

A CONTRIBUTION TO THE BIOLOGY OF WARTHOG

(PHACOCHOERUS AFRICANUS, GMELIN)

IN THE SENGWA REGION OF RHODESIA.

by

D. H. M. CUMMING B.Sc. (Hons.)

Department of National Parks and Wild Life Management  
Rhodesia.

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# T A B L E O F C O N T E N T S

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## INTRODUCTION.

To the amaZulu a warthog is "inhlovudawana" or "little elephant"; to arrogant hunters it is the "poor man's rhinoceros"; to some writers of encyclopaediae it is a "grotesque and hideous beast"; to stockmen it has long been a carrier of diseases. Injury was added to insult with the discovery that the blood of these self-assured, often comical and certainly engaging animals supports the greater proportion of tsetse flies in the African savannas. Their significance as the primary hosts of Glossina morsitans Westw., the vectors of trypanosomiasis, justified an extended field study of warthog biology. This thesis reports four years of field work on warthogs, together with complementary observations of hand-reared warthogs (and their offspring) which roamed freely in the vicinity of the remote field station on which I live.

The Sengwa Research Project, of which this study forms a part, was initiated in 1965 to study relationships between game animals and tsetse flies. One of the main problems investigated in the Sengwa Project is that of "host encounter" (Glasgow, 1967; Bursell, 1970) and how the distribution, abundance and behaviour of game animals may affect their availability to hungry tsetse flies. I have, accordingly, been concerned with discovering how warthog are dispersed in the Sengwa area and have attempted to gain some understanding of the factors, both environmental and social, which may affect or govern their dispersion and possibly population number.



Warthog density and population structure have been monitored and their distribution in the Sengwa area described (Chapter II). The animals' feeding habits were studied and the availability of food was examined, as were their use of holes and their daily patterns of activity (Chapter III). Group structure and pertinent aspects of social behaviour were studied in an attempt to examine how far social behaviour might influence dispersion (Chapters IV and V). Finally, the spatial relationships of animals and groups of animals living in a limited area were studied (Chapter VI):

The main results and observations are brought together in Chapter VII which discusses social organisation and dispersion in the Sengwa warthogs.

Warthogs were first made known to science by Pallas in 1766 who described a live specimen sent to Holland from the Cape Colony by Governor Tulbagh in 1765 (Sclater, 1900). The Cape warthog Phacochoerus aethiopicus Pallas has since become extinct and the living warthog, Phacochoerus africanus Gmelin, 1788, is still referred to as P.aethiopicus in most works but not by the palaeontologists who have studied African suids (Cooke, 1949; Ewer, 1958a, 1968; Ewer and Cooke, 1964).

Observations and records by early explorers, hunters and naturalists on warthogs are well summarised by Shortridge (1934) who also gives records of their historical distribution in Southern Africa. Bigourdan (1948) appears to have been the first to examine warthog biology at any length; he studied

warthog in the field in West Africa. Geigy (1955) published extensive observations made in Tanzania during a study of the vectors of African relapsing fever. Ewer (1958) examined features of the skulls of African suids and described a specialised mode of feeding in warthog. Fradrich (1965) studied warthog behaviour in Kenya and in European zoological gardens. His is the most complete account of warthog ethology and he provides some information on warthog home ranges. Sowls and Phelps (1966) made important observations on body temperature of young warthog and bushpig in relation to ambient temperature. Aging criteria for warthog have been described by Child et al. (1965), and Child, Roth and Kerr (1968) used material collected from hunting operations in a study of reproduction and recruitment in warthog populations. Growth patterns in captive warthog were studied by Roth (1965). Valuable information on warthog density and habitat preferences appeared in work by Lamprey (1963 and 1964) on a number of ungulate species in Tanzania. Child (1968) and Jarman (1968) both studied large mammal populations in the Kariba basin and provide further information on warthog populations and their biology.

The above paragraph refers to the more important literature dealing with warthog; further summaries of pertinent literature are given at the beginning of each chapter. Figures and tables are bound in Volume 2. Two figures, Appendix 1 Fig. 1 and Appendix 3 Fig. 1 are loose sheets in the back folder of Vol. 2.



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The Sengwa Project has been a joint undertaking between the Department of National Parks and Wild Life Management and the Tsetse and Trypanosomiasis Control Branch of the Department of Veterinary Services and I wish to thank Dr. G. F. Cockbill, Assistant Director of Veterinary Services (Tsetse and Trypanosomiasis Control) for the assistance I have received from his department and for his interest in my work.

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## C H A P T E R I.

STUDY AREAS AND METHODS.

## A. STUDY AREAS

The Sengwa Research Area, 145 square miles (c.376 km<sup>2</sup>) in extent, is situated in the north-west of Rhodesia on the Sengwa River and about 60 miles (c.96 km) west of Gokwe (Fig. 1). Before the base station was established at Sengwa Gorge in 1965 the area was little touched by man and civilization. The presence of tsetse fly has precluded the entry of domestic livestock into the district and apart from small transient villages African settlement has been absent from the Research Area for the past three to four decades.

The area lies between 2,600 and 3,100 feet above sea level (c.790 to 945 m a.s.l.). Base rocks and exposures are predominantly Karroo sandstones and mudstones. A clearly defined south-west to north-east faulted scarp, dissected by the Sengwa, Lutope and Manyoni Rivers, divides the area into two distinct levels. The Lutope and Manyoni Rivers join the Sengwa a few miles below the escarpment and much of the Research Area falls into a basin with an escarpment on the south and east and flat-topped, island-like hills on the west (Fig. 1). Thaba Mance ("Mountain of the vultures") forms a similar, smaller, but prominent, feature in the centre of the basin.

Climatically the area is hot and dry and corresponds to the low or middleveld areas of Southern Africa. There is a single



rainy season which extends from November to April, a cool dry season from May to July and a hot dry season from August to October. Although the research area falls between the 24 to 28 inch (610mm to 711mm) mean annual rainfall isohyets only 16 to 24 inches (406mm to 610mm) of rainfall may be expected in four out of five years. Mean annual temperature is  $22.2^{\circ}\text{C}$ . while in October the mean maximum temperature is  $32.2^{\circ}\text{C}$ . -  $35.0^{\circ}\text{C}$ . and mean minimum is  $17.3^{\circ}\text{C}$ . -  $20.0^{\circ}\text{C}$ . In July the mean maximum is  $25.0^{\circ}\text{C}$ . -  $27.8^{\circ}\text{C}$ . and the mean minimum is  $4.4^{\circ}\text{C}$ . -  $7.2^{\circ}\text{C}$ . (Torrence, 1965).

Vegetation in the area is, generally, deciduous and dry deciduous savanna woodland (Wild and Grandvaux Barbosa, 1967). Above the escarpment and on higher ground the main vegetation is a mixed Brachystegia/Julbernardia woodland (Fig. 2). The basin supports a more varied and prolific flora with Colophospermum mopane woodland, Acacia riparian and grassland communities predominating. Eroded slopes carry mixed Combretum associations while on gentler sandy slopes Combretum thickets and degenerate Baikiaea woodlands occur. A fuller description and map of the vegetation is provided in Appendix 1 and main vegetation types are illustrated in Fig. 3.

Permanent surface water is widespread even at the peak of the dry season. It occurs in pools along the rivers and in perennial springs in the hills west of the Sengwa River.

A wide variety of game species is to be found in the research area and these are listed in Table 1, together with an indication of their abundance in the area.

The Sengwa Area now forms the southern part of the newly created Chirisa Game Reserve. Before 1965 the research area was a hunting centre for tribesmen living to the south of Sengwa. Both snares and firearms were used by these people and game was consequently very wary of humans. Even after a five year embargo on hunting most species are more wary of humans than are their counterparts in established game reserves and national parks. The research area is now fenced on its eastern, southern and western boundaries (Fig. 1); outside the fence Tsetse controlled hunting operations have taken place since 1965. The perimeter of the Research Area has thus been subjected to considerable disturbance over the past five years. Although immigration of game may have occurred in 1965 tsetse control hunting operations appear to have had little effect on the behaviour of game animals within the Sengwa Research Area.

#### 1. Intensive study areas.

Two experimental areas, associated with the study of game/tsetse relationships, have been established within the Sengwa Research Area. Much of the warthog work and particularly the tagging of warthog has been centred on, but not confined to, these two areas viz., the Sengwa Experimental Area and the Lutope Experimental Area. Home range studies have been confined to the Sengwa Experimental Area where all radio tracking occurred. Little of the data derived from the Lutope Experimental Area is included in this report and the area will not be described in any further detail.

Observations of tame free-ranging warthog were made in the vicinity of Sengwa Gorge, the base station for the Research Area.

a) Sengwa Experimental Area.

Work in this area has been confined to within 9.5 sq. miles ( $25 \text{ km}^2$ ). The terrain is dominated by the Sengwa River in the east, the Lutope River in the west and a faulted escarpment to the south (Figs. 4 and 6). The drainage pattern is mature, the terrain generally flat and large areas of alluvial soil are present. This area was selected for its high density of warthog, wide variety of vegetation types and year-round accessibility. The southern escarpment provides valuable sites for radio tracking base stations.

Vegetation types within the experimental area are shown in Fig. 4 and described in Appendix 1. C.mopane-Combretum sp.-Tristachya superba wooded and bushed grassland is well represented and forms an important dry season feeding area for warthog. Interspersed with it are areas of C.mopane woodland which provide species of grass well used by warthog during the rains. Acacia communities on alluvial soil are also well used by warthog and are a significant component of the Sengwa Experimental Area. Large deciduous thickets are absent from the Experimental Area.

Other features of particular significance to warthog are :

(a) Old river terraces of the Sengwa and Lutope. These rise from a few feet to 20 feet above the river plains and are the site of many well-used and persistent warthog holes. (b) Areas of sodium rich, seasonally waterlogged soil which give rise to extensive subterranean erosion gulleys; these provide refuges



for warthog.

Surface water is always available in the Sengwa River and in ox-bow pools on the flood plain. Numerous temporary pools occur in the mopane woodland; some of them hold water well into the dry season. The greatest distance an animal has to travel to water, at the peak of the dry season, is approximately 4 km. An artesian borehole in the south of the Experimental Area is well used by warthog during the dry season.

b) Sengwa Gorge

This area lies above the escarpment and although within a Brachystegia woodland area (Fig. 2), C.mopane woodland is well represented near the gorge and C.mopane-Combretum sp.-Tristachya superba wooded and bushed grassland also occurs. Grasses important to warthog are common in the latter two habitats. Eroded areas and gulleys near the gorge contain holes used by the tame warthog.

The Sengwa Gorge, a spectacular, deep and narrow cleft through sandstone, dominates the area. A small concrete bridge forms the main crossing point used by the warthog.

Two African staff villages (B and C in Fig. 5), composed mainly of traditional "pole and dagga" huts, provide shady resting sites for the tame warthog. Water is available at garden taps near the author's house where wallows are maintained. Water is always available in the river below the gorge and during the rains it is available in temporary pools in the surrounding bush. Lawns and flower beds in the camp are fenced to keep warthog away from them. The animals do, however, move readily through the

stranded game fence along the main road.

## B. METHODS

### 1. African Field Assistants.

I have been assisted by a team of 16 trained African Field Assistants or Game Scouts. Without their help in routine field recording much of the work reported here would not have been possible. Lamprey (1961) has already drawn attention to the valuable contribution such men can make to ecological research in Africa. Most Scouts at Sengwa are in their twenties and all have a minimum of six years primary school education. Their formal educational qualifications should not however be equated with their ability or their intelligence. Lack of opportunity has usually precluded further education.

Most of the Game Scouts were recruited during 1965 from the main towns in Rhodesia. Few had had any previous experience with game and most grew up in tribal areas, already depleted of large mammals, or in the towns. This lack of experience (and thus of preconceived ideas) had the advantage that the men were trained to observe game and to record simple aspects of their behaviour more objectively than would have been done by local tribesmen with their background of often highly-coloured folk and hunting lore.

In Africa it is impossible to recruit men with biological training to carry out routine recording on the scale required at Sengwa and few would, in any event, be content to do it for long. An outstanding and noteworthy characteristic of the Game Scouts is the pride and interest they bring to their work. Lamprey (1961)



also remarked on this in his staff. It has not proved difficult to imbue in most Scouts a spirit of scientific enquiry and the rigorous honesty in recording which this implies. Staff in the field have never been under any compulsion to produce data. For example if a man visits a warthog hole and sees nothing he is under no pressure to fabricate an observation. Similarly if after walking a ten mile traverse no game has been seen, the Scout merely files a nil return; this happens quite frequently.

Recording procedures have necessarily been simplified and standardised as far as possible. Recording forms and cards have been designed for each particular investigation. Most recorded information is straight forward e.g. number of animals seen, date, time, locality and gross observations on behaviour such as feeding, resting, wallowing etc. Provision is made on forms for recording the age and sex of animals seen. Detailed criteria for age and sex classification of warthog in the field were established at an early stage of the study (Appendix 3) and Scouts were trained accordingly.

Some Scouts proved capable of carrying out more sophisticated field work and were trained to use radio-tracking equipment and aerial photographs. Many have provided useful information on warthog behaviour and recording forms have adequate space for additional notes and comments. Two typical, rather than exceptional, verbatim quotes from observation cards illustrate the level of reports on behaviour :

"The male yearling entered at once as it arrived at the hole. The female adult or sub-adult waited for a minute busy collecting grass into the hole. She was pulling with her front legs." (Isaac Mukuya, 18 June, 1969).

"There came an adult male at about 0650 at the hole and made soft grunts but there was no answer to his calls. In 3 minutes time he left going north. He then came back at 0740 and as soon as he arrived at the entrance the hogs (2yr. males and 3 yr. females) started emerging. Unfortunately for him there was no adult female so when he sniffed the yearlings female he did not take long with and started trotting off towards the north. The second time he came at the hole he making some grunts. Probably it is a sign of calling the females inside the hole." (John Lacha, 22 May, 1969)

Most of the Game Scouts have worked at Sengwa for four to five years and since I live on the field station the men and their specific abilities are well known to me. I can therefore view their contributions with discretion and delegate duties so as to obtain maximum efficiency and reliability from the staff.

## 2. Density and distribution (transect sampling).

To obtain information on the density and habitat preferences of ungulates in the Sengwa Research Area a system of twelve permanent transects totalling 60,000 yards (54,864 m) was established in 1965 (Fig. 6). These transects form the basis of a continuing census necessary in the study of game - tsetse relationships. The methods employed are essentially the same as those of Lamprey (1964) and Jarman (1968). However, in addition to records of game sightings, the spoor of animals crossing the transects was also recorded during the dry seasons of 1965, 1966 and 1967.

Transects were cut using the chain and compass method. Transects are 4,000, 5,000 or 6,000 yards long and are divided into 100 yard sectors. Each sector was demarcated, initially, by a numbered

aluminium disc and later by a painted number on a tree or log. Game animals seen during a traverse were recorded against the 100 yard sector on which they occurred. Each animal seen was taken as a sighting.

To determine the area sampled by transects, "visibility profiles" for each transect were measured in January, 196<sup>6</sup>~~8~~, in the manner described by Lamprey (1964). Seasonal changes in visibility in the Sengwa area are greater than experienced by Lamprey in East Africa and some vegetation types show greater seasonal changes than do others. For these reasons visibility profiles are currently being measured every second month and Jarman's (1968) method is being adopted. Two profiles are measured; the distance at which a khaki-clad man walking towards the transect first becomes visible and the distance at which a grain sack, with its long edge resting on the ground, becomes visible. The measurements are made at 100 yard intervals and on each side of the transect. The khaki-clad man gives a visibility profile for larger animals while the sack does so for the smaller game; the latter has been used in calculating warthog densities. Warthog densities reported here are based on profiles measured in November, 1969 and in January, 1970 and must be regarded as provisional.

Areas sampled on the transects have been converted from British to metric units and densities are expressed in warthog per square kilometer.

To facilitate spoor recording transects were cleared of all grass and scrub (but not trees) to a width of 6 to 8 feet (c. 2m). Each 100 yard sector was divided into three 100 ft. sections

designated a, b and c, and demarcated by shallow troughs across the path. Spoor recording teams, consisting of a Game Scout and two labourers, obliterated spoor after recording it by dragging light branches behind them. Spoor recording was practicable only during the dry season. Two basic types of information were recorded for each 100 ft. sector : presence or absence of the spoor of each species (i.e. sectors inhabited or uninhabited) and an estimate of the number of animals which had crossed each sector.

Observer variability was examined over a ten day period on two pairs of transects using six recording teams independently (Mills and Cumming unpublished data). Teams differed significantly in their assessment of the number of 100 ft. sectors inhabited per traverse by warthog, impala and elephant although they agreed on the number of sectors inhabited by kudu. Teams did not agree on the number of animals of each species crossing the transects. Disagreement on the number of sectors inhabited was very largely due to one team. The results of the test nevertheless place serious limitations on the use of spoor crossings to determine differences in abundance or activity, or both, between transects and in time.

The spoor data do, however, provide a measure of the activity at different points along a transect, e.g. over ten traverses a particular sector may be inhabited on each occasion while another sector may be inhabited only once. As a measure of the activity along a transect I have taken the number of 100 ft. sectors inhabited on each 200 yard section of transect divided by the number of traverses. Traverses are made at intervals of 24 hours. The maximum score per traverse would be 6 i.e. 6 x 100 ft. sectors



inhabited in 200 yards of transect per traverse. Recording teams showed satisfactory agreement in the distribution of activity along a particular transect over a ten day period (Fig. 7). These are the only type of spoor data used.

From August to November, 1965, traverses were made at 48 hour intervals. From January, 1966 to December, 1969 traverses were made daily. In most months 20 to 24 traverses were made.

When spoor was not being recorded teams comprised only a Game Scout and one labourer. On each recording day the teams moved out along one transect and returned along the other (Fig. 6). A pair of transects took about 5 hours to complete if spoor was being recorded and about 3 hours if sightings only were recorded.

Checks on the reliability of recorders were made at irregular intervals. The presence of sweeping on the transects during the dry season provided a further check. Recorders have never been found not to complete their traverses. When illness or elephant have prevented a traverse, or part of a traverse, from being completed the facts have been noted on the recording form or reported to me. To offset possible differences between recording teams the two teams at each field camp alternated on transect pairs every four days during the month. Teams were rotated between camps so that each spent two consecutive months on one set of transects.

### 3. Food habits and availability of food.

I have made a collection of the grasses occurring in the Sengwa Research Area and I am grateful to Mr. B. K. Simon, Systematic Botanist of the National Herbarium for identifying the

the specimens. A duplicate set has been retained on the station.

Plants on which warthog have been seen feeding have been collected by myself and by the Game Scouts and the station herbarium has been used to identify them. An accumulation of such feeding records does not however provide quantitative evidence of feeding preferences but merely a list of species eaten.

a) Faecal analysis

Fifty faecal samples were collected each month from June, 1966 to May 1967. Approximately equal numbers were collected from the vicinities of the three main sets of transects every month. Selected scouts collected two or three pellets from each batch of dung and then crushed and scattered the remainder to prevent duplicating the sample. The longevity of dung is a few weeks during the dry season but coprophagous beetles reduce it to less than a few hours during the rainy season. Samples have been sun dried and stored initially in plastic bags and finally in bottles.

Faecal pellets have been examined macroscopically under a dissecting microscope for the remains of fruits, leaves, stems, rhizomes and roots of graminaceous, cyperaceous and dicotyledonous plants. Pellets were crumbled by hand into a petri dish and examined dry. The abundance of different plant remains was established and scored according to the following frequency scale :

| <u>Score</u> | <u>Abundance estimate in sample</u> |
|--------------|-------------------------------------|
| 1            | Trace                               |
| 2            | Not abundant (up to 30%)            |
| 3            | Abundant (30 to 60%)                |
| 4            | Very abundant (60 to 90%)           |
| 5            | Almost entire sample                |

Suids pass a considerable amount of undigested material in their faeces and this allows major changes in their diet to be detected by macroscopic examination.

b. Feeding minutes

Feeding minutes were recorded on tame free ranging warthogs (page 29). The periods spent feeding on particular food species or on other activities were recorded with a stop watch over sample periods of 20 or 30 minutes. Only one animal was watched at a time and changes from one plant species to another, or from one activity to another, were recorded to the nearest 0.05 of a minute. Notes were made of the general composition of the grassland at the site where the minutes were recorded but not of the grasses "rejected". The method of recording the minutes required such attention that it was not possible to record species which the animal by-passed.

c. Distribution and availability of food

Preliminary information on the distribution of grasses has been gathered by compiling species lists of grasses occurring in different habitats. Visual, relative abundance estimates have also been made by walking through the various habitats.

Signs of warthog rooting are distinct and can be used to measure the utilization of different habitats by warthog during the dry season. Belt traverses have been run in different habitats and these took two forms :

i. Traverses 250 yards long and c. 3 feet wide in which the presence or absence of rooting, faeces and certain species of grass were recorded in each of twenty five 10 x 1 yard plots.

ii. Traverses on every second 100 yard sector of the fly grid in



the Sengwa Experimental Area (App. 1, Fig. 1). <sup>also Fig. 33</sup> Fly rounds are each a mile long and 500 feet apart, and cover an area of 1 square mile. The frequency of Tristachya superba, Digitaria milanjiana and of rooting in each 10 yard plot was measured by counting the number of 1 yard plots in which the items occurred. The results for each 100 yard section are expressed as a percentage. The number of warthog dung heaps within each 100 yard traverse was also counted by a second observer walking behind me.

To obtain a measure of the amount of rhizomatous food available, two plots, in C.mopane-Combretum sp.-Tristachya habitat, near transect 7, were examined in October, 1969. The rhizomes from 20, randomly sited, one square metre quadrats in each plot were dug out of the ground and weighed.

#### 4. Warthog holes

The density of warthog holes was measured early in 1966 by counting the number of holes within strips 60 paces wide along eleven of the transects (c. 34 miles or 55 km) in the Research Area. A total of 68 acres (c.28 ha) was examined. The distance of each hole from the transect was paced to ensure that it fell within the strip. Notes were made on the structure and type of each hole and its suitability for use by warthog.

Observations of particular warthog holes started in March, 1966. These were located by Game Scouts and later examined by myself and mapped by pin-pointing their positions on aerial photographs. Each hole was assigned a number, painted on a nearby tree, as it was discovered. Holes were usually inspected for



signs of use at intervals of one to four weeks by examining the hole entrance in the morning. A log card was kept for each hole on which the date of each visit and the status of the hole were noted.

Direct observations of warthog using holes have been made by watching these in the morning and in the evening from nearby trees. Recorders positioned themselves 2 to 2½ hours before sunset and remained there until dark regardless of when warthog entered the hole. In the morning, positions were taken up at dawn and abandoned only after the warthog had emerged or at about 0800 hours. Observations were recorded on printed, edge-punched, 6 x 4 inch cards which were completed in the field or on return to the field camp if it was too dark to write. A "master card" was maintained by the senior Scout in the field who noted which holes had been watched each day, whether warthog entered or emerged and the periods during which holes were observed. In the Sengwa Experimental Area 3,094 observation periods have been completed by myself and Game Scouts.

The capture of animals at holes and subsequent observations of tagged animals have also provided information on the use of holes.

##### 5. Capture, tagging and tracking of warthog.

Warthog are not easily distinguished as individuals and at Sengwa they are too wild for this to be a practicable field technique. It was therefore necessary to capture and tag warthog and 242 were marked between July, 1966 and January, 1970. Some animals which had lost their tags when recaptured were, if unidentifiable, re-tagged and assigned a new serial number. Conventionally tagged warthog

(those not tagged with radio collars) were seldom seen during the first  $2\frac{1}{2}$  years of this study. Radio tracking techniques were therefore introduced and most of the data on home range ~~was~~<sup>were</sup> obtained with the aid of this technique between September, 1968 and February, 1970. The full potential of the equipment has not yet been realised; construction and operation of electronic gear on remote African field stations is not easy (Hanks, 1969).

The methods developed to capture and tag warthog are more fully described in Appendices 4 and 5. A brief outline is given here only to draw attention to those features which have a direct bearing on the results.

a) Capture

Warthog were captured by setting nets at the entrances of occupied holes before dawn. This method allowed an entire sounder to be captured, tagged and released together. No immobilizing or tranquilizing drugs were used on captured animals; risk of predation due to the after-effects of such drugs was thus avoided. Sounders may be temporarily disrupted and home ranges briefly shifted as a result of this (and other) capture methods. Animals have, however, been recaptured at holes where they were caught only three to four weeks earlier.

b) Tags

The following tags, illustrated in Fig. 8, have been used on warthog : (1) Numbered metal ear tags. (2) Coloured rotating plastic ear tags. (3) Ear notches. (4) Shoulder harnesses. (5) Colour coded collars. (6) Plastic collars with painted symbols. (7) Radio-collars.

The metal and plastic ear tags have not been successful and tag losses have been high. Metal tags tore, or were torn out, and their use was discontinued early in 1967. The tear has, in some instances, been sufficiently characteristic to permit identification. Plastic ear tags break and fall out leaving a small hole in the pinna; their use was discontinued in 1969. Ear notching has proved to be the most satisfactory means of permanently tagging warthog and individuals can be positively identified in the field.

Twelve shoulder harnesses fitted to warthog in 1966 were shed within a few weeks. Twenty-two colour-coded collars (5 cm wide and made from a rayon cloth impregnated with p.v.c.; construction after Pienaar, pers. comm. 1965) were attached to warthog in 1967. These collars were easily seen and identified in the field until they became worn after c. 6 months. Some collars remained on warthog for more than 18 months.

Since July, 1968 all immature warthog and those adults not tagged with radio collars have been marked with collars made from p.v.c. tennis court tape on which symbols have been painted with a p.v.c. lacquer. The collars are similar to those used by Ealy and Dunnet (1956) on kangaroo and I have adopted their system of using readily distinguishable symbols instead of conventional numerals. Although the plastic collars remain on warthog for only two to four months they have proved very useful for recognising members of radio tagged groups and for observing changes in group composition.

Early attempts at radio tracking in 1967 were unsuccessful (Hanks, 1969). In September, 1968, radio tagged warthog were successfully tracked and, from September, 1968 to June, 1969, 17

radio-collars were fitted to 13 warthog. Maximum transmitter life realised was, however, only 40 days. Between October, 1969 and January, 1970 a further 9 transmitters were used and all but two of these were still transmitting in April, 1970 i.e. after more than 150 days.

The construction of these transmitters and radio-collars is described in Appendix 5.

c) Radio tracking

The point at which an observer locates a conventionally tagged animal largely depends on the observer's route through the study area. Unless an animal's entire home range can be observed from a vantage point the observer must either follow his animals or traverse the study area in a systematic (or, more difficult, completely random) manner. Unless one or more of these requirements can be met a biased picture of an animal's home range can emerge. Error due to the observer's route can, however, be reduced or eliminated by the use of radio tracking techniques. These techniques also greatly increase the frequency with which animals can be located; contact no longer depends on a chance encounter between observer and animal.

The whereabouts of a radio-tagged animal is determined by coupling, to the receiver, an antenna with directional properties. Bearings are then taken on the signal source from two, or more, widely spaced points. The intersection of these bearings, when plotted on a base map, will indicate the animal's position. Such triangulation techniques require accurate direction finding equipment to obtain reliable locations or "radio-fixes". An



alternative method is to "home in" on the signal with portable direction finding equipment (e.g. a loop antenna coupled to the receiver) and to observe the tagged animal and its precise locality.

Stacked 5-element yagi antennas and portable base stations with 3 or 4-element yagis (Fig. 9) were used to obtain preliminary fixes on radio-tagged animals. Accuracy of these antennas was tested by taking bearings at predetermined intervals on a radio collar carried by a man who recorded his position at the appropriate times. The antennas generally provided bearings with an accuracy of  $\pm 5$  degrees but aberrant bearings were frequent (c. 1 in 5). Little use has therefore been made of radio fixes in determining the home ranges of radio tagged warthog. Most of the information presented here has been obtained by homing in on tagged animals and observing their positions.

Storm (1965) found that radio tagged foxes soon became aware of being followed and took evasive action. I have found it possible to follow warthog for short periods without disturbing them by remaining downwind and by not attempting to keep them continuously in view. However, groups usually did become aware of the observer's presence once contacted. This was either because we wanted a classification and count of the group or because the cover was so dense that we had to move in close. Their reactions to one's presence varied considerably; in dense cover they sometimes lay low until flushed, sometimes they merely continued their activities and slowly moved away and sometimes an alarm was sounded and the group rushed away. They seldom ran very far. If a group failed to sense one's presence they were usually watched until they moved

off or until we withdrew. Tagged warthog were generally not followed immediately after they had been disturbed. They were, however, sometimes contacted later on the same day. Warthog have been successfully followed for up to 2 km to their holes after an initial contact made an hour or more before sunset.

d) Recording and mapping.

Game Scouts can easily give accurate locations of tagged animals by referring to warthog hole numbers or, if on a transect, to the sector number.

Accurate location of radio tracking observations was accomplished by using 9 x 9 inch contact prints of 1 : 5,000 aerial photography of the Sengwa Experimental Area. These can be conveniently carried in the field. A grid of approximately 100 x 100 yards was drawn on each photograph in red waterproof ink. One axis of the grid was designated A to L while the other was designated 1 - 12. The locality of an observation is specified by reference to the photograph number, the grid square and one of four quadrants within the grid square which are denoted by lower case letters a, b, c or d. For example a full reference would be Photo No. 0123, Grid Ref. H4a. This allows an observation to be placed within a square of 25 x 25 yards. This system has been remarkably useful and it allows locations to be described precisely even in generally featureless bush country.

Magnetic bearings of the grid lines are also marked on the photographs; by stationing oneself at two or more grid intersections it is thus possible to take a radio fix on an animal and plot this in the field. The sometimes serious disadvantage of the

bi-directional loop antenna can thus be readily overcome without having to return to an identifiable point on a map.

Localities recorded in the above manner are easily transferred to aerial photographs at other scales and then to maps which have been drawn from these photographs. In this instance the original field records have been transferred to a 1 : 12,700 aerial photograph of the Sengwa Experimental Area on which the 1,000m Universal Transverse Mercator grid has been marked. Sightings of radio tagged warthog have been finally designated by a Universal Transverse Mercator Grid reference giving the animal's locality to the nearest 10 (or sometimes to the nearest 100) metres. Grid references are easily plotted on maps drawn at other scales.

e) Continuity of records.

Short transmitter life has led to inevitable gaps in the continuity of the records. Animals could not always be recaptured to replace their collars and delays in the supply of components for new transmitters occurred. It must therefore be borne in mind that not all of the transmitters were functioning at the same time and that home ranges of animals have been determined at different times and for varying durations (Table 31).

f) Numbering of animals.

Each animal on being captured, tagged and released was assigned a serial number without regard to age or to sex. Animals are referred to by their serial number prefixed by their sex and age at the time the observation was made e.g. Ad. ♂ 175. The age prefix for a particular animal may change, e.g. Sub-adult female 171 (S.Ad. ♀ 171) was first captured in February, 1969;



by October she had become an adult and on recapture was designated Ad. ♀ 171. The system of age classification used in this study is described in Appendix 3. and the following age classes have been recognised :

| <u>Age Class</u> | <u>Age</u>               | <u>Abbreviation</u> |
|------------------|--------------------------|---------------------|
| Juvenile         | Less than 12 months      | Juv.                |
| Yearling         | Between 12 and 24 months | Yr.                 |
| Sub-adult        | Between 24 and 36 months | S.Ad.               |
| Adult            | Older than 36 months     | Ad.                 |

#### 6. Tame free-ranging warthog.

Hand-reared animals (have) proved immensely valuable and instructive in behavioural research (Lorenz, 195<sup>0</sup><sub>2</sub>; Ewer, 1968, page xii). The value of such animals can be enhanced if they are given their freedom at an early age, and, as has happened with our warthog, they remain only loosely attached to their foster parents but firmly attached to their home area, so that they go about their normal activities and visit their initial home every day or two.

Four "generations" of warthog have been reared at Sengwa (Fig. 10) by my wife and I. Animals were obtained at ages of between one and two weeks. At the outset they were given free run of the house to which they needed to be confined for only 7 to 10 days. Once they followed us about the house they were taken for walks out-doors. For the following 6 weeks the animals were continuously in our company. This was of their own volition for they were free to wander outside the house. In the early stages the young animals were kept separate from the older warthog. Meetings between the newly acquired animals and older hands inevitably



occurred but did not present any difficulty for the young warthog readily returned to us when called ("Come on" was a signal to which they soon responded). After about 6 weeks the animals were encouraged to spend more time out of our house and small fenced garden. They were weaned from the bottle at about three months by which time they were grazing extensively, and had also been introduced to "Chick mash" or "Growers mash". They were given a plate of this three times a day. At four months they were banished from the house because they became too destructive indoors. After their evening plate of mash they were closed in a pen, which contained an artificial warthog hole, for the night. They were released each morning when they were again given a plate of mash.

Initial care of the young animals was time-consuming as they were fed on a demand schedule which in practice was a feed every two to three hours. They were fed on powdered milk ("Nespray" made up to normal strength) with added vitamins and minerals; after about two weeks a little "Pronutro" was added to the milk. The young were provided with a hog hole in the form of a cardboard box which contained a hot water bottle and an old blanket (Fig. 11). Young warthog are not able to maintain their body temperatures effectively (Sowls and Phelps, 1966) and become cold even on warm tropical nights. The hot water bottle had therefore to be constantly warm and without it they did not retire to their "hole" to sleep during the day. The box was available to them at all times. When they were between a month and six weeks old the mid-night and pre-dawn feeds were eliminated. While the animals were living in the house they received a good deal of handling, scratching and

fondling, as well as discipline. These social activities continued afterwards but to a lesser extent.

The amount of mash given to the animals was decreased from three plates to two plates once they were about five months old. No other supplementary food was given so that they were responsible for feeding themselves. By the time the warthog were 7 to 8 months old they had usually started sleeping in natural holes away from the pen or had joined with the older warthog. When sleeping out they missed their evening plate of mash but usually arrived in the morning between 7 and 8 o'clock for food. The morning visit was usually made directly to the kitchen door. They soon learned that only one plate of mash was forthcoming and after eating this went about their usual activities. This feeding was continued throughout their lives in order to maintain contact with them. The amount of food given was sufficient to ensure contact but small enough to avoid any dependence on us for their livelihood. The animals frequently missed their meals, sometimes for long periods.

This system of rearing warthogs has produced remarkably tame and even-tempered animals. MacSweeney, who was without a warthog companion for his first month, showed signs of being so firmly imprinted on humans that he attempted to court them in preference to warthog when he became sexually mature. We were forced to evict him at the age of twenty months when he weighed 185 lbs. and was clearly likely to inflict serious injury. None of the other male warthog have<sup>s</sup> shown similar sexual or aggressive tendencies towards us. Of the female warthog Susan became aggressive at 2½ years old, but only towards strangers (people who did not live at Sengwa). She had to be evicted when she was 34 months old.

Although not aggressive towards us the animals have, in appropriate situations, fought seriously with each other. For example neither Rosemary nor Susan showed the least concern at us approaching and even touching their litters whereas both attacked the male yearling warthog (MacDuff and Mackintosh respectively) when they approached.

The hogs could be accompanied in the field; they took no evasive action and appeared to be little influenced by human observers and company once older than 7 or 8 months or when they were with older warthog. Despite being very tame and tolerant of humans I believe their attachment to us to have been sufficiently loose to justify their use in detailed studies of their daily patterns of activity and movement.

a) Recording procedures.

i. Daily patterns of activities

Observations started in April, 1969 on Susan, Mackintosh, Sophie and Gladys. These animals formed a cohesive sounder under the leadership of Susan with MacDuff occasionally joining them. Sophie and Gladys were unfortunately taken by crocodiles in mid-April so that subsequent observations were confined to Susan and Mackintosh until Susan farrowed in November, 1969. Activities were recorded for either twelve or eighteen consecutive days in each month from May to November (Table 2). Two Game Scouts were trained to carry out routine observations. An observer waited outside the sleeping hole for the hogs to emerge in the morning and stayed with them until mid-day when he was relieved by an observer who watched them until they entered their hole at night.

Breakfast was taken to the man on the morning shift at about

8 a.m. and the Scouts were issued with water bottles and suitable hats.

The activities of each animal were recorded at ten minute intervals by simply entering an initial in one of a number of columns on an appropriately designed form. Additional notes were made on the reverse of the form. A whirling psychrometer was used to determine wet and dry bulb temperatures at 20 minute intervals.

This method of sampling activity patterns assumes that the activity at the end of a ten minute interval reflects the activity over the previous ten minutes. The technique was developed for use on domestic livestock where it was found that even sampling intervals of 30 minutes provided a reliable picture of the daily pattern of major activities of cattle (Hull et al. 1960). A ten minute interval was selected for warthog recording because it was below the 15 to 30 minute interval suggested by Hull et al. and it worked well in practice. Shorter intervals demanded greater vigilance and consequently increased fatigue. Other workers have used shorter intervals (4 minutes) but were working on single animals and over shorter periods (Spinage, 1968). Minor activities of special interest such as drinking and wallowing were recorded, whenever they occurred, on the reverse of the form.

A test between intermittent versus continuous recording for warthog behaviour has not however been made. Hull et al. (1960) found significant differences between the activity patterns of different individuals and considered a minimum of four animals per group, for cattle, to be sufficient. The behaviour of warthog in a group is generally synchronous and will be discussed under the results.



## ii. Home range

The location of each 10 minute activity record was also noted by referring to a grid square on a 1 : 5,000 scale aerial photograph of the study area. A 100 x 100 yard grid was drawn on the photograph which was carried by the observer. Grid squares were divided into quadrants and the locality given to the nearest 25 x 25 yard square. The number of observations in each square was plotted for each monthly set of observations. Periods of observation are given in Table 2.

Home ranges before May, 1969 (i.e. before systematic observations of daily activities began) were plotted by walking over the area and marking, on an aerial photograph, points at which I, or the Game Scouts, could clearly remember having seen the warthog.

## iii. Behaviour

Notes have been kept of various facets of the behaviour of the tame warthog and of interactions which have occurred between the groups. Some 3,000 feet of 16 mm cine colour film has been taken (with a Beaulieu R16 camera) of the various aspects of behaviour of the tame warthog and the bushpig. My interests have tended to focus on those aspects of behaviour most directly related to dispersion viz., aggressive behaviour and scent marking.

Drawings of postures and descriptions of movements have been derived from the 16 mm film record where possible or from sketches made at the time of the observations. Except where otherwise stated, film was taken at 24 frames per second.

## CHAPTER II

WARTHOG ABUNDANCE, DISTRIBUTION AND  
POPULATION STRUCTURE

Field work began with a census of the game community and questions asked for each ungulate species were : How many?, How are they distributed?, and What is their population structure?. A more specific study of warthog biology developed from this general survey.

Complete counts of game inhabiting 150 square miles of bush country are impracticable. A system of permanent transects was therefore established in 1965 and has been maintained since. Information on warthog derived from these transects and from field observation records over a five year period is presented in this Chapter under three sections : Abundance, Distribution and Population Structure.

Warthog are widely distributed over Africa within the savanna and savanna woodlands south of the Sahara. Schläter (1900) claims that warthog live in fairly open country and never far from water. Ansell (1960) states that in Zambia their habitat is woodlands, dambos (vleis), plains and also montane grassland. Vesey-Fitzgerald (1960) found warthog confined to Acacia parkland and certain woods on the perimeter of Lake Rukwa in Tanzania.

Lamprey (1963), in the only quantitative study so far, reports that in the Tarangire Game Reserve (Tanzania) warthog occurred in woodland, dense woodland and grassland in decreasing order of preference. He states, in the same communication, that they show a slight avoidance of dense Commiphora woodland but occur

"showing no marked preference" in all other zones. His transects passed through a wide range of habitat in an area of c. 5 square miles. Stewart and Stewart (1963) describe warthog habitat in Kenya as "scattered tree - grassland and open grassland, desert grass-bush and scrub from sea level to 8,000 ft." Fradrich (1965), in Nairobi National Park, considered the two main requirements of warthog habitat to be open grassland and nearness to water points. Although he saw warthog in wooded areas it was on the open flats, dissected by small rivers lined with xerophytic shrubs, that the highest populations occurred.

Other authors consulted include Vaughn Kirby (cited by Lydekker, 1908), Bigourdan (1948), Stevenson-Hamilton (1947) and Shortridge (1934). Guiraud (1948) found warthog living in densely forested areas and leading a nocturnal existence but this is the only reference I have found to their occurrence in forest habitat.

The habitat preferences of warthog are far from clear and apart from Lamprey's data there is little on warthog abundance in relation to habitat.

#### A. ABUNDANCE.

Monthly densities of warthog in the transect area are illustrated in Fig. 12 and the annual data are summarised in Table 3.

Each monthly density figure was calculated by :

$$\frac{\text{Monthly total of warthog seen}}{\text{Number of traverses}} \\ \text{Area sampled on each traverse}$$

Lamprey (1963) found that his transects provided an accurate estimate of warthog, and other species, in his transect area. The accuracy of estimates on the Sengwa transects has not yet been



established and density figures given here are therefore provisional.

### 1. Annual variations in density.

Fig. 12 shows an initial drop in warthog density early in 1966, a marked increase during 1968 (see also Table 3) followed by little change during 1969. Some of the changes can be related to seasonal variations of rainfall and the incidence of fires.

The initial decline in density was associated with drought at the end of 1965. Conditions for grazing animals were particularly harsh by the end of December and were only relieved in February, 1966, by heavy rain. Grass fires had swept through most of the Research Area during the 1965 dry season and the subsequent green flush was severely wilted by lack of rain.

Observations of tame warthog suggest that juveniles may suffer acute, and possibly fatal, diarrhoea if they feed on badly wilted grass. A three week dry spell at the end of 1967 resulted in some wilting of grass near the Sengwa Gorge. Two tame yearling warthog had diarrhoea at this time but appeared to be little affected whereas two juveniles, 2 to 2½ months old, were very ill and one nearly died.

The prolonged and widespread wilting which occurred during the 1965 breeding season could have resulted in high juvenile mortality. Good rains fell throughout the 1966 - 1967 rainy season and satisfactory rainfall occurred in subsequent seasons.

### 2. Seasonal changes in density

Marked and consistent seasonal changes of density are not



shown in Fig. 12 and neither is a dispersal of warthog from the area at the onset of the rains. Densities do however tend to be highest at the end of the dry season and lowest during the wettest months which are February and March. Lamprey (1963) also found warthog densities were highest at the peak of the dry season and lowest at the height of the rains in his transect area. A slight dispersal of warthog however occurred from his transect area during the rains. My observations show that warthog often remain in their holes on wet mornings or when it is raining; this may account for the lower densities recorded during the wettest months in the Sengwa area. Seasonal changes in visibility would affect the number of animals seen on transects. Data obtained so far show that the area sampled during the wet season is c. 85% of that sampled during the dry season, i.e. a seasonal change of 15%. Appropriate corrections have however been made in calculating monthly densities.

The marked increase in the variability of the data after August, 1967, (Fig. 12) is not understood. However, despite the difficulties surrounding the interpretation of this type of data they do indicate that warthog densities declined early in 1966 and subsequently showed an upward trend at the end of 1967 and during 1968. This information is important to later discussions on changes in population structure and social structure observed during the study period. (Section C of this Chapter, page 454, and Chapter IV, Sounder Structure).

## B. DISTRIBUTION

Warthog occur throughout the Research Area so that any description of their distribution in different habitats requires

careful treatment. A systematic form of sampling such as that carried out on the transects could provide data on distribution in relation to habitat provided the transects were sited with a view to including as many vegetation types as possible. Proportions of the different habitats in the transect area are shown in Table 4.

Transect records have been treated in the following ways to describe warthog distribution in relation to habitat :

- a) Sightings of warthog on each of two adjacent 100 yard sectors of the transect have been summed and then divided by the number of traverses made on that transect. The data have not been corrected for variations in visibility along the transect.
- b) The spoor datum "Number of sectors inhabited per traverse" has already been described under methods on pages 16 to 18.
- c) The density of warthog ( $\text{warthog}/\text{km}^2$ ) in each of thirteen habitat types occurring in the transect area has been calculated for dry, wet and cold seasons in each year. For example the area of C.mopane woodland on transects 5 and 6 = 130.5 ha, the number of warthog seen per traverse during the dry season of 1965 was 5.66 and  $\text{Density} = 5.65/130.5 \times 100 \text{ warthog per km}^2$ .

#### 1. Distribution along transects.

The distribution of warthog sightings and of sectors inhabited on each transect is shown in Figs. 13 - 15. Favoured habitats appear to be C.mopane vleis, Acacia-Grewia and C.mopane, Combretum sp., Tristachya wooded and bushed grassland. Warthog

numbers in C.mopane woodland habitat show considerable variation. Brachystegia, Combretum and Baikiaea woodlands show the lowest numbers of warthog and Combretum and Baikiaea also show a very low incidence of spoor activity.

Interpretation of the distribution graphs (Figs. 13 - 15) of warthog sightings and spoor crossings is largely speculative. The 1965 -1966 and 1966 -1967 distributions are very similar but differences between sightings, or between spoor crossings, in different habitats may not be significant. I have not been able to find a statistical test that could be confidently applied to the distribution curves.

## 2. Densities in various habitats.

A wide variety of indices or occupance<sup>y?</sup> ratios can be computed from the transect records to express habitat preferences or utilization. The data can also be tested by chi-square in a contingency table where the expected values for each cell are calculated by assuming that the numbers of animals seen in each habitat are proportional to the area sampled. (Expected value = Total number seen x Area of habitat/Total area sampled). The data, when tested on this hypothesis, provide highly significant chi-square values showing that sightings in various habitats are not proportional to the area sampled. The excessively high chi-square values, greater than 1,000, throw some doubt on the validity of applying this test to the transect data. The hypothesis that warthog distribution is not associated with habitat in the transect area is, on the evidence in Figs. 13 to 15 most unlikely to be true; one would be erecting a null hypothesis which would be

extremely difficult to accept. Thus while a chi-square test may be applicable to limited amounts of observational data on distribution in relation to habitat (Dzieciolowski, 1969) its use on the transect data seems unrealistic. Overall habitat preference ratios and the chi-square test tend to obscure the real variability of the data. For these reasons more elementary statistical parameters have been used.

Areas of the same habitat on adjacent transects have been treated as a single unit, for example, densities of warthog in Acacia tortilis-Grewia communities on transects 3 and 4, 7 and 8, and 11 and 12 have been treated as three rather than six units or samples.

The mean and standard error of the seasonal density determinations in each habitat type have been calculated (Table 5) and plotted in Fig. 16. Warthog have been seen in all habitats sampled by the transects and, despite the evident variability of the data, the following general pattern of distribution in relation to habitat emerges :

High density habitats (greater than 5 hogs/km<sup>2</sup>)

Drainage line grassland in C.mopane (Mopane vleis)

Acacia tortilis - Grewia communities

C.mopane - Combretum sp. - Tristachya W.B.G.

Intermediate density habitats (2 - 5 hogs/km<sup>2</sup>)

"Various Contacts"

C.mopane woodland

Setaria - Andropogon Grassland with A.tortilis

Acacia albida - Hyparrhenia W.G.

Combretum woodland and W.B.G.



Low density habitats (less than 2 hogs/km<sup>2</sup>)

Brachystegia woodland

Brachystegia - C.mopane contacts

Sengwa flood plain grassland

Combretum thickets

Baikiaea woodland (and Baphia thickets)

The most striking common factor in the high density habitats is that they occur on alluvial soils carrying a good cover of palatable grasses or species with edible rhizomes, or both. The habitats with low densities are mostly characterised by sandy soils. Baikiaea woodland, which has the lowest density, grows on a few isolated remnants of Kalahari sand.

The pattern of distribution shown on the transects is in accordance with field observation records and general impressions gained over a five-year period of working in the area.

3. Seasonal density changes within habitats.

Average habitat densities for each season are plotted in Fig. 17 and shown in Table 5a. Considerable density fluctuations are apparent in the high density habitats while in others, such as C.mopane woodland and Brachystegia woodland, average densities show little change from season to season.

Densities in C.mopane-Combretum sp.--Tristachya habitat are highest in the cold and dry seasons and lowest in the wet season (Fig. 18). Spoor data recorded during the cold and dry seasons show this habitat to be more highly used than any other. Signs of rooting also indicate a high utilization of this habitat during the dry season suggesting that food influences the seasonal changes in density which are significant at the 5% level. The

C.mopane woodland areas on transects 7 and 8 which are adjacent to the main C.mopane-Combretum sp.-Tristachya habitat sampled by the transects show clear wet season peaks in warthog density (Fig. 20b). The grassland is predominantly short (Chloris and Sporobolus) and warthog feed extensively in these areas during the rains. A seasonal shift in habitat or of feeding areas is indicated by these data with warthog feeding in short grass areas in C.mopane during the rains and in the taller perennial grassland of C.mopane-Combretum sp.-Tristachya habitat during the dry season.

Density fluctuations in C.mopane vleis and Acacia-Grewia habitats are not obviously associated with season ( $P = 0.07$ ) and no clear seasonal trends are evident in other habitats or areas on the transects.

In some habitats exceptional dry season increases in density have occurred in certain years. These have usually been associated with fires. For example, both C.mopane woodland and Brachystegia woodland showed little change in average density from season to season except during the dry season of 1968 (Fig. 17). Both increases in density were related to local fires which occurred during that season : one on transects 1 and 2 in Brachystegia woodland and another on transects 9 and 10 which affected the C.mopane habitat on transect 9. The effects of these fires on the local density of warthog in the two areas are shown in Fig. 19. The marked increase in density, in both areas, during the 1968 dry season is evident. Both areas were also burned in 1967 but no concentration of warthog occurred because fires were widespread in the Research Area and green grass was widely available. Thus

the effect of burning on local densities of warthog may vary from area to area and from season to season depending on the timing and extent of the burn.

From these observations it is possible to understand two causes behind seasonal density changes : (1) a consistent seasonal change in density, as in C.mopane-Combretum sp.- Tristachya and the adjacent C.mopane areas, which is possibly associated with the availability of rhizomes for which they root during the dry season and grasses on which they may graze during the wet season, and (2) a very variable change associated with fire and rainfall and the local effects these may have on the availability of green grass during the dry season.

#### 4. Density variations within habitat types.

Warthog density in different areas within the same habitat varies considerably. For example the number of warthog seen per traverse in Acacia tortilis-Grewia on transects 3 and 4, 7 and 8, and 11 and 12 differed greatly (Fig. 13 - 15). No two areas of bush are quite the same and even within a fairly uniform vegetation type, such as C.mopane woodland, marked differences in warthog density occur which are associated with variations in the form of the woodland and particularly the grass cover.

Seasonal densities of warthog in C.mopane woodland habitat have varied from less than 1 hog/km<sup>2</sup> to 37 hogs/km<sup>2</sup>. Mean densities, over thirteen seasons, for each of the six transect areas of mopane are shown in Table 6 together with the main features of the habitat in each area. Densities in the six areas differ significantly at the 0.1% level. Without

measurements of the many environmental variables in each area of mopane it is not possible to relate density to particular environmental factors with certainty but the nature of grass cover and the availability of holes appear to be the most important factors (Table 6).

That the relationship between warthog density and area is not straight-forward is exemplified by the differential trends and fluctuations in density within each of the mopane areas (Fig. 20). Much of the variability may be due to the sensitive nature of the grasslands (Rattray, 1957) which can be greatly affected by fires and by differences in the distribution of rainfall during a particular season.

These observations suggest that further analysis of warthog densities in relation to habitat would need to be based on measurements of grassland composition and soil type (which would also affect availability of holes), rather than on vegetation types defined largely by the more easily mapped woody vegetation.

### C. POPULATION STRUCTURE.

Warthog in the Sengwa area and elsewhere in Rhodesia have a short, well-defined breeding season (Child, Roth and Kerr, 1968) and three classes of warthog can be distinguished in the field throughout the year. (See Appendix 3, "Age and sex classification of warthog in the field") Results presented here have been derived entirely from field classifications of warthog in the Sengwa Research Area. The structure of the population is therefore expressed in terms of ratios which represent the number of immature animals (juveniles and yearlings) relative to the



adult population. No absolute data are available; changes are described as changes in the proportion of immature to adult animals. Furthermore it has not been possible to describe the scatter about the age and sex ratios obtained.

Child et al. (1968) have studied reproduction and recruitment patterns in warthog. They found no significant difference in foetal sex ratio and also concluded that sex ratio in adult warthog approaches parity. Results from two hunting operations (in Botswana and in the Nagupande area of Rhodesia) and from Lake Kariba islands indicate an equal sex ratio. They consider the disparity reported from field studies to be the result of an inherent bias in favour of observing females. The possibility of bias in kill records is not examined except to point out that a uniform sex ratio occurs in all age classes. Litters range from 1 - 8 animals with an overall mean (from 231 pregnancies from various parts of Africa) of 3.0 fetuses. From Nagupande (c. 50 km west of Sengwa) the following results of Child et al. (1968) are of interest: prenatal mortality was estimated to be 16.9%; of a sample of 173 mature females, 72% had farrowed; average little size was 3.75; the authors consider 316 young per 1,000 mature females to be the "theoretical maximum reproductive potential" for the population after taking farrowing percentages and pre-natal loss into account.

The authors suggest that "juvenile mortality is sensitive to habitat conditions". A juvenile mortality rate of more than 95% was found on a Kariba island, 70 - 80% in the Nagupande population (considered to be stable and on which most of the reproductive work was done) and less than 60% in a Chobe

Game Reserve population (considered to be expanding). The latter figure was derived from field classifications.

Female warthog reach sexual maturity at approximately 18 months i.e. as yearlings. Male warthog are considered, on evidence of epididymal smears, to reach sexual maturity a year later. However the authors (Child et al. 1968) did not examine testes from yearling males between the months of April and December (inclusive). The rut in Rhodesia is reported to occur in May. Clough (1969), in Uganda, found warthog breeding throughout the year and males reached sexual maturity about a month later than females which did so at 18 - 19 months of age.

Child et al. (1968) consider warthog to be monogamous. Their evidence is based on observations of equal sex ratio in warthog and on the numbers of mature males and farrowing females killed during October and November in Nagupande. (Number of mature animals in sample = 239; number of mature females = 173; number of males which would have been mature at previous rut = 122; number of pregnant or lactating females = 124; the number of males which would have been yearlings at the previous rut was = 44). The correspondence between mature males and farrowing females (122 : 124) is held to be good evidence in support of Fradrich's suggestion that warthog might be monogamous.

#### 1. Collection and validity of population data.

October 1 is taken as the start of the warthog annual cycle and the date on which animals pass from one age class through to the next (Appendix 3). Each year-class is identified by the year

in which the animals were born e.g. the 1965 year-class refers to those warthog born during October - November, 1965. These animals are classified as juveniles until September 30, 1966. On October 1 the same animals are classified as yearlings (of the 1965 year-class) even though many are less than 12 months old. The 1965 year-class pass through to the adult class (properly, sub-adult class) on October 1, 1967 when they are approximately 2 years old. Records (Table 7, and Fig. 21) start with the 1963 and 1964 year-classes and end with the 1968 and 1969 year-classes.

Classifications during 1965 - 66 were drawn from the entire Research Area but since 1967 they have been increasingly drawn from the Lutope and Sengwa Experimental Areas. The December, 1968 sample was drawn from the entire area but most of the 1969 classifications were made in the Sengwa Experimental Area, except during a special capture operation in August when 95% of the observations were made in the Lutope Area.

Selective recording of sounders was reduced to a minimum by recording all groups encountered in the field. Classifications before May, 1966 were recorded by myself and supplemented by Mr. G. Davison during the dry season of 1965. After May, 1966 a few trained Game Scouts equipped with binoculars increased the monthly records. Classifications made at warthog holes since 1967 have been included in the results but not those made on the transects.

An opportunity to test the accuracy of a sample of field classifications has arisen only once. In the Lutope Experimental Area during August, 1969, we caught as many warthog as possible regardless of group composition. Selection of groups, as occurred

during normal capture operations, was reduced to a minimum. The ratios derived from field classifications are compared with those from the captured sample in Table 8. Agreement between the ratios is good. The field classifications in Table 8 do not represent observations of 609 separate individuals but the sum of animals classified in the capture area during August, 1969. Many individuals were seen and classified more than once during the 24 day operation.

Field classifications have been collected whenever and wherever possible in the Sengwa area during the course of other field work. The data obtained are considered to be representative of the warthog population in the Sengwa area but their validity rests on two main hypotheses : that sampling has adequately covered possible differences in the dispersion pattern of age classes and sexes and that there is not a marked inherent bias against observing males in the field.

If dispersion patterns differ within the population then changes in age and sex structure may be a reflection of changes in sampling rather than of changes in the population. Dispersion of warthog at Sengwa is still being investigated but no clear evidence of differential dispersion is available (Chapter VI). Jarman (1968) suggests however that males predominate in marginal habitats or those areas where densities are low while females predominate in "population centres" where density is highest. Jarman found an overall sex ratio of 1 : 1 in 560 warthog classified in his transect area but sex ratios differed on different parts of his transect. In an area of low warthog density 157 males : 100 females were observed while 69 males : 100 females occurred in an adjacent area of higher density on the same transect. Population centres may



thus be rather small areas depending on the extent and proximity of favourable and unfavourable habitats.

If Jarman's observations of differential dispersal apply to the Sengwa area and if our data, because of the high proportion of females observed, have been drawn from a "population centre" then the sex ratio should change during the rutting season because males would move into predominantly female habitats at this time. No marked changes in the proportion of males have been observed during the rut (Table 9) which suggests that differential dispersal of the sexes is not marked or, if it does occur, both male and female areas have been adequately sampled. Increases in the proportion of males in some years have been associated with increases in the proportion of young males accompanying matriarchal sounders (Chapter IV). Observed changes in sex ratio are thus not likely to be due to changes in sampling area. Those months during 1968 and 1969 in which sampling covered areas outside the Sengwa Experimental Area have produced age and sex ratios not greatly different to those observed in the Sengwa Experimental Area. Warthog home ranges are about  $1 \text{ km}^2$  in extent (Chapter VI), they overlap considerably and male home ranges occur with and sometimes within those of matriarchal sounders. Sampling has covered, even when most limited, an area of more than  $10 \text{ km}^2$ .

Child et al. (1968) suggest that disparate sex ratios from field classifications are due to an inherent bias against observing males and that sex ratios of warthog should approach parity. If Child et al. are correct and if, as they also suggest, warthog form stable breeding pairs during the rut then a 1 : 1

sex ratio should be observed in the field at this time of the year but not necessarily at other times. This prediction is not supported by our data which show a preponderance of females during the rut (Table 9). Furthermore, the most frequently contacted sounders are those of one, two or three animals (Fig. 51 and Chapter IV) and these groups are predominantly solitary males or bachelor sounders. It seems more realistic, on present evidence, to accept the sex ratio data from field observations and with it the possibility that sex ratio in warthog populations may be disparate.

Although our field sampling appears to have adequately covered possible bias due to differential dispersion and behaviour of age classes and sexes these issues have not yet received rigorous analysis and study. The population data presented here and the conclusions drawn from them must therefore be viewed with caution.

## 2. Results.

### a) Age structure

Numbers of warthog classified in each two month period between April, 1965 and December, 1969 are given in Table 7. Ratios of juveniles : adult and of yearlings : adult are plotted in Fig. 21.

#### i. Natality, juvenile mortality and breeding success.

A seasonal breeding peak is confirmed by the increase in juvenile : adult ratio during October - December each year (Fig. 21). Litters possibly born as late as February or March have only twice been observed. There is a time lag between birth and observation of hoglets in the field because they spend most of



their first month in holes (Chapter V).

Confinement of the young to holes and a rapid increase in grass cover during December and January preclude a realistic measure of natality. The juvenile : adult ratios in February - March or in April - May indicate natality less pre-weaning mortality. Decreases in the proportion of juveniles after weaning are not marked, which suggests a very low mortality rate after the age of 4 - 6 months and during the first year. Small increases in the 1967 and 1968 year-class juvenile : adult ratios indicate a possible decline in the proportion of adults or that mortality or emigration rates, or both, were greater for adults than for juveniles.

Breeding success is measured by the survival of juveniles to the end of their first year i.e. by the juvenile : adult ratio in September each year. This ratio may also be taken as a measure of potential recruitment into the yearling age class. It was 1.85 juveniles to each adult for the 1964 year-class (Fig. 21, September, 1965, and also Fig. 22). Breeding the following year was less successful with a survival rate of 0.93 juveniles to each adult. This drop in juvenile survival was associated with a decline in population density and a drought at the end of 1965 (page 37 ).

In 1966 - 67 good rains occurred and fires were very limited. Survival of the 1966 year-class juveniles was high at 1.76 juveniles to each adult in September, 1967.

Breeding success in the two subsequent years, 1967 - 68 and 1968 - 69, declined despite apparently equable seasons. Severe frosts occurred in June, 1968 but no evidence of juvenile



mortality was noted at the time and marked juvenile mortality is not apparent from the data in Fig. 21. Reduced breeding success in these two seasons was however associated with an increase in population density (Fig. 12 and 22) which suggests that a density dependent mechanism may be operative.

ii. Yearling mortality and recruitment into the adult class.

The decrement between recruitment into the yearling class, measured by the juvenile : adult ratio in September each year, and the yearling : adult ratio a year later provides a measure of yearling loss for that year-class. The decrement may be due to mortality or emigration or to both; the data do not allow the distinction to be drawn.

Losses in the yearling population appear to be greater than those observed in the weaned juvenile population (Fig. 21). There is a rapid decline in the yearling : adult ratio from October to December each year. The decline coincides with the breeding season and the onset of the rains and it may reflect a dispersal of yearlings. An increase in mortality rate is also possible.

Percentage annual decline in the yearling population is calculated from the following expression :

$$\% \text{ yearling loss} = \frac{a - b}{a} \times 100$$

Where a = recruitment of juveniles into the yearling class  
(juvenile : adult ratio in September).

b = recruitment of yearlings into the adult class  
(yearling : adult ratio of the following year).

A yearling loss of 75% in the 1964 year class coincided with a drought and decline in warthog density during 1965 - 66. Losses



were lower the following year but recruitment had been lower (Table 10). Recruitment into and losses from the 1966 year-class yearlings was high. Recruitment into and losses from the 1967 year class were smaller. Yearling loss could be proportional to recruitment but the data are too meagre to determine this (Table 10).

Recruitment into the adult class shows an upward trend from September, 1967 (Fig. 22) while recruitment into the yearling class showed a downward trend over the same period. The decline in breeding success, as indicated on page 53, may be associated with the observed increase in population density; one might then expect, a priori, that recruitment into the adult class would also decline as population density increased. It is however possible that environmental and, particularly, social influences act differently on the juvenile and yearling components of the population.

#### b. Sex ratio

Sex ratios for each age class over the four year period of observation are shown in Table 11. Sex ratios for each year (age classes lumped) are shown in Table 12 and changes in the proportion of adult, sub-adult and yearling males each year are given in Table 13.

More females than males were observed over the entire period of observation (Table 11). Sexual parity was shown in juveniles at the end of their first year and in yearlings. Sub-adults showed a preponderance of males while adults + sub-adults and adults alone showed a greater number of females. The anomalous preponderance of sub-adult males is discussed in Chapter IV, page 123.

Sex ratio differed in the population from year to year

(Table 12). The proportion of males was lowest in 1966 - 67 at 34 % ♂♂ : 66 % ♀♀ and highest in 1968 - 69 at 47.8 % ♂♂ : 52.2 % ♀♀.

Changes in the overall sex ratios were largely due to changes in the sex ratios of sub-adults and yearlings. A high proportion of sub-adult males (73.1%) was recorded in 1968 - 69. The proportion of adult males between 1966 - 67 and 1968 - 69 showed no significant change, while annual changes in the younger age classes were significant (Table 13).

Since sex ratios of 1 : 1 have been reported from the same broad geographic area as Sengwa (Child et al. 1968; Jarman, 1968) the information needs reappraisal. The findings of various workers are summarised in Table 14.

Field classifications of various workers indicate a sex ratio of about 34 % ♂♂ : 66 % ♀♀ and, apart from those of Jarman (1968) who recorded 50 males : 50 females, agree fairly well. Records from kills or captures from Kariba are confused. Sample sizes quoted by the authors differ and are presumably derived from sources within the rescue operation records. Junor's data were collected by himself during the initial stages of Operation Noah and come from the riverine area of the Zambesi, now flooded by Lake Kariba (Junor, pers. comm. 1968). Child's data are from two islands formed during the flooding of the valley and the sample (163 warthog) is small. Jarman (1968) quotes figures from Operation Noah journals as indicating sexual parity but says that sex ratio differed significantly between 1959 and 1960 at the 5% level. I have however calculated a sex ratio of 43.6 % ♂♂ : 56.4 % ♀♀

from data provided on page 119 of his thesis, viz:

Adults

143 males : 196 females

Juveniles

61 males : 95 females.

The sex ratio differs significantly from parity at the  $\frac{1}{0.01\%}$  level.

Child's (1968) sample from Nagupande was 491 animals with 242 males and 249 females. A sample of 1,271 skulls from the same hunting operation was examined to establish aging criteria for warthog (Child, Sows and Mitchell, 1965). Only those animals killed during the first two months of the Nagupande operation (October - November, 1962) were used in this sex ratio sample.

More extensive kill records from the Sebungwe controlled hunting area (which includes the Nagupande area) for 1964 - 67 are given in Table 15. In the overall sample of 3,506 warthog the sex ratio was 47 % ♂♂ : 53 % ♀♀, which differs significantly from parity at the 0.5% level. However, similar data from the Gokwe - Sanyati - Sessami Controlled Hunting Area for the same period shows a sex ratio of 48 % ♂♂ : 52 % ♀♀ which does not differ significantly from parity (Table 15).

The contention that field classifications are biased in favour of females has already been examined (page 50). The reliability of kill records vis a vis those from field classifications requires some comment. Trained observers classify, as far as possible, all animals seen when sampling a population whereas African hunters engaged in control operations must, when faced with more than one animal, select their quarry. Two factors which might result in a greater selection of males by hunters are :

(a) Male warthog, being more solitary than females and usually less wary, are more readily shot. (b) Adult males, when with a

sounder, are normally the most conspicuous members and thus the most likely targets (a factor which should also enhance their proportion in field classifications).

It would seem that errors in determining sex ratio are as likely to arise from kill records as from field classifications and unless the entire population has been obtained, and emigration prevented, kill records may be of dubious value. Hunted populations are also highly disturbed and behavioural responses not fully known. Field classifications, on the other hand, are usually derived from undisturbed populations and are more likely to provide realistic population structure data than those from extensive control operations.

The available evidence indicates that while warthog populations generally show a sex ratio of nearly 1 male : 2 females, this is not necessarily static and may be 1 male : 1 female. The Sengwa evidence indicates that sex ratio may vary with time in the same population. The disparity between sexes was greatest when population density was low (1966 - 67, Fig. 12 and Tables 11 and 12 for sex ratios) and approached 1 : 1 when population density increased. Child's observation of a 1 : 1 sex ratio on Kariba coincided with an over-crowded population. The Nagupande population was considered stable and initially showed a sex ratio of 1 : 1 (if we accept that the data from the kill sample provide a reliable estimate of sex ratio). Field classifications from Botswana (Child *et al.*, 1968) showed the lowest proportion of males and the population was considered, on other grounds, to be expanding. Thus the apparently conflicting information on warthog sex ratio can be accommodated within the



hypothesis that sex ratio changes with population status, being disparate in favour of females when the population is expanding and approaching parity when stable or at excessive densities. The situation of males being more numerous than females (except in the sub-adult class of the Sengwa data) has not been reported.

A disparate sex ratio may arise in two ways : differential sex ratio at birth or ~~by~~ differential mortality. The following data do not support the hypothesis of a differential sex ratio at birth although Fradrich's sample, in isolation, does indicate more females than males at the 5% confidence level :

| <u>Author</u>              | <u>Type of sample</u> | <u>No. of Males</u> | <u>No. of Females</u> |
|----------------------------|-----------------------|---------------------|-----------------------|
| Fradrich (1965)            | Births in zoos        | 17                  | 31                    |
| Cumming (this report)      | Births in tame hogs   | 7                   | 1                     |
| Child <u>et al.</u> (1968) | Foetal (Rhodesia)     | 43                  | 35                    |
| Cumming (unpublished)      | Foetal (Sengwa)       | 13                  | 14                    |
| Geigy (1965)               | Foetal (Tanzania)     | 9                   | 12                    |
|                            |                       | <u>89</u>           | <u>93</u>             |

Sex ratios from Sengwa field classifications indicate parity in juveniles at the end of the first year and also in yearlings, although the yearling sex ratio may differ from year to year (Tables 11 - 13). Of 90 juvenile warthog captured at Sengwa 47 were males and 43 females. Juveniles are the only age class in which there is probably no bias in capture operations which is why, apart from the August, 1969 sample (Table 8 and page 48), capture records are not quoted for other age classes. Sex ratio at birth and in the juvenile age class appears to be 1 : 1. The data are however very meagre. Sex ratios at birth showing a slight

preponderance of males have been reported for many species of mammals but not the domestic pig (<sup>3</sup>Adsell, 1946). The disparate sex ratio in older age classes of warthog suggests that differential mortality occurs.

Observations on radio-tagged adult males indicate that their behaviour may make them more susceptible to predation by lion. Two traits which seem to be significant are that older males tend to be largely solitary and they frequently do not go into holes until well after dark. They may spend the night resting up in a hollow in the ground or in long grass. One radio-tagged male (Ad. ♂ 175) was in fact killed by lion in such a situation.

Predation records have been collected at Sengwa but the data are too inadequate to show sex differences in kills. Records from some of the other species do suggest a higher predation rate on males. A major problem in assuming that the proportion of males in a population is regulated by predation is that of explaining how, in one species, predators may keep the sex ratio in adults at 1 male : 2 females while in another they maintain the ratio at 1 male : 4 females as in <sup>k</sup>Kudu (Jarman, 1968). It seems more likely that behavioural changes within the population and particularly changes in social organisation may provide the basis for changes in sex ratio or for differences in sex ratio between species. These may operate so as to increase the chances of certain individuals falling prey to predators. Intra-specific conflict and consequent injuries may also play a role. Adult <sup>k</sup>Kudu bulls which have been gored and have later died of peritonitis have been found on four occasions in the Sengwa Area and others with broken

legs have been killed by predators. Similar observations have not however been recorded for warthog in the Sengwa Area.

## C H A P T E R   I I I .

ENVIRONMENTAL   FACTORS.

Distribution patterns of warthog in the transect area showed that certain vegetation types or areas supported more warthog than did others. The transect data also indicated that marked variations in density may occur within a single habitat; warthog density is thus not simply related to vegetation type. The environmental factors which appeared most likely to influence distribution were food, water, and holes in which the animals sleep at night, and possibly climate. It was not feasible to study all the other environmental factors which may affect warthog populations such as predators, disease and parasites.

Food, water and holes will be considered in turn. Climate impinges on these factors and is considered where appropriate and also in the final section on daily patterns of activity.

A.   FOOD.

Published information on warthog food habits was meagre and studies had to begin at a very simple level. Detailed studies of nutrition, while of considerable importance in African wildlife work, were beyond the resources at Sengwa. Questions asked were therefore :

- i)   What do warthog eat and how do they feed?
- ii)   Does their diet change with the seasons?
- iii)   What, in general terms, is the distribution and availability of the main items of warthog diet?

Only within the last decade have plant species eaten by warthog been reported in the literature (Pienaar, 1962; Lamprey, 1963).



Earlier statements about warthog feeding, with the notable exception of Ewer's (1958) study of suid cranial anatomy in relation to feeding, have been limited to whether warthog grazed or rooted and the extent to which they were omnivorous.

While Bigourdan (1948) considered warthog to be omnivorous with a primary diet of roots, notably those of aquatic plants, supplemented by grass, the general consensus of early opinion is that warthog are grazers but may also eat roots. Stevenson-Hamilton (1947) suggests a seasonal change from grass once it ceases to be fresh and succulent to roots and tubers. Pienaar (1962) states that during the dry season in the Transvaal they subsist entirely on juicy rhizomes, corms and grass roots. Vesey-Fitzgerald (1960) reports warthog rooting for the rhizomes of perennial grasses and for the bulbs of Cyperus usitatus in the Lake Rukwa region of Tanzania. Of 291 feeding records reported by Lamprey (1963), grass roots (? rhizomes) comprised 5%; aerial portions of grasses 78%; sedges 6% and the remaining 12% was made up of dicotyledonous plants of which only 1% was on fruits.

Fradrich (1965) considered warthog to be grazers and did not see them rooting in the Nairobi National Park. Clough (1969, citing pers. comm. from C. R. Field) states that warthog in the Queen Elizabeth National Park, Uganda are mainly grazers. Mitchell (1963) reports that in the Kafue National Park, Zambia the rhizomes of Tristachya superba (Loudetia superba) form the staple diet of warthog during the cold season. Child (1968) examined the stomach contents of warthog shot during the late dry season in the Nagupande area of Rhodesia and found them to

contain approximately 90% rhizomes, mainly of Tristachya superba. Child (1968) also reports on a tame animal which, although it had access to green grass at a spring, continued to root for rhizomes. He suggests that rooting is not an emergency measure (cf Ewer, 1958) but that rhizomes provide the most nutritive food during the dry season. Warthog confined to islands in Lake Kariba made little use of the available carrion and Child has queried suggestions in the literature that warthog are characteristically omnivorous.

Roth's (1965) studies of growth in captive warthog indicate a decline in growth rate during the dry season in Rhodesia, despite a supplemented diet, and he suggests that the dry season may be one of considerable hardship for feral warthog. Ewer (1958) suggests rooting may be an emergency mechanism in an otherwise typically grazing species. On the basis of cranial anatomy and field observations in Zululand, Ewer (1958) characterises the warthog as a highly specialised "grass plucker". This idea is examined in some detail later in this section.

#### 1. Plants eaten by warthog in the Sengwa Area.

A list of the grasses collected in the Sengwa Research Area is provided in Appendix 2. Species on which warthog have been found feeding in the Sengwa Area, and elsewhere in Africa, are also shown. The grass collection contains most of the species occurring in the Sengwa Area.

Grasses eaten by warthog, the part of the plant eaten and whether the record was derived from tame or wild animals are shown in Table 16. Records from the more easily observed tame animals

predominate.

Wild warthog have not been observed feeding on dicotyledonous plants but tame hogs have been seen feeding on Commelina sp., Ipomea sp. and Portulaca hereroense. Neither wild nor tame warthog have been noted feeding on sedges. In 1967 two tame warthog frequently fed at a tree (Hexalobus sp.) whose fruits they were able to reach. Tame warthog did not eat fruits of Commiphora mollis or dry Acacia albida pods offered to them; both of these fruits were eagerly consumed by the tame bushpig. Unidentified remains of dicotyledonous plants were found in only 15 of 600 warthog faecal samples whereas remains of these were evident in all of the few bushpig pellets I have been able to examine.

Meat offered to the tame warthog was sometimes eaten but the tame bushpig always ate meat given to him and waited for more. One female warthog readily ate a litter of rats found in a grain-store while another ignored them. A tame warthog has been seen to nibble at a civet carcass. <sup>Mr. V.J.</sup> Wilson (pers. comm.) has seen warthog kill and eat snakes. I have found the claws of either a young antbear (Orycteropus afer Pallas) or a young springhare (Pedetes capensis Forster) amongst the well digested remains of a small mammal in the stomach contents of a warthog. Only 2 faecal samples of the 600 examined contained bone fragments; in both cases they were very small bones possibly belonging to a rodent or insectivore. Both species of tame pig have frequently, and at all ages, chewed bones. In young warthog this behaviour appeared to be a function of "teething". Young warthog (and the young bushpig) have eaten winged termites attracted to the lamps in

the house at night (Fig. 23). I have not seen older warthog eating termites which swarm in the late afternoon at the start of the rainy season.

Despite these observations of warthog eating non-vegetable matter it must be emphasized that they are rather rare and isolated occurrences. Noting them, because they are unusual, imparts to them a greater significance as dietary items than they deserve.

## 2. Seasonal changes of diet

Three main types of feeding are shown by warthog in the Research Area : grazing, rooting or digging for rhizomes, and "shredding" during which the flowering heads of grasses are ingested (Figs. 24 - 26). Quantitative information on the importance of these methods of feeding, which also involve changes of diet, has been obtained from two sources :

### a) Faecal samples

An examination of 600 samples collected at the rate of 50 per month between June, 1966 and May, 1967 revealed marked seasonal changes in the relative abundance of graminaceous leaf, seed and rhizome fragments in the faeces of warthog (Fig. 27). The data show that warthog feed mainly on grass leaves during the rainy season but also extensively on grass seeds when these were towards the end of the rains (February - March) and that they subsist largely on perennial grass rhizomes during the dry months (April - October). The high proportion of rhizomatous remains in faeces during the dry season may be partly a reflection of their indigestibility rather than the true extent to which



they are ingested by warthog.

b) Direct observation of tame free-ranging warthog

While observing diurnal patterns of activity in tame hogs feeding was recorded as "grazing", "rooting", "shredding" or "other". Since activity is recorded at ten minute intervals the record also provides a measure of the time spent feeding in different ways (Methods page 33). Animals were observed for 12 to 18 days in each month over a year; the proportions of ~~the~~ time spent grazing, rooting, shredding or feeding on other items (mash, meal and items from rubbish pits in the villages) are shown in Fig. 28. The data confirm the results of the faecal analysis and show that, in the tame warthog at least, the major food item during the dry season is rhizomes.

The month of the year at which grazing changes to rooting, and vice versa, depends largely on when the rains start and cease. Thus in 1966 rains started in mid-November and a change from rooting to grazing occurred shortly afterwards (Fig. 27). During 1969 rains began unusually early and heavy falls occurred before mid-October; the resulting early flush of green grass lead to an earlier change from rooting to grazing than had been observed in 1966 (Fig. 28).

### 3. Wet season foods

The wet season diet of warthog is characterized by a wide range of species. The number of species eaten is probably greater than listed (Table 16). Observations on wild and tame hogs indicate that species favoured during the wet season are

Sporobolus marginatus, S.festivus, Chloris virgata, Urochloa trichopus, U.pullulans, Panicum maximum and possibly Setaria pallide - fusca. The extent to which the various Eragrostis sp. may be used is not known. Some support for these general observations is provided by a sample of 290 feeding minutes recorded on six tame warthog in February - March in five different parts of the area. The actual times and percentage of total time spent feeding on each of the 19 species is given in Table 17. Approximately 76% of the time was spent feeding on the following six species : Chloris virgata, Setaria pallide-fusca, Sporobolus festivus, S.marginatus, Urochloa pullulans and U.trichopus. Feeding minutes were recorded in C.mopane woodland, Sporobolus-Chloris grassland and Acacia tortilis-Grewia sp. wooded and bushed grassland (all favourable habitats).

Warthog were also taken to areas thought to be unfavourable for feeding at that time of the year. For example Sophie, Gladys and Mackintosh were taken into C.mopane-Combretum sp.-Tristachya wooded and bushed grassland where they did not feed. Mackintosh spent only 1.4 minutes out of 14 occasionally nibbling at D.milanjiana, T.superba, Aristida sp., Sporobolus panicoides, Setaria pallide-fusca and Urochloa trichopus; the Sporobolus, Setaria and Urochloa species occurred infrequently in the pasture which was composed primarily of Digitaria, Tristachya, Andropogon and Aristida. On completion of the 14 minute sample Mackintosh and the other two hogs were immediately taken to an adjacent area of Sporobolus-Chloris grassland only 80 paces away. Mackintosh started grazing at once, spending 5.75 out of 6 minutes

feeding on Chloris virgata. The behaviour of Sophie and Gladys followed the same pattern and feeding in Sporobolus-Chloris grassland continued for another half an hour. On again passing through C.mopane-Combretum sp., Tristachya W.B.G. the animals showed no inclination to feed.

Many grasses which are generally tough and unpalatable for warthog may be acceptable in their young stages following a fire at the end of the dry season. Tame warthog have been recorded feeding on Tristachya superba leaves in November after a burn, but not later in the season. The species which fall into this category are Heteropogon contortus, Hyparrhenia sp., Andropogon sp. and the large Setaria sp.

Both the faecal analysis and the gross seasonal pattern of feeding seen in the tame warthog (Figs. 27 and 28) have indicated that grass seeds (before they drop from the plant) form a major food item during February and March. The flowering heads of Urochloa sp., Chloris virgata and Echinochloa colonum (Fig. 25) appear to be the most important. (Identifications of seeds in faecal samples have not been made). Warthog have been observed feeding on the seeds of Sorghum versicolor, Panicum maximum and possibly Leersia hexandra seeds. Seeds of Setaria sp. are evident in the faecal material.

Warthog have been seen to wade into shallow pans to feed on the fleshy stems of Sacciolepis sp. (parts of this plant offered to a tame warthog were readily eaten). Pans containing Sacciolepis show signs of heavy utilization by the end of the rains.

Warthog thus feed on a wide variety of grass species during



the rains but appear to prefer the shorter tufted perennials and certain annuals (Sporobolus, Chloris and Urochloa). Short grasses are, in the Sengwa area, most abundant in the poorly developed or "downgraded" grassland areas - particularly in C.mopane and seasonally waterlogged soils. Petrides and Swank (1965) found the greatest densities of warthog in the most heavily grazed and short grass areas of the Queen Elizabeth National Park in Uganda. Sporobolus marginatus and Cynodon dactylon formed a high proportion of the feeding records reported by Lamprey (1963). Cynodon is not common in the Sengwa area but tame warthog graze on our lawns whenever they can. The grazing habits of warthog in the Sengwa area (apart, perhaps, from the eating of grass seeds) conform with observations made in East Africa. The warthogs' apparent preference for short grasslands may be due not to the grasses they contain but to a disinclination to move through tall grass. The animals are short and visibility in tall grass would be severely restricted. However, since the animals dig for rhizomes in tall and fairly dense (but dry) grassland the latter possibility is unlikely. There is some circumstantial evidence to suggest that warthog will avoid moving through rank wet grassland but such conditions only obtain in the morning (dew) and on rainy days during the wet season.

Warthog at Sengwa make effective use of mature grass seeds before they fall; it is unlikely that they would be able to gather fallen grass seeds. They eat the highly nutritious seeds at a time when the nutritive value of leaves is declining at the end of the rainy season. Warthog are not alone in using this food



resource ; impala have been seen feeding on flowering heads and grass seeds are sometimes very evident in the faeces of elephant.

#### 4. Dry season foods.

The marked change from grazing in the wet season to rooting in the dry season has already been demonstrated. Rooting is virtually confined to the rhizomes of three grasses : Digitaria milanjiana, Tristachya superba and Oryza barthii with very occasional records of Echinochloa pyramidalis, Hyparrhenia sp., Phragmites sp. and the swollen bases of Heteropogon contortus and Setaria sphacelata. Digitaria, Tristachya and Oryza are the only grasses that are both widely distributed in the area, and which possess, so far as I know, well developed rhizomes. Echinochloa pyramidalis is limited to a few moist areas in heavy clay soils which are extremely hard in the late dry season. Phragmites is restricted to the banks of the Sengwa River. Oryza barthii grows in pans and temporary drainage line pools in C.mopane woodland; by the end of June the areas where it occurs have been thoroughly rooted and the rhizomes depleted (Fig. 29). Thus Digitaria milanjiana and Tristachya superba form the main items of food for most of the dry season.

Although warthog spend much the greater proportion of time feeding on rhizomes during the dry season they nevertheless also graze. Green leaves are eaten where available e.g. the basal portions of such tufted perennials as Hyparrhenia rufa, Schizachyrium jefreysii, Eragrostis sp. and Andropogon gayanus occasionally have green leaves even in September; along the banks of the Sengwa River and in some areas where sparse but still

green Sporobolus marginatus occurs. There is however no indication, with the notable exception of burned areas, that warthog congregate on limited areas of green grass. Little information has been gathered on the extent to which warthog feed on dry fodder but tame warthog have been seen feeding on the dry leaves of Urochloa bolbodes.

These observations are supported by a sample of 158 feeding minutes recorded over a period of four days in September, 1969 on Susan and Mackintosh (Table 18). Sites at which the records were made were not selected in any way by myself but depended on where I found the animals feeding; they were entirely unrestricted. The observations represent an accumulation of six samples of 20 or 30 minute observation periods plus one of 50 minutes. Table 18 shows that the animals spent over 94.4% of their feeding time rooting for Digitaria milaniana and Tristachya superba. While it would have been desirable to separate time spent rooting from time spent ingesting rhizomes this proved extremely difficult in practice. Occasions when animals rooted but did not ingest the rhizomes and then moved to a new rooting site, even if only a metre or less away, were not included in the feeding time. The remaining 5.6% was spent grazing on fragments of green grass and rooting the basal portion of a Urochloa bolbodes plant. This is a very small sample but there is no reason to suspect that it differs greatly from what has been observed in a less systematic manner on numerous other occasions.

Ewer (1958) has characterised warthog as highly specialised grazers. Because of the importance of rooting to warthog in the

Sengwa area, and probably in much of Southern and Central Africa (Child, 1968; Mitchell 1963), it is desirable to re-examine Ewer's ideas at this point.

5. Anatomical adaptations of warthog and bushpig (Potamochoerus porcus Linn.) in relation to their manner of feeding and their habitat.

The manner in which warthog and bushpig feed has been described and discussed by Ewer (1958) in her consideration of the adaptive features of the skulls of African suids. Her conclusions were based on a discerning analysis of the cranial anatomy of these animals with some supporting field observations of warthog in a Zululand game reserve. She has characterised warthog as highly selective "grass pluckers", feeding predominantly on the growing tips of short grasses. Ewer demonstrates that the unique structure of warthog incisors can be understood in terms of this method of grazing. Rooting is considered by Ewer (and others) to be relatively unimportant to warthog but of major importance to bushpig and she says of warthog, "the characters of the snout are explicable in terms of the large upper canines and the reduced importance of digging with the rhinarium".

It is argued here that the emphasis is misplaced in assigning the short rigid structure of the warthog snout to the presence of large upper canines and the reduced significance of the rhinarium in digging. The feeding habits and diet of a species may, as Ewer notes, vary in different parts of its range. Ewer did not see warthog rooting in northern Zululand where this manner of feeding is apparently of little importance. In Kenya and in Uganda rooting



observations have seldom been reported (Eradrich, 1965; Clough, 1969). Rooting is, however, of major importance to warthog in the Sengwa Area and is clearly the dominant manner of feeding for much of the year. Re-examination of certain aspects of the cranial morphology and anatomy of the suids is therefore desirable. The differences between warthog and bushpig snouts might be due to differences in the manner in which they dig rather than to the extent to which they do so.

Tame free-ranging warthog and bushpig have provided the major source of material for the observations reported below.

The anatomical features of an animal are often a compromise between a number of functional demands and adaptations. In addition to feeding, fighting and defence with their attendant armoury, the disposition of sense organs may also play a significant role in determining cranial anatomy. Observations of behavioural aspects other than feeding which supplement Ewer's analysis have been made but will be discussed under "Agonistic behaviour" in Chapter V.

a) Observations on feeding and digging.

Both warthog and bushpig show two distinctive types of feeding, namely, grazing and rooting or grubbing for foods in the soil. Feeding in a more generalised manner on fruits and such-like need not concern us here since in neither animal do these appear to be of major importance and no specialised adaptations appear to be involved. The manner in which tame warthog and bushpig have been seen feeding is described first and the observations are then discussed in relation to the anatomical features of the two



animals.

Grazing in warthog. Three fairly distinct methods of grazing are recognised, each being dependent on the growth form and part of the plant being eaten. The modes of feeding are termed : grass plucking, coarse cropping and shredding.

Grass plucking has been described by Ewer, (1958). It has been observed at Sengwa in both tame and wild warthog and occurs when feeding is on low, finely tufted species of grass or on the spring shoots of taller, often less palatable, species (Fig. 24b). Warthogs may either walk along slowly from tuft to tuft or progress on their fore-wrists while plucking short, more densely covered swards.

Coarse cropping refers to grazing performed on taller and frequently broader and longer-leaved species of grass. Leaf blades are taken into the side or front of the mouth and then broken off with a sideways or upwards movement, or both, of the head. Protruding ends of severed grass are gradually drawn into the mouth during chewing and as the next mouthful is taken. The role of the incisors during this process is not clear. The lips seem to play a major role but are rather firm and inflexible and movements are in no obvious way comparable to the rapid and often deft movements of some bovids (e.g. a tame impala reared and often running with the warthog used its lips and tongue to a much greater extent in working grass blades into its mouth; once in, a distinct bite, using the incisors, accompanied by a jerk of the head, served to sever the leaf). Use of the tongue in the prehension of food by warthog is limited by its length. I have never seen either of the suids lick their lips in the way a bovid can. It is difficult to

see the tongue at all while the animals are feeding.

Tame warthog have frequently been observed coarse cropping. Indeed many of the species on which warthog are known to feed, both at Sengwa and elsewhere, are too tall and long leaved to warrant plucking e.g. Panicum maximum and Urochloa pullulans.

Shredding refers to feeding on the flowering heads of grasses (Fig. 25). The movements involved are akin to those of coarse cropping but are modified to deal with a source of food usually above and out of the animal's limited reach. A stem bearing an inflorescence is grasped in the mouth which is then worked up along the rachis (often by simply drawing the still anchored rachis through the mouth) until the seeds are reached; the flowering head is then pulled off with a sideways and upwards sweep of the head. A number of stalks may be grasped at the same time. Sometimes the stalks are drawn out of their sheaths before the seeds have been reached. A sound often accompanying this feeding is the squeak of a stalk being drawn from its ensheathing leaf base (a sound familiar to all who have drawn and chewed the succulent bases of such stalks). Flowering heads within reach are taken straight into the mouth.

Feeding on grass seeds constitutes an important feeding pattern in the Sengwa area during the latter part of the wet season (Figs. 27 and 28) and does not appear to have been reported elsewhere.

Bushpig. I have frequently seen our tame bushpig feeding on grass in a manner approaching the coarse cropping of warthog. He appeared to be much less efficient at it than the warthog and his

cropping was more reminiscent of a dog taking grass. He was not seen grazing short tufted grasses although he often nosed these out of the ground and ate the entire tuft.

#### Rhinarium digging

The terms "rhinarium digging", "rooting" or simply "digging" are applied to both warthog and bushpig and the literature contains no information on differences of style or sites of digging between the two species. The chief differences are highlighted in Table 19, and probably stem from the contrasting diets and habitats of the two species. Warthog tend to live in areas where soil is dry for much of the year while bushpig live in moister habitats. Rhinarium digging by warthog is shallow while in bushpig it is deeper. Phillips (1926) notes that in the Knysna Forest (Cape Province) bushpig "snout the soil to a depth of several inches, thus obtaining supplies of buried seeds, roots, rhizomes and insects".

#### b) Anatomical features.

An external examination of bushpig and warthog reveals the following main differences in the oral and snout region:

The anterior part of the mouth is slightly less inferior in warthog than it is in bushpig (Fig. 30). The profile of the warthog lower jaw and the point at which it apposes the snout is not greatly different from cattle.

The lower lip of warthog is broad, rounded and shows little flexibility (Fig. 31a). In bushpig the lip is thinner and a great deal more flexible; it is possibly partly prehensile (Fig. 31b).

The distal end of the bushpig snout is markedly bulbous by

comparison with the flatter, harder warthog snout. Mobility of the rhinarium is greater in bushpig which are capable of lateral and dorsoventral changes in the inclination of the plane of the rhinarium. In warthog lateral changes in inclination of the rhinarium are less marked and dorsi-ventral flexion is limited to the dorsal edge; the ventral edge of the rhinarium appears to be fixed. These observations are based on watching live animals and manipulating fresh carcasses. Bushpig almost continuously twitch their noses this way and that, while the warthog rhinarium is more static. Bushpig also have a "wet nose" while in warthog it is dry.

The dorsal edge of the warthog rhinarium is more acute in section but projects less above the general line of the snout (Fig. 30) than it does in bushpig. The end of the snout is also flatter, more spade-like and harder than the rounded protruding nose of the bushpig.

In warthog the bridge of the snout is broad and flat and almost hairless. The bushpig snout is much narrower, more rounded and covered with short erect bristles except on, and just behind, the rhinarium (Fig. 30). Warts in older males result in a flattening of the more proximal region of the bushpig snout.

In warthog the position of the mouth, the structure of the lower lip and, as Ewer has shown, the structure of the incisors are clearly associated with grazing. However, the short, sharp, firm and broadly pointed dorsal aspect of the rhinarium is admirably suited to shallow digging in hard soils. This view differs from that advanced by Ewer who bases many of her views on the skeletal architecture of the warthog snout. She



writes :

"In the bushpig the dominating importance of rhinarium digging is reflected in the elongated and vertical sided snout; in the warthog the dominance of the upper canine is reflected in exactly the reverse characters; the snout is relatively short, and the nasals are rounded, so as to give maximum strength and rigidity without undue increase in weight, the weight carried by the snout in the upper canines already being considerable" (underlining mine).

Shovelling must place a considerable bending strain on the maxillary and nasal regions of the warthog snout. The longer the snout the heavier and thicker it would have to be to withstand this strain. Since a tubular structure is the most economical with respect to weight in terms of strength then a short snout with a tubular cross section in the skeletal supporting structure, such as Ewer describes, would be well suited to resist the strains imposed by shovelling with the tip of the snout. It is my contention, therefore, that the snout was shaped primarily by the demands of shovelling and grazing rather than by the influence of the tusks and exclusive specialization for grass plucking.

Ewer indicates that ancestral omnivorous suids rooted and that, in the evolution of the Phacochoeroids, the importance of rhinarium digging declined as they became more specialised herbivores. The warthogs' diet in the Sengwa region (and probably much of Southern Africa) is almost entirely herbivorous rather than omnivorous, despite its digging. Plucking of tender grass shoots by warthog is no more likely to demand highly specialised cheek teeth than is the soft dicotyledonous diet of Hylochoerus. The latter shows little specialisation in its

cheek teeth (Ewer, 1958). The rhizomes<sup>mes</sup> eaten by warthog during the dry season probably require grinding molars as efficient as those developed for grazing (the grinding cheek teeth of many rodents bear ample testimony to this probability). The evolution of a grazing-rooting complex, both aspects of which may be highly specialised, is feasible. Incompatibility would arise only if the prehension movements required and the nature of the food were dissimilar. The warthog rhinarium is modified so as to act as a shovel but this does not obstruct selective prehension of grass by plucking with the incisors. No additional modifications to the mouth or incisors are required by the mode of digging which does however allow for the development of tusks. Excavations are shallow and the tusks would be well clear of the ground when rooting whereas in the bushpig the snout is thrust well into the earth and its shorter tusks do not hamper deep excavations and probing in loose or moist earth.

Simultaneous specialisation for rooting and grazing makes ecological sense. An ancestral form of suid invading the arid savanna and becoming a more proficient grazer would be unlikely to dispense, immediately, with its ability to root for food. The harsh dry season common to much of the savanna of Africa would have placed a grazing non-ruminant unable to supplement its diet at a disadvantage. The vast and probably largely untouched reservoir of perennial grass rhizomes would have been at its disposal were it able to dig for them. (I have seen elephant laboriously kicking out tufts of grass at the peak of the dry season but, apart from this, grass rhizomes appear to be a source of food

no certain  
evidence from  
that warthog  
require grinding  
molars for  
grazing.  
If that is the  
case, then the  
rhizomes would  
be good teeth  
as good teeth  
as good teeth.  
How?

untapped by ungulates other than suids.)

The great importance attached by Ewer to the incisors and to grass plucking is called into question by the considerable variability in warthog incisor number recorded by Child et al. (1965). They found that in 400 specimens with permanent, moderately worn incisors, 53.5% had two incisors in each lower jaw, 33.5% had three and 13% had three on one side and two on the other. All except one specimen had a single incisor in each upper jaw. It would be interesting to know whether variability in incisor number is associated with aridity of the habitat and the extent to which rooting predominates over grazing during the dry season. One of our tame warthog, Rosemary, possessed no upper incisors but this was not evident from her behaviour; the lack of upper incisors was discovered only after her death. Field (1968) states that hippopotamus are able to graze very short grassland by using their lips and it is possible the lips may be more important to warthog when grazing than either Ewer or I have observed.

The form of the bushpig snout is also adapted to the way the animal digs and feeds. The long, rounded and hairy snout is generally worked well into the soil. If the earth is sufficiently tractable the snout is then pushed, plough-like, through it. As a result the major forces in digging act not on the point of the snout, through the rhinarium, but chiefly on and through the bridge of the snout i.e. proximal to the rhinarium. As Ewer (1958) states, this region of the bushpig snout shows evidence of strengthening by the horizontal nasals and vertically placed

maxillae which abut onto a strengthened palatal maxillary region. The nasals are also placed higher in relation to the canine roots than in the warthog. The bridge of the snout is effectively well clear of the canines which are thus less likely to obstruct digging.

Bulbs, grubs and other food are unearthed by lifting the snout and the earth with it. The protruding nose is placed over a morsel which can only then be ingested into the inferiorly situated mouth. The foods eaten and the precise method of ingestion are extremely difficult to observe (even from six inches) because the anterior part of the mouth is usually buried in the soil.

Our tame bushpig was incapable of digging, or even enlarging warthog scrapings, in hard compacted ground. He was frequently seen examining warthog diggings for left-over rhizomes. In the Knysna Forest area, Phillips (1926) found that bushpig preferred the moister portions of the climax forest.

Thus the bushpig with its omnivorous habits, soft rhinarium, narrow snout and mode of digging seems fitted for moist forested areas. The warthog on the other hand shows adaptations for dry, almost arid habitats. It has twin specialisations for grazing short, seasonally succulent pastures and for digging perennial grass rhizomes in hard dry soils. It is a herbivore which has capitalized on the suid ability to dig with the rhinarium and this has probably enabled it to compete successfully with ruminants in dry savanna regions which it might not otherwise have been able to invade.



## 6. Availability of food.

Three important facets of food availability are : distribution, quantity and quality of the food resource. The quality of warthog food has not been investigated in this study. Clear seasonal changes in warthog diet have been shown (2. above): the animals graze during the rains, eat quantities of grass seeds towards the end of summer and subsist largely on rhizomes during the dry months. Anatomical and behavioural observations by Ewer (1958) and later by myself (5. above) indicate that warthog show two specialised modes of feeding, grass plucking and shallow rhinarium digging for rhizomes in hard dry soils. The stance in both methods of feeding is typically one of resting on the forecarpals. Grass plucking permits selective cropping of short pastures while shallow rhinarium digging permits utilization of perennial grass rhizomes in dry savanna regions. Wet and dry season food requirements differ and the availability of foods in each season is discussed separately.

### a) Wet season.

Warthog feed on a wide variety of grasses during the wet season (Table 16) and available evidence indicated a preference for Chloris virgata, Sporobolus marginatus and Urochloa trichopus. Species such as Brachyachne patentiflora, Brachiaria grossa and Setaria pallide-fusca are also taken. All are short grasses (in the Sengwa Area) which occur mainly in downgraded grasslands (those lower in the succession) and on saline soils. C.mopane woodland forms about 50% of the Research Area and although its

grass cover varies greatly (Table 6) Sporobolus, Chloris and Urochloa are important and widespread species in this habitat. C.mopane woodland type 4b (Appendix 1, Fig. 1) is particularly rich in Chloris virgata and Sporobolus marginatus (Fig. 32a) while these two species and Urochloa are the main grasses in the rather bare C.mopane type 4c (Fig. 32b). Sporobolus-Chloris grassland (Figs. 4 and 3g) although included in C.mopane woodland habitat for the transect analysis, is attractive to warthog during the rains; wet season increases in density are evident in the small part of this habitat sampled by the transects. Important wet season foods are thus widely available in the most extensive habitat of the Research Area.

Favoured wet season foods are plentiful in Acacia tortilis - Grewia communities on the Lutope alluviums. Here the seasonal and distributional pattern is more varied than in C.mopane woodland. High utilization of this habitat by all ungulates results in heavy trampling and much of the habitat is "short grass" by the end of the dry season. At the onset of the rains a spring flush results in a low carpet of palatable species particularly Panicum maximum, Setaria sp., Urochloa pullulans and annuals such as Dactyloctenium. These areas are effectively short grass swards until early January. Tall swards are formed after December consisting mainly of Panicum maximum. The grassland is however very diverse and is well used by warthog either by plucking short grasses or by cropping such species as Panicum, Setaria, Dactyloctenium or Urochloa pullulans.

Patches of favoured species and species on which warthog will

feed during the wet season occur in all habitats. Grassland habitats with low warthog density such as the Sengwa flood plain are mainly medium to tall grasslands dominated by Aristida or Hyparrhenia species. There is a general but not complete lack of favoured wet season foods in C.mopane-Combretum sp. Tristachya habitat where transect densities are low during the rains (Fig. 18)). Our tame warthog showed little inclination to feed there. Grass cover in the wooded habitats on sandy soils is sparse. Palatable annuals do occur but the grass cover is mainly Aristida sp., Chloridion, Loudetia flavida and other similarly wiry species.

Despite there being many areas which do not contain optimal grazing for warthog there is, within the Research Area, sufficient favourable grazing over a wide area, to suggest that food is plentiful and readily available during a normal wet season.

It was suggested in Chapter II (page 37 ) that widespread fires followed by drought may have affected the warthog population at the end of 1965. Under such conditions perennial grasses would have mobilized their storage reserves in an abortive flush after fires. Food reserves below the ground would have been depleted. Subsequent drought and wilting would also have reduced the quality of available grazing, particularly the growth of annuals such as Chloris and Urochloa triphopus. In the 1965 - 66 season Panicum maximum was only 10 to 25 cm high and yellowed or browned in mid-January whereas in a normal season it would have been a metre or more high. Fire and very late rains may markedly reduce the availability and quality of grasses on which warthog feed but whether these factors reduced food to below a critical level in

1965 - 66 was not established.

Towards the end of the rains, when grass leaves begin to dry out and seeds begin to ripen warthog turn to shredding Urochloa, Sporobolus, Echinochloa and other species. The seed crop of annual species is probably largely dependent on season. The distribution of species shredded follows that of the main species grazed i.e. C.mopane areas, particularly drainage line depressions and temporary pools, and Acacia-Grewia areas. The latter habitat also has an abundance of Panicum, Dactyloctenium and Urochloa pullulans of which the flowering heads are also eaten.

b) Dry season

Dry season diet is, in contrast to that of the wet season, more restricted and confined largely to the rhizomes of three species of grass; Digitaria milanjiana, Tristachya superba and Oryza barthii. Little green fodder is available during the dry season.

Digitaria is widespread in the Research Area as a sub-dominant but stands of up to 5 ha are found where Digitaria is dominant. These stands occur on heavy black soils such as in C.mopane vleis and on alluviums of the Lutope River. It is also a major constituent of the grassland in C.mopane-Combretum sp.-Tristachya habitat and occurs widely in C.mopane woodland areas in depressions, drainages and around termite mounds. It is generally absent in habitats based on deep sands such as Brachystegia woodland, Combretum thickets and Baikiaea woodland, except on or near termitaria and in some drainages in Brachystegia woodland.



Tristachya is more limited in its distribution, occurring on red loam (alluvial) soils in the basin below the escarpment and near the main rivers. Habitats in which it forms a co-dominant with Aristida, Andropogon or Hyparrhenia are C.mopane-Combretum sp.-Tristachya W.B.G. (Types 11 and 13 in Appendix 1, Fig. 1). It is also found in patches in the Acacia-Grewia habitats and on the Sengwa flood plain. Tristachya occurs widely in the Brachystegia woodland above the escarpment but is little used by warthog in this habitat. The reason for this is not understood. Where the rhizome is rooted in Brachystegia woodland C.mopane trees are almost always within a few paces of the rootings.

Oryza barthii is limited in its distribution to temporary pools and drainage line pools in C.mopane areas. It is heavily utilised by warthog at the end of the rains as pools dry out and during the cold season. Areas containing this rhizome show a ploughed appearance by June (Fig. 29a) and the resource is all but depleted.

Warthog rooting sign is easily recognised and intensive feeding areas are readily located. Traverses through feeding areas show a very close coincidence between rooting sign, abundance of Digitaria and Tristachya and frequently of warthog dung heaps. The results of systematic traverses over an area of one square mile (the fly round grid in the Sengwa Experimental Area, Appendix 1, Fig. 1) are summarised in Fig. 33. An association between the distribution of rooting sign, warthog dung heaps and suitable rhizomes emerges clearly. Rooting is

almost entirely confined to habitats containing Digitaria or Tristachya, or both. Dung heaps are most abundant in these areas. Rooting along the main drainage through the grid on Fly rounds 1 and 2 is apparent as is the small amount of warthog feeding sign and faeces in the bare C.mopane area and C.mopane woodland west of the drainage and south of Fly round 2. The number of dung heaps in Acacia tortilis-Grewia habitat in the north west of the grid (Fly rounds 1 and 2, Fig. 33) is not clearly associated with food, i.e. there was little rooting sign and rhizomatous grasses occurred on few sectors. There are, however, a number of holes, a water point and plentiful shade in this area, all of which may have been used by warthog.

Step point transects in C.mopane-Combretum sp.-Tristachya habitat show that between 20 and 50% of the ground may be rooted by the end of the dry season. The quantity of rhizomes in the ground at the end of the dry season in this habitat is however remarkably high despite apparently excessive utilization by warthog. Two well rooted plots (20 m x 20 m, Fig. 34) were selected and within each 20 quadrats of 1 m<sup>2</sup> were located at random; the rhizomes of Tristachya and Digitaria were removed and weighed. These two plots provided an estimate of 3 - 5 tons (wet weight) of rhizome per hectare. At a daily intake of say 2 k per day (the full stomach of an adult warthog which has been rooting weighs about 1 k) a density of 10 hogs per hectare for 150 days would be required to deplete the food available. The greatest local seasonal density recorded in the Research Area was 0.38 hogs per hectare.

These preliminary observations indicate that an extremely high rooting pressure would be required to deplete rhizomatous food reserves. Close observation of tame animals reveals that they do not remove the entire rhizome-root system of a plant when digging. A good proportion of rhizome is left in scrapings and certainly enough to ensure regeneration of the plant. Rooting and consequent tilling of the soil would also serve to bury seeds which, in consequence, would be better protected from fires.

The degree to which warthog might, by heavy utilization of limited areas, deplete their food resource over a few seasons has not been measured. However the grassland in C.mopane-Combretum sp. Tristachya habitat in the Sengwa Experimental Area has, over a five year period, shown no obvious signs of degradation.

Traverses through the C.mopane vlei area on Transect 7 (Traverses 5 & 6, Fig. 34) have confirmed a high utilization of Digitaria in this area. Again utilization has been high year after year with no signs of grassland degradation. Further traverses in Acacia tortilis-Grewia habitat and areas of C.mopane-Combretum sp.-Tristachya habitat provided similar data to that obtained on the Fly round grid in the Sengwa Experimental Area (Table 20 and Fig. 34).

These observations on dry season food distribution and quantity suggest that despite a restricted dry season diet, there is, in high density habitats, ample food for warthog even at the end of a dry season. One low density habitat, Brachystegia woodland, contained rhizomes but these had not been used extensively (Table 20). Parts of the area, e.g. C.mopane type 4c and the

thickets are generally devoid of rhizomes and show low dry season densities of warthog. There is little indication that warthog in the Sengwa Area are using the dry season food reserves to the full. This suggests that factors other than food are keeping the population below the level at which over-exploitation of the food resource might occur.

#### B. WARTHOG HOLES.

"The mouse that always trusts to one poor hole  
Can never be a mouse of any soul."

Pope. "The Wife of Bath"  
Imitations from Chaucer

Holes feature prominently in the lives of warthog. They are used as a retreat in which the animals sleep at night (Bigourdan, 1948; Geigy, 1955). The young are born in holes where, according to Bigourdan (1948), they spend their first few days (cf. maternal behaviour, page 178). Holes also provide protection from cold for young, as opposed to new born, warthog whose body temperature regulation is imperfect (Sowls and Phelps, 1966). Warthog are reported to use holes as retreats from the mid-day sun (Stevenson-Hamilton, 1947). They seek refuge in holes from predators and inspect them during the day (Fradrich, 1965). Fradrich considers holes to be the most important points in a warthog's home range and reports them using the same hole night after night although occasionally they slept in other holes. Geigy (1955) reports on the structure of a hole and Walton (1957) describes the structure of porcupine (Hystrix) warrens which were also used by warthog.



Work reported here differs from that of authors cited above mainly in that holes have been studied over a long period, preliminary experimental holes have been built in the field and the behaviour of tagged animals in relation to both natural and constructed holes has been observed. The behaviour of tame free ranging warthog at holes has also been observed. As a result it is now possible to place the "hole", in warthog biology, into a more realistic perspective.

1. Number of holes.

Counts of holes which warthog would have been able to enter and use, were made along the permanent transects early in 1966. The density of holes far exceeded density estimates of warthog in the transect area. An area of  $2.78 \text{ km}^2$  was covered on 11 transects and 146 suitable holes were found, i.e. 52 per  $\text{km}^2$ . An additional 117 holes were recorded, mainly antbear diggings, which were either very short or had partially collapsed. These were considered unsuitable as sleeping dens for warthog. The number of holes judged to have been used by warthog during the fortnight prior to the count was 43 or approximately 15 per  $\text{km}^2$ . Even the density of used holes exceeded the estimated density of warthog. Since holes are used by groups of warthog their availability is even greater than the figures indicate.

During the Nagupande game elimination experiment, 32,213 holes were blocked in an area of c.  $565 \text{ km}^2$  (Lovemore, pers. comm. 1970). Not all of the area was covered and the data represent a minimum rather than an absolute density of 57 holes per  $\text{km}^2$ .

The densities obtained at Sengwa are not greatly different from the more extensive Nagupande data.

Density of warthog was not correlated with density of holes on different transects (Kendall rank correlation coefficient - Siegel, 1956). However, since there are more holes than there are warthog using them, it is unlikely that warthog density will be related in a simple manner to density of holes. The results of this initial survey suggested that type of hole and the dispersion of holes used by warthog may be more important than hole number.

## 2. Types of hole used by warthog in the Sengwa Area

Field observations of both mapped (Fig. 35) and unmapped holes have provided the main source of data. Excavation of holes was avoided because this would have involved destroying holes still under observation. Some holes have been partially opened and then repaired and I have also crawled into these and others.

According to Clough (1969) warthog in Uganda will dig their own holes. Blancou (1958, cited by Fradrich, 1965) reports that captive animals may make their own sleeping places. A. Osborne (pers. comm. 1968) had two tame warthog which dug a tunnel-like hole of about 1.5 m in a night (see also page 105). Thirty wild warthog confined for up to 14 days in pens at Sengwa before translocation to another area did dig open hollows but not burrows, up to 60 cm deep. Fradrich (1965) found no evidence of warthog digging holes in the field. I have also found no evidence that warthog excavate their own holes in the Sengwa Area. They do however modify holes and have been seen shovelling soil or mud out

of holes with their snouts. They will use their forefeet in digging; the animal rests on the carpals of one foreleg and scrapes earth backwards with the free foot. In the absence of clear observations to the contrary it is assumed that warthog at Sengwa use holes created by other animals or by natural agencies such as erosion.

Three main types of hole are used :

- i) Caves in rock
- ii) Antbear holes
- iii) Erosion-gulley holes.

Caves are the least common type in the Sengwa Research Area and only two (Numbers 30 and 30a, Figs. 35 and 36) have been mapped in the Sengwa Experimental Area. Hole 30 is on a hillside under an eroded rocky overhang and it is walled off in front by fallen rock. It has three entrances and is very well used.

Antbear holes have a small, usually round, opening with a mound of earth at the entrance, caused, in new holes, by the antbear and, in older holes, by warthog. This type of hole generally has a single entrance opening onto level ground or onto the side of a slope or embankment (Figs. 37a and b). Entrance tunnels are seldom straight and seldom descend more than 1 to 1.5 m below ground level. Examination of collapsed holes and those into which I have crawled indicates that antbear holes used by warthog usually end in a simple chamber such as is illustrated in Fig. 37a. However, some holes on the edge of the Sengwa flood plain, apparently of antbear origin, are much larger and more complex. Some have two or even three entrances. Holes 9 and 10 (Fig. 35) were two separate holes in 1966 but have since been linked underground into a single complex. These holes (9 and 10) are also occasionally used by porcupines.

Erosion gully holes are, by contrast, usually large, with two or more entrances (Fig. 37c). In some cases the hole is a maze of sub-terranean tunnels. Such holes are found in C.mopane woodland areas and are associated with seasonally waterlogged, sodium-rich soils. Numerous sink holes, many of which open into sub-terranean tunnels, are also characteristic of these soils. (Fig. 38). Despite the fact that many of these warrens carry water when it rains, warthog still use them during the wet season. An example of this type is shown in Fig. 37c. The hole is adjacent to an even more extensive sub-terranean gully system which has been grouped under holes 20, 20b and 20c (Fig. 35). Porcupine have occasionally been seen using these and other erosion gully holes but their possible role in the origin of this type of hole is not known.

Some extensively used holes appear to be antbear digging-cum-erosion gulleys. Hole 19 provides an example (Fig. 39~~0~~). This hole opens through two adjacent entrances in the bank of a shallow drainage gully in C.mopane woodland. Superficially the hole appears to be a sub-terranean erosion tunnel but excavations into the main chamber revealed that a termitarium had existed there. The ground over the hole was level, with no tell-tale mound. It seems probable that a hole was created initially by an antbear and subsequently used and maintained by warthog. The present openings may have been caused by erosion or a change in the course of the drainage passing the hole.

Hole 22, which has two openings, appears to have been created both by an antbear digging and by subsidence (Fig. 39a).

Holes used by warthog thus reveal a wide variety and



preferences for the various hole types are examined below.

### 3. Permanence of holes

Cave-like holes in rock are obviously the most permanent, although the least common, type.

The most transient holes are antbear diggings in sandy soils such as occur in Brachystegia woodland areas and on the Sengwa flood plain. Entrances frequently collapse and, less frequently, the rooves of chambers may cave in, especially towards the end of the rains. Subsidence need not necessarily destroy a hole; partial collapse may merely modify it. For example, a long single entrance hole may change to one with two entrances and vice versa.

Holes in old, large, termitaria appear to be very durable and this is probably due to the structure of the soil. Termite mounds in Central Africa may be up to about 700 years old (Watson, 1969) and the possibility of warthog holes lasting several or more decades in these mounds exists.

Some subsidence and erosion gulley holes have altered each rainy season. Changes have usually been slight and, in more extensive hole complexes, have had no marked effect on warthog. Other well-used holes have been completely sealed during the rains and not used again (e.g. Hole 34, Fig. 35).

Other animals occasionally destroy warthog holes. Elephant walking over shallow holes during the rainy season may cause them to collapse. Lions dig warthog out of smaller holes and in so doing

usually destroy the hole. At larger or deeper holes lion have merely enlarged the entrance.

Some warthog holes are frequented by porcupines. No information on the extent to which porcupines affect hole structure has been obtained but they may well modify the interiors extensively since they are better equipped than warthog to do so. Walton (1957) describes porcupine burrows as being very large and complex with a multitude of chambers and interleading tunnels with by-passes.

#### 4. Artificial warthog holes.

Two sets of warthog holes, about 2 km apart, were constructed in the Sengwa Experimental Area in November, 1968. This was a pilot experiment and the simplest design of hole, a single standard-sized chamber with minor variations in the entrance tunnel, was used. Each set comprised three separate holes spaced about 15 m from each other. The size of the chamber was the same for each hole but the shape and number of entrance tunnels differed (Fig. 40a). Hole 1 in each set (designated A1 and A2) had a single straight tunnel leading to the entrance. Hole 2 had a single curved tunnel and hole 3 had two curved tunnels. The two sets were situated in similar vegetation and soil but A2 had large trees closer to it than did A1. The construction of these holes is illustrated in Fig. 40b.

The aim in constructing these holes was to discover :

- (a) whether warthog would use holes erected by man (the tame animals had used holes of a similar construction).
- (b) whether a clear preference for one of the basic designs existed.

- (c) how durable the holes would be and whether warthog would use them over a period sufficiently long to yield data about preferences.

Within a month of the holes being completed some had been used for sleeping and all had been visited by warthog. A further four holes of single-entrance, curved-tunnel, design and numbered A3 to A6 in Fig. 35, were erected in September, 1969 for another purpose. These were also used shortly after completion. One was inspected, if not used, by warthog two days after erection.

The holes have not been used frequently enough to provide evidence of preferences between the three designs but the results (Table 21) suggest that they are equally acceptable to warthog.

The experiment demonstrates that hole preferences could be investigated by simple field experimental methods. Constructing holes fitted with sensors to monitor activity and behaviour of warthog is feasible. However the frequency with which holes (not only artificial holes) are used indicated that experimental holes would have to be observed for a year or more to yield useful results.

## 5. Frequency of use.

Measures of the frequency with which warthog use particular holes have been obtained from two types of observation : the presence or absence of fresh spoor in holes, i.e. a "spoor index" of use, and the number of times warthog have been seen using a hole, i.e. a "sighting index" of use. For both indices the number of times the hole has been used is expressed as a percentage of the total number of observations (inspections in the case of spoor or

observation periods in the case of sightings) made at that particular hole.

An average of the spoor and sighting index for each hole is given in Table 22 and Fig. 41 shows the distribution of holes within the Sengwa Experimental Area according to four classes of use : 70% or more, between 50 and 69%, between 30 and 49% and less than 30%. Only those holes at which inspections plus observation periods exceeded 30, between November, 1966 and December 1969 have been included in Table 22 and Fig. 41.

Holes were not randomly selected nor were observation periods at registered holes made on a random basis. Holes were only registered (mapped and numbered) once their use by warthog had been established. Holes were seldom watched if the initial spoor inspection indicated that they were not in use at the time. The sighting index is thus higher than if the holes to be watched each day had been chosen at random.

The overall spoor index from 3,751 inspections of 74 holes was 48%, while 3,094 observation periods provided a sighting index of 31%, i.e. warthog were seen entering, or emerging from, holes on 31% of the observation periods. The overall spoor index and that for particular holes is usually higher than the sighting index (48% as opposed to 31% for the overall indices). This is because a hole is judged to be "in use" on the basis of spoor left by hogs over a number of days prior to inspection.

Indices of use show that some holes are used more frequently than others. The most frequently used holes are larger erosion-gulley holes and the larger multiple entrance antbear type holes. A non-



parametric ranking test (Mann-Whitney "U" test; Siegel, 1956) on the sighting indices of erosion-gulley versus antbear holes shows that indices for erosion-gulley holes are larger than those for antbear type holes ( $z = 3.50$  and Probability = 0.00023). However few holes are used more than 50% of the time which suggests that warthog seldom use the same hole for long continuous periods but change holes frequently. This suggestion is amply supported by observations of both tagged and tame warthog.

Resightings of tagged animals at holes have shown that a sounder uses a number of holes, in some cases as many as 10. Tame warthog also changed holes frequently and the various groups have used 19 different holes. Individuals or groups return at intervals to particular holes e.g. Ad. ♀ 4 was first captured at Hole 19 in September, 1966, recaptured there in March, 1967 and was seen using it again during September, 1967. Ad. ♀ 145 was captured at Hole 24 in September, 1966 and twice again in 1969. She has been recorded using Hole 24 on 14 other occasions. Similar data are available for other animals. Particular holes may be used intermittently by different sounders e.g. Hole 20 has been used by 7 different sounders over three years and Hole 29 by 5 different sounders. These observations do not include the many untagged groups which have also used these holes. Only occasionally have two tagged sounders been seen using the same hole on the same night and then it has not been established that they slept in the same part of the hole.

The data contained in Fig. 41 indicate that those holes which have been used by a number of sounders (shared holes) are generally those with high indices of use.

Few holes have very high indices of use and those that do (e.g. Holes 29, 23, 39 and 30, Figs. 35 and 41) are generally more than 0.5 km apart. Holes with slightly lower, but still high, indices, tend to be grouped about the most frequently used holes or "centres". The remaining and greater proportion of holes with low indices are scattered between these centres. Dispersion of centres appears to be based on the distribution of large erosion-gulley or more durable and persistent holes.

Hole structure or type appears to be the factor governing intensity of use. However this relationship is not established by the data available and would require experimental verification, perhaps by the use of more elaborate artificial holes. It may be that a high use index is merely a function of the proximity of a hole to favourable feeding areas i.e. warthog make most use of holes closest to their feeding areas. This would imply that warthog dispersion and hole use are controlled by the distribution of food. A further alternative is that the pattern of dispersion indicated by hole use is based on social factors such as territoriality or even an element of "traditionalism" which in turn may result from the durability of certain holes and their use by successive generations. The idea of tradition playing a role in the movements of social mammals is not without precedent (Darling, 1937; Etkin, 1964, p 273). Permanence of hole rather than structural details may be the more important factor.

A marked relationship exists between warthog sightings on the transects and the proximity of large erosion-gulley type holes: the peak in warthog sightings on transect 3, sector 28 (Fig. 13) is

associated with erosion-gulley holes. Regular inspection of these holes every few days in 1966 showed them to be very well used. Spoor indices <sup>were 70% and</sup> ~~were 70% and~~ higher. On transect 7, sectors 28-36 (Fig. 14), the peak is associated with well-used erosion-gulley holes, 27, 27a, 27b and Hole 23 (Fig. 41). On transect 8, sector 30, the peak may be associated with the erosion-gulley complex of Hole 39 and 40 (Figs. 14 and 41); on sector 42, with Hole 22 and on sectors 48-50, with Hole 29. On transect 9 peaks in warthog density also occur near well-used erosion-gulley holes.

Striking though the coincidence between erosion-gulley holes and density is, it may be spurious. A similar coincidence between density and availability of food is evident (pages 82 to 89 and Figs. 13 - 15). Both the grassland and erosion-gulley holes are to a great degree dependent on soil type. Soil in which the holes occur does not provide much suitable forage for warthog, except possibly during the rains, but these eroded areas are often immediately adjacent to favourable feeding areas. The soil-plant-erosion complex has not been studied but it does seem likely that a relationship between food and holes may be based on the overall drainage pattern of these areas. Thus the degree to which warthog density or dispersion is influenced by food or holes cannot be effectively separated in these high density areas. The following simple model clarifies the relationship between food, holes and density; three simple situations can be recognised.

$$A. \quad \left\{ \begin{array}{l} + \text{ food and } - \text{ holes} \\ \text{or} \\ - \text{ food and } + \text{ holes} \end{array} \right\} = \text{few or no warthog}$$



$$B. \quad \left\{ \begin{array}{l} + \text{ holes, move to food} \\ \text{or} \\ + \text{ food, move to holes} \end{array} \right\} = \text{moderate warthog density}$$

$$C. \quad ( + \text{ food and } + \text{ holes } ) = \text{high warthog density.}$$

Situation A would obtain where suitable food and suitable holes were too widely separated for daily movement between the two to occur, as in B. Situation C appears to obtain in the high density areas sampled along the transects.

Examples showing the association between population densities and fewer holes, or less favourable feeding areas, or both, can be found in the transect area. These would correspond with A and B of the above model. However, fully quantitative data on food, holes and hole use is lacking for the entire transect area and, until home range size and behaviour have been discussed, further elaboration of these possibilities is unwise.

Data on the intensity of hole use and the behaviour of tagged animals do, however, show :

1. That warthog sounders use numbers of holes, return to particular holes at intervals and may use these holes over periods of as long as three years.

2. Holes with high indices of use are rather widely spaced in the study area. They are usually complex permanent holes and are used by a number of sounders but not usually shared in the sense that the same part of a hole is used by different sounders on the same night.

3. Warthog also use a number of other holes but less frequently and, so far as is known at present, they are used by fewer groups. In one instance a hole is known to have been used more frequently by males than by females.



4. Warthog are also known to inspect holes within their home ranges and females become solitary towards the end of pregnancy (Fradrich 1965, and this report).

These data suggest that holes might be classified in terms of how they are used by the population in the Sengwa Experimental Area and the following ecological model is proposed :

Well-used holes form "centres" for a number of sounders. These holes are long-lived and safe from attack by predators. They cannot, however, house all the warthog living in their respective areas and a number of well-used secondary holes therefore exist about the central holes or within the home areas of central hole occupants. Other holes in the area, the less well-used and less permanent tertiary holes, might be used by farrowing females and serve as occasional sleeping dens and as emergency refuges from predators.

#### 6. Ecto-parasites and mammals using warthogs holes.

Use of holes by other mammals and ecto-parasites inhabiting warthog holes have not been studied but might account for the frequency with which warthog change holes. Nevill~~l~~ (1964), for example, remarks that sand tampan. (Ornithodoros savignyi Audouin) infestations of resting sites can prevent domestic livestock seeking shade from the mid-day heat.

Warthog holes often carry infestations of mites, fleas and haematophagous "floor maggots" (Auchmeromyia or Pachychoeromyia, Calliphoridae, Diptera). Mites are notoriously long lived and Walton (1957) found 100% survival after 28 months of once fed virgin female Ornithodoros moubata which he obtained from a warthog hole.

No information on the fleas inhabiting warthog holes has been found but these are probably capable of withstanding long periods of starvation (cf. rabbit fleas which live in stops from one spring to the next; Allan, 1956). Floor maggots appear to survive from 3 to 6 weeks without food depending on their size and number of blood meals (Zumpt, 1965). Thus, while frequent changes of hole by warthog might serve to offset extreme parasite populations it is unlikely that vacating holes for even two or three months will greatly affect the presence of parasites in holes. The wet and often muddy floors of erosion-gulley holes during the rains may however be <sup>e</sup> unfavourable habitats for these parasites.

Porcupines have been seen using warthog holes, sometimes at the same time as warthog. Only one observation of a hyaena using a warthog hole has been made and warthog were not seen using this normally well-used hole for the subsequent two months. A leopard has been seen entering a hole in the late morning. However, changes of hole occur too frequently and evidence, even circumstantial, of other animals influencing these changes is so infrequent as to suggest that they have little effect on warthog behaviour.

Our activities do on occasion cause warthog to change their particular sleeping hole at the time but the behaviour of tame warthog and of radio-tagged animals shows that the phenomenon is not an artefact of our field procedures.

#### 7. Behaviour in relation to holes.

Holes are clearly a dominant feature in the ecology of warthog and behavioural patterns associated specifically with their use are



to be expected.

a) Times of entry and emergence

The distribution of 409 records of emergence and 679 records of entry times are shown in Fig. 42. There is a slight shift in the modal time of entry with seasonal change in time of sunset. Changes in time of emergence follow changes in time of sunrise but the distribution during December-January is more scattered than at other times of the year. The reasons for this are not known but many of the late emergences are due to nursing mothers which tend to emerge from their holes in the mid- or late-morning period. (Chapter V, "Maternal behaviour" and Fig. 68<sup>9</sup>). Warthog will also remain in their holes on wet rainy mornings. Both tame and wild warthog have been seen seeking refuge in holes when it rains. At the onset of a rain storm they will rush headlong for a hole where they will remain until the storm has passed.

Some ruminants e.g. cattle and horses, adopt a special stance during rain. A tame impala regularly assumed his "rain stance", even indoors, when it was raining. Similar behaviour has not been observed in warthog; rather, having gained shelter, either indoors or in a hole, they huddle together. This behaviour, in young animals at least, is probably associated with imperfect body temperature control (see below).

Geigy's (1955) observations that warthog go into their holes at about sunset and emerge at sunrise are confirmed by the data in Fig. 42. The question arises, however, as to whether warthog always sleep in holes. Sowls and Phelps (1966) demonstrated daily fluctuations in the body temperature of young warthog but not in

bushpig. The authors concluded from this and other evidence that young warthog must sleep in burrows in order to survive. A. Osborne (pers. comm.) lost two warthog, approximately 8 months old, after an abnormally cold night in the Matopos National Park, Rhodesia. The animals were in a pen furnished with a large wooden box containing an old blanket. They were found dead within a short hole they had excavated during the previous night.

Measurements of the body temperature of adult warthog in relation to ambient temperature do not appear to have been made. Sowls and Phelps (1966) state, "Observers who have spent many years in the Rhodesian bush agree that warthog are strictly diurnal and seldom if ever are seen above ground after sundown". At Sengwa warthog are frequently seen between sundown and nightfall. Observations also show that some may not retire into holes. Signals from radio tagged adult males have frequently been heard as late as two or three hours after sunset. The signals from transmitters are usually inaudible, except at very close range, when animals are in holes. Changes in signal can indicate whether or not an animal is active and active adult males have been monitored after dark. Adult males have also been tracked to resting sites in long grass or slight hollows shortly after dark. Susan and Mackintosh (Fig. 10) have frequently "gone to bed" in a depression near a hole but have entered their hole later in the evening. During June, 1969 both animals slept in the



pen on a number of nights without entering the hole. The pen was a pole stockade offering little if any protection from the wind and ambient temperatures dropped to  $10^{\circ}\text{C}$ . in the early hours of the morning. During October, the warmest month, capturing warthog is frequently difficult because the animals often fail to enter holes before darkness falls; this has been established by their emergence the following morning. Sometimes warthog have arrived at holes after sunset but bedded down outside the holes. Local Field Officers have reported warthog feeding at 10 p.m. on moonlit October nights.

Sowls' and Phelps' (1966) important observations of body temperature fluctuation clearly require to be extended and information on survival at low temperatures is required.

b) Nest building

Warthog have been seen carrying and scraping grass into holes during the winter months in the Sengwa Area. Dry grass has been carried to the hole in the mouth or scraped into it with the forefeet. Both male and female warthog have shown this behaviour. Mr. G. Davison (pers. comm.) observed warthog building nests from grass on Redcliff Island, Lake Kariba (Fig. 43). The barren rather rocky island was devoid of holes and grass-cover was sparse. Grass was gathered and carried in the mouth to the nest. On cold mornings the animals (an adult male, 2 adult females and their young; the only sounder on the island) were frequently seen, up to two hours after sunrise, still huddled together in their open nest.

Nest building behaviour has been observed in domestic swine (Hafez, 1962) and has been described for Sus scrofa L. (Gundlach,

1968). Ewer (1968), citing Fradrich (1965), says that female warthog carry grass into their holes before farrowing. However, Fradrich states that he never saw pre-parturient females carry grass to their holes. Warthog at Sengwa have not been observed carrying or scraping grass into holes during the breeding season and Susan, who was under observation for the week before she farrowed, did not do so.

Thus, Sus builds nests before parturition and at other times while Phacochoerus appears to do so only in response to cold; where holes are available nest material is carried into holes. It would be interesting to know the extent to which nest building patterns differ in the suids.

c) Inspecting holes

Fradrich's (1965) observation that warthog visit and enter holes, apparently to inspect them, during the day has been confirmed by observation of both tame and wild warthog. In the field I have only seen young animals actually entering to inspect holes while the parent or older hogs have remained at the entrance. Hole-inspecting behaviour has been very marked in young tame warthog from 4 to 8 months old. During the course of walks with these animals all holes encountered have been inspected. The hogs reverse into holes, rush out and enter again, sometimes shovel soil at the entrance or deep inside the hole; the sequence is often repeated a number of times. On occasions, while walking with them, they would rush off some 50 paces directly to a hole which had last been visited some weeks before. Their memory for holes appears to be acute. Behavioural observations of tame animals suggest that the pattern is innate and

provide some indication of the releasers which may be involved.

*20004*  
A marked interest was shown in any new digging (e.g. new flower beds, furrows, road sidedrains on bush tracks and building foundation trenches) by tame warthog. They inspect and may even reverse into these "holes", shovel loose soil with their snouts and behave in much the same way as they do at the entrance to a hole. Young warthog have also been observed inspecting mounds of termitaria. These often possess holes which may not be visible until the hogs have climbed the anthill (Fig. 44).

A subjective impression of play is gained while observing hole-inspection behaviour in young animals; they all join in. Exploration of holes is not as marked in older animals and the considerable exuberance shown by the young is lacking, nor have they been seen rushing out of holes with their heads swinging! Reversing in, coming out, digging and shovelling out soil does however occur in adults. Hole inspections by young warthog appear to contain elements of both play and exploratory behaviour while the play component fades as animals mature.

The rapidity with which artificial holes in the Sengwa Experimental Area were found has already been mentioned (page 96 ). These had large and obvious mounds over the roof. Since warthog do not generally construct their own holes one might expect them to show innate patterns which lead them to investigate holes, and particularly new holes, within their home ranges. One needs to know whether other suids show an interest in mounds of soil to determine whether these patterns in warthog have evolved specifically in association with their use of holes. Percival, the bushpig, did not show any

particular interest in mounds or holes; he never entered them despite growing up with two warthog. He would root around in loose soil at the entrance to a hole but this was clearly looking for food and not comparable to the warthogs' digging behaviour.

d) Behaviour at holes in relation to predators.

Lydekker (1908) records that warthog hunted by dogs or chased on horseback seek refuge in holes. They presumably do so when threatened by predators. Inspecting holes and knowing their precise location within the home range would have clear advantages to warthog. Hole inspections by tame warthog were sometimes preceded by a head-long rush for a hole with a last minute speedy reversal into it.

Reversing into holes has been described by many authors (Shortridge 1934) and warthog are reported to do so not only when hard pressed but regularly when entering their sleeping holes at night (Geigy, 1955; Fradrich, 1965) though young animals may enter head first (Fradrich, 1965). At Sengwa both adult and half-grown animals by no means always enter <sup>holes</sup> by reversing into them. The behaviour is very variable. One animal in a group may enter head first, another reverse into the hole; at a particular hole animals may all reverse in on one occasion but enter head first on another. Factors governing the manner in which holes are entered are not known and while reversing into holes may be to face predators we need to know why warthog do so when no predators are about.

Warthog generally approach their holes against the prevailing wind; they may even circle around a hole at a distance to achieve this. Leopards have on two occasions been seen lying in wait at a



hole. On one occasion the leopard waited on an overhanging branch while on the other it lay near the hole entrance. Both observations were made at the same hole (Hole 34) and were reported by Scouts who had arrived at their observation post in a nearby tree before the leopard. No warthog arrived on either evening.

Lions have often been found waiting outside occupied warthog holes in the morning and coming out of a hole may clearly be a vulnerable time for warthog. From tree observation sites it is usually difficult to observe warthogs' behaviour immediately prior to emergence from holes. I have however observed it clearly on two occasions from behind the bole of a tree opposite a hole entrance. The leading animal paused for a while, well within the entrance, only its head being visible. The animal moved its head very slowly, apparently sniffing and listening for a few minutes before cautiously edging out until its head and shoulders were out of the hole. Only then did it move more freely and was followed in quick succession by 5 other animals. On some occasions, when watching from a nearby tree warthog have burst out of the hole at speed, only to stop some 10 metres from the hole and move off at a walk.

Observations while catching warthog at holes indicate that they respond in two ways to being trapped within a hole. The first is to rush out of the hole at great speed and, in the case of a group, in very rapid succession, rather like an express train out of a tunnel. Sideways slashing movements of the head are often evident as they leap out. This response is most frequent at smaller and shorter holes where hogs have rushed out even at 2 or 3 a.m. The second response is to "sit tight" within the hole; this they may do for

an entire day and through to the following day. In the case of one group we breached the main chamber at 4 p.m. after waiting from 3 a.m. for the animals to emerge. Smoke, burning grass and poking the animals (an adult female and a yearling female) with a pole failed to force them from the chamber. The hogs did not attempt to attack, or flee from a man who had entered the hole and inadvertently crawled alongside the adult female. Both animals had to be dragged from the hole by placing ropes around their snouts. Lions attempt to dig warthog out of holes and the almost cataleptic behaviour described here, and observed on other occasions, may in these circumstances be significant. Warthog have been recorded staying in a hole until the following day after lions had spent a morning waiting outside their hole.

### C. DAILY ACTIVITIES.

Warthog, because they sleep in holes at night, are probably more markedly diurnal than other African ungulates. Fradrich (1965) found warthog to be active throughout the day in Nairobi National Park. Gundlach (1968) found Sus scrofa to be active in the morning and in the afternoon; animals rested during the middle of the day and were largely inactive at night. Bushpig (Potamochoerus porcus) are known to be nocturnal in developed areas where they raid crops at night. A tame free ranging bushpig, Percival, was mainly diurnal until he was about a year old and until he separated from the warthog with whom he was reared. Thereafter he was nocturnal or crepuscular; being seen abroad in the early morning and evening and at night. Observations on the activity patterns of tame free ranging warthog

and some observations of feral warthog between the time they emerge from and enter their holes are described below.

The general daily pattern was characterised by morning and evening activity with a period of rest during the middle of the day (Fig. 45). Feeding was most intense in the late afternoon before the animals retired to their hole for the night. Walking, drinking, wallowing and social activities have been placed under "Other activities" in Fig. 45.

Drinking may occur at any time of the day but the tame animals drank more frequently between 0700 and 0800 hrs. in the morning and between 1400 and 1600 hours in the afternoon, from May to September, 1969 (Fig. 46a). These data conform with those of Weir and Davison (1965) on times at which warthog arrived at water holes in Wankie National Park during October. The morning peak is more pronounced in my data than in Weir and Davison's and this may be because the tame animals visited the camp in the morning for mash. They frequently drank after eating mash which was given to them between 0700 and 0800 hours. During the rains, December to March, water was more widely available and although drinking still occurred more frequently in the afternoon, the marked bimodal pattern of the dry season was not evident (Fig. 46b).

Wallowing was not observed before 0700 hours in the morning although it was seen as late as 1800 hours in the evening. Wallowing during the dry season showed a clear peak between 1400 and 1500 hours while during the wet season it was most frequent between 1000 and 1700 hours with a slight peak between 1300 and 1700 hours (Fig. 46).

Social activities occurred too frequently or were too brief, or



both, to provide an adequate measure of their frequency at 10 minute observation (recording) intervals.

The broad daily pattern, characterised by a quiescent mid-day period, occurred throughout the year. Changes in the proportion of time spent on various activities and absolute changes in times spent feeding and resting did occur. Susan and Mackintosh were feeding, on average, 4 to 6 hours a day during the May to November period (Fig. 47). Time spent feeding by Susan changed markedly after she farrowed, and increased from c. 2 hours a day shortly after parturition to between 6 and 7 hours a day by the time her juveniles were weaned in April (Fig. 47).

Resting by Susan and Mackintosh increased between June and November from an average of  $2\frac{1}{2}$  hours a day to  $5\frac{1}{2}$  hours a day during the week before Susan farrowed in November. Average mid-day temperatures also increased from June to November. Susan was however pregnant and this may have affected the activity of the sounder, comprising her and Mackintosh. Susan and her juveniles spent more time feeding, but only slightly less time resting, during April to June, 1970 than she and Mackintosh had done during May to June, 1969. Susan and her juveniles were in exceptionally good condition in July, 1970. Mackintosh also spent slightly more time feeding during February and March than he had during the previous dry season. He was however resting very much more than Susan and her family, probably because of an injured leg.

The amounts of time spent feeding and resting by tame warthog may well differ from those shown by wild warthog; however, the daily patterns of activity conform with general field observations.



# 1. Activity in relation to temperature.

The average daily patterns presented in Figs. 45 and 47 obscure a considerable day to day variation. Time spent resting by Susan and Mackintosh increased as average mid-day temperatures increased between May and November, 1969. An examination of daily records also indicates that ambient temperatures may have a marked effect on warthog activity. This is illustrated by the activity and temperature records for three days in September, 1969. Hogs were very active on a cool day, <sup>15</sup>~~1st~~ September (Fig. 48) and activity was less on hotter days particularly when ambient temperature approached or exceeded 90°F. Periods of mid-day activity on the two hot days (Fig. 48, 13th and 26th September) followed a visit to a wallow.

Temperatures at which warthog have been recorded wallowing are presented in Table 23. No wallowing was seen at temperatures below 70°F between April and November, 1969. Only 3 observations of warthog wallowing at above 100°F were made but then temperatures in excess of 99.9°F were only recorded on two days during November, and on one of these the animals wallowed twice. It should be noted that temperatures were recorded by the observer using a whirling psychrometer so ambient air temperatures were recorded rather than standard Stevenson screen temperatures. Table 13 indicates that wallowing was most frequent above temperatures of 80°F. Apart from the effects wallowing might have on ectoparasites it almost certainly serves to cool the animals. No measurements of body temperature have however been made. Ba~~y~~<sup>l</sup>drédin and Ghany (1952) have drawn attention to the high evaporative cooling effect of a layer of mud on wallowing buffalo.

On cold and overcast days or on cool mornings warthog will often bask in the open (Fig. 49). Young animals may rest on top of their mother. Resting was recorded as being either in the shade or in the sun. Data from Susan and Mackintosh between May and November, 1969, are summarised in Fig. 50. As the hot dry season advanced animals spent a greater proportion of their time resting in the shade. Records of resting in the sun during the hot weather were made in the morning before 0800 hours. On fine cold winter mornings tame warthog frequently basked in the sun after emerging from their hole.

Warthog in the Sengwa Research Area use a variety of sites in which to rest during the heat of the day : next to the bases of large baobab trees (Adansonia digitata); under well developed shade trees such as Diospyros mespilliformis and Acacia albida; thickets and bushes of Caparis tomentosa. Grass under such resting sites is often flattened by trampling of many game animals. Warthog, however, do not necessarily rest in situations from which they may have a clear view. They have been found resting in dense grass either with or without additional tree shade. During the wet season animals have been found resting in dense swards of tall grass in depressions and where the soil is slightly damp. Sometimes only a minimal amount of shade might be present. It is worth noting that holes in baobab trees and the boles of Diospyros trees form favourite resting sites of tsetse flies (Glossina morsitans Westw.) during the dry season (Pilson and Pilson, 1967).

A number of African game animals have been shown to be thermolabile (Haarhoorn et al. 1970). Sowls' and Phelps' (1966) observations of body temperature in young warthog suggest this

species is also thermo-labile but that bushpig are not. Observations described here indicate that warthog daily patterns of activity show some degree of temperature dependence and that behavioural thermoregulation may occur. The adaptive significance of thermo-lability, which has yet to be properly established in adult animals, has still to be determined.

## CHAPTER IV

SOUNDER STRUCTURE.

The social unit in suids is generally a family group. In wild boar (Sus scrofa L.) familial bands of 15 or more animals may be formed by the aggregation of two or three mothers and their offspring into a social unit (Altmann, 1963; Gundlach, 1968). Warthog family groups are generally smaller than those of other suids and, according to Fradrich (1965), usually comprise an adult male, an adult female and three or four young animals. However opinions differ as to the composition of warthog groups - mainly on whether adult males are attached to the family unit or not. Bigourdan (1948) reports "bachelor herds" of 2 - 6 animals in Nigeria. No published information on the frequency of different types of warthog sounder has been found. Fradrich (1965) lists the composition of five warthog groups whose home range he studied; only one of these groups contained both an adult male and an adult female.

An attempt has been made, at Sengwa, to obtain information on the occurrence and composition of different types of sounder at different times of the year. This information has been gathered largely from classifications of warthog sounders in the field over a period of four years. Observations of tagged animals and tame warthog have provided more direct information on permanence of social groupings and on group interactions.



1. Group size.

The percentage occurrence of sounders of different sizes seen during 1967 is given in Table 24 and during 1969 in Table 25. Overall percentage occurrence for 1967 and 1969 is illustrated in Fig. 51a. Although sounders of up to 9 and 10 animals have been seen throughout the year the greater proportion contained five or fewer warthog. Groups of 16 warthog have been recorded on four occasions. Two of the groups were recorded entering holes while a third, apparently single unit, was seen feeding in the late afternoon. Only one of the three groups (one was recorded twice) contained an adult male.

The largest sounder recorded by Fradrich (1965) in Nairobi National Park was 6 and, in Murchison Falls National Park 9, but he could not say whether the latter was a single social unit.

The incidence of large groups (6 or more animals) varies during the year being highest during the rainy season and lowest at the end of the dry season (Table 26). The latter period also marks the onset of the farrowing season.

The data in Table 26 suggest that large sounders fragment during, or just before, the farrowing season. Child et al. (1968), drawing on samples from many areas, give an average litter size of 3 juveniles per adult female which would result in a basic sounder of four animals if limited to a female and her immediate offspring. The modal sounder size, in terms of the percentage of the population, is however 5 or 6 animals (Fig. 51b). The incidence of larger sounders is greatest during December - March suggesting some regrouping of animals after the breeding season.

Fradrich's (1965) observations of greater numbers of solitary adult females during or just before the farrowing season and his conclusion that pregnant females desert their young of the previous year when about to farrow are confirmed by my data. Consequent disruption of the family group could account for the decreased incidence of large sounders during the breeding season.

## 2. Types of sounder.

Ungulate groups are most simply described by the number, age and sex of individuals comprising a group. These features can readily be observed and the terms do not necessarily impart functional or social roles to the individuals observed.

Various combinations of four age-classes, adults, sub-adults, yearlings and juveniles allow one to distinguish 19 types of warthog sounder which are listed in Table 27. Further sub-division into male, female and heterosexual sounders is possible. The sexes of juvenile members of a group have been ignored when assigning sounders to a particular sex category. A distinction has also been made between heterosexual groups containing a fully mature male (older than 36 months) and those with males younger than 36 months (sub-adult or yearling). Not all sounders fully classified with respect to age have been fully classified with respect to sex which accounts for the smaller number of complete age and sex classifications as opposed to age classifications.

### a) Age structure.

All of the 19 possible sounder types have been recorded.

Ordinarily transient forms of sounder are necessarily recorded e.g. a yearling hog and 3 juveniles may be temporarily separated from their mother and one has no way of knowing whether the individuals were a transient fragment of some larger social unit or not. Some groupings are seldom seen which fact suggests they are transient or unstable social units.

The high incidence of solitary sounders, about 19%, is apparent from the data on sounder size (Fig. 51a) as well as from Table 27. Age classifications show solitary animals to be mainly adults and sub-adults; very few yearlings and even fewer solitary juveniles are encountered (Table 2<sup>7</sup>~~6~~, types 1 - 4).

Sounders of only one age class (types 5 - 8) and those without juveniles<sub>(types 9-12)</sub> form approximately 36% of the total sample, being highest in 1965 - 66 at 45% and lowest in 1966 - 67 at 27%. Sounders which included juveniles formed 44.6% of the entire sample and varied between 35.7% in 1965 - 66 and 52.1% in 1966 - 67. Adults + juveniles (type 13) were more frequent than adults + yearlings + juveniles in all but the last year when more groups of adult + yearlings + juveniles were seen (Table 2<sup>7</sup>~~6~~).

b) Seasonal changes in sounder type.

Incidence of solitary adults and sub-adults changed seasonally and peaks coincided with the farrowing season (October - December) and, in some years, with the mating season (April - June) (Fig. 52a). The increase in solitary animals during the farrowing season is largely due to an increase in solitary females (Fig. 52b). These are breeding females which have left their half-grown young or their

sounders in order to farrow. A corresponding increase in the incidence of abandoned, or evicted, immature animals (juveniles up to September each year and <sup>which</sup> become yearlings from October) is evident during the breeding season (Fig. 52c). The reason for an increased occurrence of solitary adults, mainly males, during some mating seasons is not known; possibly it is due to a fragmentation of bachelor groups or to greater activity of males, or both, at this season.

The farrowing season is marked by major changes in age composition of sounders. Changes are largely the result of the transition of animals from one age class to the next, an artefact of the classification system, and birth of young animals. That adult + juvenile sounders change to adult + yearling sounders at the beginning of October is merely a descriptive convenience. Groups of adult + yearlings decrease as groups of adult + yearlings + juveniles increase during the breeding season. A residue of adult + yearling groups after the breeding season is made up of females which have not bred during the current season and of adult and immature males. The decline in the percentage occurrence of groups of yearlings after December suggests that animals evicted during farrowing probably rejoin family groups or emigrate.

Percentage occurrence of most sounder types was similar during the four years. There were, however, markedly more adult + yearling groups in 1969 than in 1967 and fewer sounders of adults + juveniles. Differences were consistent throughout the year (Fig. 53a). Population density was higher in 1969 than in 1967. Social groupings appear to have altered too, showing a greater proportion of sounders



with three or more age classes (adults, yearlings and juveniles) and a lower proportion of adults with young only. There were also slightly more groups of mixed age classes without juveniles after October, 1967 than in the two previous years (Table 27 types 9 - 12). These changes coupled with a lower proportion of juveniles per adult in 1969 than in 1967 (Fig. 21) suggest that changes in the incidence of sounder types may occur with changes in density and age and sex structure of the population.

The proportion of heterosexual sounders, those with both males and females older than 12 months, changed markedly between May, 1966 and December 1969 (Fig. 53b). After an initial decrease in 1966 - 67 there was an increase in the proportion of heterosexual sounders after the 1967 breeding season, i.e. after January, 1968. Within this overall trend, peaks during the mating season are discernible. A high proportion of adult males with groups of adult females and their young was recorded in December, 1966 but not in subsequent years. Most heterosexual sounders contain yearlings rather than fully mature males. The incidence of adult males seen with females shows a marked increase during the mating season. This, and the very low incidence of adult males with female groups at other times of the year, indicates that fully mature males are not attached to family groups (Fig. 53b). The increase in heterosexual sounders after January, 1968 is thus due to an increase in the occurrence of yearling and sub-adult males with family sounders rather than to a change in the behaviour of fully mature males. Adult males differ in their behaviour from yearling and sub-adult males and it is therefore desirable to separate heterosexual sounders into :

- (a) Those which include females and a fully mature male(s); sub-adult or yearling males may also be present.
- (b) Those which include males and females older than 12 months but not an adult male.

A major difference in social structure between 1966 - 67 and 1968 - 69 was the increased numbers of yearling and sub-adult males with family groups in 1969. Densities were lower in 1966 - 67 and the population expanding. Males appear to have left family groups at a younger age, and females with juveniles, but without accompanying young of the previous breeding season, formed a higher proportion of sounders (Fig. 53a). The prolonged attachment of immature males to the family group could account for observed changes in sex ratio in the population (Chapter 2, Tables 11 - 13).

c) Sex and age structure

Proportions of male, female and heterosexual sounders with adult males and heterosexual sounders without adult males in each of the 19 sounder types are illustrated in Fig. 54 (Table 28). These data are for the 1968 - 69 period only and have been taken as an example because the sample of complete classifications was greatest in that year. The following points emerge from the data :

(a) Solitary animals. 27.2% of all sounders seen were solitary animals and males accounted for 75% of these or 20% of the total sample.

(b) All-male sounders. 20.7% of all sounders classified contained only males. Sounder types 5 (adults), 6 (sub-adults), 9 (adult + sub-adults) and  $1\frac{1}{10}$  (sub-adults + yearlings) were

predominantly male or "bachelor sounders". The existence of bachelor sounders in the Sengwa warthog population is clear. Approximately 50% of yearling groups but only <sup>19.8%</sup>23% of adult + yearling groups (types 7 and 10 respectively) were bachelor groups.

(c) Heterosexual groups. Only 2.5% of all sounders classified (8% of all heterosexual sounders) contained an adult male as well as an adult female. Most observations of this sounder type were made during the mating season; on this fact alone, family units composed of an adult male together with a female and her young cannot be considered a stable social unit.

While only 8% of the heterosexual sounders contained adult males, 72% included an adult female but no adult male. Of the heterosexual groups, 20% were either sub-adult (type 6), yearling (type 7) or sub-adult + yearling (type 11) sounders. Sounders consisting of an adult female with yearlings (type 10) or with yearlings and juveniles (type 17) or with sub-adults, yearlings and juveniles (type 19) were mainly heterosexual.

(d) Female sounders. While most sounders containing juveniles as well as yearlings or sub-adults, or both, are heterosexual about 25% are, apart from the juveniles, exclusively female. Female sounders without any juveniles do occur and may be adult females, sub-adult females or a combination of these with yearling females. These sounders without juveniles may be referred to as "spinster groups".

On the basis of age and sex composition and on frequency of occurrence, the following tentative types of warthog sounder are proposed:

A. Solitary. (27.1%)

Adult male ( 13%) (Sub-adult male 6%)

Adult female or sub-adult female ( 8.1%)

B. Bachelor groups. ( 20%)C. Spinster groups. (4.5%)D. Sub-mature heterosexual groups. (5.5%)E. Matriarchal groups. (40%)

i) Adult female + juveniles ( 9.3%)

ii) Adult female + juveniles + yearlings (23.7%)

iii) Adult females + sub-adult + yearlings, but NO juveniles ( 7.0%)

(ii and iii may be heterosexual).

Other types account for 3%.

The validity of these groups as social units must be examined in the light of their stability and also the role, or roles, they may play in the social organisation of a warthog population.

3. Stability and longevity of sounders.

Information derived from tagged animals and from the tame warthog is available for some of the sounder types defined above. The data are fragmentary and best given in fairly detailed note form. Pertinent case histories are outlined and commented upon below.



a) Solitary Malesi) Adult ♂ 175.

Captured March, 1969 and observed during April.

April 2 - 19

Seen 6 times and solitary on each occasion

" 22 - 23

Contacted twice and with an Ad.♀ on both occasions, heard courting on the 23 April.

" 24

Killed by lion.

ii) Adult ♂ 176.

Captured 20 April, 1969 with Yr. ♂ 177.

April 21 -

Six contacts and solitary on each occasion.

May 5

" 14

Emerged from Hole 20 with Yr. ♂ 177 and seen later in the morning running with a group of 4 unclassified warthog. An hour later had left this group and was solitary.

June 2

Contacted at 1255 hours resting on his own in dense grass from which he was flushed. At 1345 hours he was with a matriarchal sounder (Ad.♀ 182) which he had left by the following morning.

" 4

Solitary.

" 7

Solitary.

July 11 - 13

Seen at Hole 8d with a yearling or sub-adult female. Not, however, a positive identification.

iii) Adult ♂ 189.

Captured 28 June, 1969. Solitary.

July

Seen 8 times and solitary on each occasion.

Sept.

Seen once at artesian borehole in company of an untagged yearling male.

Dec.

One contact, solitary.

iv) Adult ♂ 41.

Captured February 1967 as a sub-adult and with an adult female and two juveniles which escaped. Only one uncertain sighting during 1967. None during 1968.

May 31

Found with Ad.♀ 145. The two animals were followed from 1620 hours until darkness and they probably slept in the same hole (Hole 76).

June 3

Solitary. Arrived at Hole 20 at 0625 hours to inspect the hole. At 1245 hours was found resting with matriarchal sounder of Ad. ♀ 182. Remained with this sounder until shortly before sunset.

|           |                                                                                     |
|-----------|-------------------------------------------------------------------------------------|
| June 24   | Solitary. Arrived at Hole 20 in early morning.                                      |
| Oct. 1969 | Solitary on one occasion and temporarily with a sub-adult male on another occasion. |

All of the above males were fully mature animals during 1969. They were seen with mature females occasionally during the breeding season, sometimes they were with younger males, but most frequently they were solitary. Ad. ♂ 41 was seen with two different females but courtship was not observed. The data indicate that fully mature males are mainly solitary and there is no evidence to support the contention that pair formation occurs during the rutting season.

No information is available from tagged animals on the behaviour of solitary sub-adult males.

b) Bachelor groups.

|                            |                                                                                                                                                                                                        |
|----------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| i) <u>Adult ♂ 161.</u>     | Captured 14 October, 1968, with Ad. ♂ 162 and S.Ad. ♂ 163. Observed in Oct. and Nov. 1968 and again in Jan., April, May, June and July, 1969.                                                          |
| Oct. 15                    | Solitary.                                                                                                                                                                                              |
| Oct. 18                    | Solitary but arrived at artesian borehole 3 mins. after Ad. ♂ 162 and S.Ad. ♂ 163 had departed.                                                                                                        |
| Oct. 20 to<br>Nov. 21 1968 | Seen on 11 occasions with a sub-adult male. S.Ad. ♂ 163 was positively identified on only two of these occasions. On two other occasions an additional male was with Ad. ♂ 161 and the sub-adult male. |
| Jan. 1969                  | Seen on three occasions and solitary on each.                                                                                                                                                          |
| April                      | Seen once with a matriarchal sounder.                                                                                                                                                                  |
| May                        | Seen once - solitary.                                                                                                                                                                                  |
| June                       | Seen once with an adult female.                                                                                                                                                                        |
| July                       | Seen twice, once with a yearling female and once with an unclassified sub-adult or adult.                                                                                                              |

- ii) Yearling ♂ 169 Captured with a matriarchal sounder (Ad.♀ 100) on 15 February, 1969. Seen on his own later the same day and the next day at Hole 20.

March - Seen 6 times and on each occasion was with a  
May sub-adult male. It is not known whether the same individual accompanied him on each occasion. All observations were at Hole 20.

Records of Ad. ♂ 161 suggest that bonds between adult males and younger males are of a temporary nature lasting perhaps two to three months. Bachelor sounders of younger males (sub-adults or yearlings, or both) may be more durable and possibly last until full maturity or until the rutting season which is likely to disrupt male-male bonds. There is however no direct evidence for the latter contention. The quantitative data from field observations and those of untagged groups at particular holes suggest that sub-mature bachelor groups may be stable between the main disruptive periods of mating and breeding. Bachelor sounders of up to five animals and which have included adult males have been seen during the dry season.

o) Spinster groups.

- i) Adult ♀ 145. First captured on her own as a yearling on 12 September, 1966 (was Yr. ♀ 12).  
Recaptured Feb. 1967, with Ad. ♀ 58 and 4 juveniles. S.Ad. ♀ 145 had suckled young i.e. she had bred as a sub-adult.
- Sept. 11 1968 Recaptured and numbered 145. Captured with 2 juv. ♂♂ (146 and 147) and a juv. ♀ 148.
- Sept. 12 to  
Oct. 20 1968 Observed on 18 occasions with her young; 146, 147 and 148.
- Oct. 22 Solitary.
- Oct. 24 Solitary.
- Oct. 25 Solitary.
- Nov. 16 Seen with Yr. ♂ 146, Yr. ♀ 148 and a yearling male which was probably 147 but without its collar. Three further observations of group during November.

|       |        |                                                                                                                                                                                                                                                                                                                                                          |
|-------|--------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Jan.  | 1969   | Three observations of Ad. ♀ 145 with Yr. ♂ 146 and Yr. ♀ 148.                                                                                                                                                                                                                                                                                            |
| Feb.  |        | Three observations. Group as in January.                                                                                                                                                                                                                                                                                                                 |
| March | 13     | <u>Recaptured</u> with Yr. ♂ 146 and Yr. ♀ 148.                                                                                                                                                                                                                                                                                                          |
| "     | 19     | Group had reformed. By 22 March, Yr. ♂ 146 was no longer with Ad. ♀ 145 and Yr. ♀ 148. On 23 March Yr. ♀ 148 was seen alone and on 24 March Ad. ♀ 145 was seen alone.                                                                                                                                                                                    |
| "     | 25     | <u>Recaptured</u> . Ad. ♀ 145. Solitary.                                                                                                                                                                                                                                                                                                                 |
| April | 4      | Seen with a Yr. ♀. Latter not identified.                                                                                                                                                                                                                                                                                                                |
| "     |        | 9 further contacts and on each occasion with a Yr. ♀. On one occasion with a second adult female and 3 juveniles.                                                                                                                                                                                                                                        |
| May   | 21     | <u>Recaptured</u> . The yearling female with her escaped and was not identified.                                                                                                                                                                                                                                                                         |
| "     | 22     | Solitary.                                                                                                                                                                                                                                                                                                                                                |
| "     | 24     | Contacted twice; once in a.m. and once again in p.m. with Ad. ♂ 41. Was with an unidentified Ad. ♂ in the a.m.                                                                                                                                                                                                                                           |
| "     | 25     | Seen with a Yr. ♀. No adult male.                                                                                                                                                                                                                                                                                                                        |
| "     | 31     | Seen with an Ad. ♂ and a Yr. ♀.                                                                                                                                                                                                                                                                                                                          |
| Sept. | 11     | With Yr. ♀.                                                                                                                                                                                                                                                                                                                                              |
| Oct.  |        | Observed on 7 occasions and each time with a S.Ad. ♀ (Change from yearling to sub-adult on 1 October.)                                                                                                                                                                                                                                                   |
| Nov.  | 12     | Seen with S.Ad. ♀. and again on 16 and 17 Nov.                                                                                                                                                                                                                                                                                                           |
| "     | 18     | Solitary.                                                                                                                                                                                                                                                                                                                                                |
| "     | 20     | With S.Ad. ♀ and 3 juveniles. The juveniles belonging to Ad. ♀ 145.                                                                                                                                                                                                                                                                                      |
| Dec.  | 7      | With S.Ad. ♀ and 3 juveniles.                                                                                                                                                                                                                                                                                                                            |
| "     | 12     | As on 7 Dec. but S.Ad. ♀ positively identified as 148 from ear notch on left ear. This is a shallow notch on the lower edge of the ear and this might account for it not being seen on previous occasions - i.e. if so this female is the same animal that has been with Ad. ♀ 145 since 4 April. Two further observations of the group during December. |
| Jan.  | 1 1970 | Groups as above and S.Ad. ♀ 148 positively identified.                                                                                                                                                                                                                                                                                                   |

While it is not positively established that the female accompanying Ad. ♀ 145 between April and November, 1969, was



number 148 it is extremely likely that this was so. If accepted, the example shows a persistent bond between an adult female and a younger female which was almost certainly one of her offspring. The two animals remained together for 16 months despite considerable disturbance resulting from 4 recaptures. The example also illustrates the stability of a spinster group without juveniles from one breeding season to the next. Although it would seem that Ad. ♀ 145 did not breed at the end of 1968 it is possible that she did so and lost her litter. She was seen on her own three times towards the end of October and could have farrowed between then and the next time she was contacted in mid-November, 1968. In the 1969 farrowing season she might only have been separated from S.Ad. ♀ 148 for two days (18 and 19 Nov.) but it is not known whether she farrowed before or after 16 November.

The longest recorded attachment between two animals is one of 34 months. The evidence is however to some extent circumstantial. Ad. ♀ 18 and Yr. ♀ 17 were captured on 5 October, 1966. The entire pinna of Ad. ♀ 18's right ear was missing and a metal tag was affixed to her left ear. Yr. ♀ 17 was tagged with a plastic rotating ear tag in each ear. When Ad. ♀ 18 was recaptured in August, 1969, she had lost her metal tag but the tear left by the tag and the missing right ear allowed her to be identified. She was accompanied by a younger but adult female which had a hole in each ear resulting from plastic ear tags. If, as seems highly probable, the younger female was number 17, then both were recaptured only 150 metres from the point of original capture in 1966.

d) Sub-mature heterosexual groups.

No evidence is available from tagged animals on how long-lived these groups may be. They are probably formed when deserted by a parent in the breeding season or alternatively by the death of a parent. Young animals from different litters may, of course, also join together into a group. However these bands seldom consist of more than three or four animals and since males, once they leave the family unit, tend to move into bachelor groups it is likely that sub-mature heterosexual groups are composed of siblings. The behaviour of tame animals suggests how these groups may be formed.

Rosemary's three juveniles, a female and two males were orphaned in December, 1968 at the age of three months. Although occasionally fed by us these animals were unprotected and were invariably driven off by tame hogs in the camp. The three juveniles were together until July, 1969, when one of the males disappeared. The female was severely injured, probably by a gunshot wound, at the same time and only the remaining male visited the camp. Later in July the injured female arrived at the camp with the male which we had marked with paint and it was thus possible to piece together the probable course of events viz. that one male had been killed when the female was injured. The young male and female remained together for the rest of the year and were still together in March, 1970. By April they had separated and by July the male and Mackintosh, one of the tame hogs of the same age, had joined to form a bachelor group. Although we seldom saw Rosemary's young other than in the camp (any wild warthog they may have joined would not have ventured into camp) they were never seen with other

warthog. They did not join with the tame warthog sounder even though this comprised only Susan and Mackintosh for most of 1969.

MacSweeny and Rosemary grew up together but separated on reaching sexual maturity. Similarly, Susan and MacDuff separated completely in May, 1969, when both were approximately 18 months old and sexually mature. It should be noted that tame male warthog have reached sexual maturity earlier than wild males appear to do, although Rosemary's young male copulated with Susan in May, 1969 at the age of 20 months.

Thus it seems that while heterosexual groups of young animals, particularly if they are litter mates, may be fairly long-lived their association is unlikely to proceed beyond the first season after the animals become sexually mature. Males and females are likely to separate at this time.

e) Matriarchal sounders.

These groups may comprise one or more adult females. Ad. ♀ 145 provided, during 1968 (see above), an example of an adult female and her immediate offspring. These remained with her until about fifteen months in the case of males and longer in the case of the female number 148. The bond between females may last some years as shown by Ad. ♀♀ 17 and 18. The following example is of a large matriarchal sounder which on capture comprised two fully adult females and it also illustrates the filial nature of large sounders with four age classes.

- i) Adult ♀♀ 182 and 183 Captured together on 25 April, 1969 with Yr. ♂ 181; a Yr. ♀ and 3 juveniles escaped.
- May 7 Contacted Ad. ♀ 182 who was with two yearlings and 3 juveniles and was being courted by an Ad. ♂. A sub-adult ♂ also appeared on the scene twice during the day.
- " 8 Ad. ♀ 182 on her own. Rooting.
- " 11 Ad. ♀ 182 and Ad. ♀ 183 and Yr. ♂ 181 together plus a yearling ♀ and 1 juv. ♂ and 2 juv. ♀♀.
- " 14 Ad. ♀♀ 182 and 183 together plus four other hogs which were not seen long enough to establish their identity or to classify them.
- " 16 Group as above but a sub adult male seen with them in the a.m.
- " 19 0650 hours. Group as above emerged from Hole 24 with an Ad. ♂ waiting outside. Ad. ♂ joined the group.  
0750 hours. Male seen copulating with Ad. ♀ 183 and keeping yearlings and juveniles away from Ad. ♀♀ (Hole 20).
- " 20 1613 hours. Ad. ♂ mated with Ad. ♀ 183. Ad. ♀ 182, 3 yearlings and 3 juveniles and a sub-adult male present. Sub-adult male chased off by the adult male.  
1735 hours. Ad. ♀ 182, 2 yearlings and 3 juveniles arrived at Hole 20.  
1738 hours. Ad. ♀ 183 and Ad. ♂ arrived at the hole. Ad. ♀ 183 joined the rest of her group and entered the hole while the male moved off.
- " 23 Ad. ♀♀ 182, 183, Yr. ♂ 181 and 3 juveniles as well as a S.Ad. ♂ entered Hole 20. On emerging the following morning the S.Ad. ♂ was trailing behind the group.
- June 3 Ad. ♂ 41 was with the group resting at mid-day and remained with them until c. 1735 hours. The group entered Hole 20 without the adult male. No sub-adult male was seen with the group. Ad. ♂ 41 was not with the group when they emerged the following morning.
- " 5 Group composed of Ad. ♀♀ 182 and 183, Yr. ♂ 181 a yearling ♀ and 3 juveniles.



|                       |         |                                                                                                                                                                                                                                                                      |
|-----------------------|---------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| June                  | 26      | <u>Recaptured.</u> Ad ♀♀ 182 and 183 together with Yr. ♀ (190), juv. ♂ (191) and a juv. ♀ (192). Yr. ♂ 181 was not with the group but was seen at another hole, on his own, the previous evening.                                                                    |
| July                  | 2       | Ad. ♀ 182, a tagged Yr. ♀ and a tagged juv. seen. Ad. ♀ 183 not in the group.                                                                                                                                                                                        |
| "                     | 9       | Group had reformed, 182 and 183 together again.                                                                                                                                                                                                                      |
| "                     | 12      | Ad. ♀♀ 182, 183, Yr. ♂ 181, Yr. ♀ 190, juv. 191 and 192 identified. (i.e. Group composed of 2 Ad. ♀♀, 2 yrs. and 2 juv.)                                                                                                                                             |
| Sept.                 | 4       | Group seen once; composition as on 12 July.                                                                                                                                                                                                                          |
| Oct.                  | 10      | Group as above.                                                                                                                                                                                                                                                      |
| "                     | 11 - 12 | Ad. ♀ 183 killed by predator. Immature animals seen separately in the evening but 182 not seen on evening of 12. Tag and carcass of 183 recovered on morning of 12 Oct.<br><br>No further contact with group until December despite efforts to locate them at holes. |
| Dec.                  | 7       | Ad. ♀ 182, a sub-adult female and 4 juveniles entered Hole 20.                                                                                                                                                                                                       |
| "                     | 11      | <u>Recaptured.</u> Ad. ♀ 182, S.Ad. ♀ 190 and 4 juveniles.                                                                                                                                                                                                           |
| "                     | 16      | Group as on the 11 December and intact.                                                                                                                                                                                                                              |
| "                     | 28      | Ad. ♀ 182, S.Ad. ♀ 190 and 4 juveniles, S.Ad. ♂ 181, Yr. ♂ 191 and Yr. ♀ 192 also with group.                                                                                                                                                                        |
| Jan. to<br>March 1970 |         | The group remained intact as seen on 28 Dec. apart from S.Ad. ♂ 181 who was only occasionally seen with the sounder.                                                                                                                                                 |

The history of this group illustrates the continued attachment of two fully mature females; 183 was the older animal. No adult male was attached to the group except temporarily during the rutting season and when one or other of the females was in oestrus. The young animals, both yearling and sub-adult, rejoined Ad. ♀ 182 after she had farrowed but S.Ad. ♂ 181 was only loosely attached to the group. S.Ad. ♀ 190 might have been with Ad. ♀ 182 throughout the farrowing period but this could not be established since contact

with the group was lost after it had been disrupted by a predator attack and the death of Ad. ♀ 183 in October, 1969.

Regrouping of a sounder after the dominant female or matriarch has farrowed~~has~~ been observed in other radio tagged groups. In one instance the breeding female (Ad. ♀ 232) lost her litter and was rejoined two weeks later by two sub-adult males and a sub-adult female who had been with her the week before she farrowed. Yr. ♀ 236, who was with 232 a week before farrowing and was also seen with 232 and her juveniles, disappeared, presumably when the juveniles did. The sub-adult animals (233 - 235) were not seen with Ad. ♀ 232 when she was accompanied by juveniles. In another instance, however, three yearling males did not rejoin the female (Ad. ♀ 110) after capture in October or after she had farrowed in November. They did however visit a hole where she had her young on at least one occasion in November.

Both Ad. ♀ 145 and Ad. ♀ 182 were the only members of their respective sounders which farrowed. Some sounders contain two or three females, each of which has bred in the same season. It is not known whether pregnant females part company, farrow in different holes and only later rejoin, or whether they may farrow in the same hole. The evidence at present available suggests they probably do part company but rejoin shortly after farrowing.

ii) Ad. ♀♀ 178  
and 179

Captured at Hole 24, on 25 April, 1969, with Yr. ♀ 180. Seen together in May, June and July 1969.

|       |        |                                                                                                                                                                                                                                         |
|-------|--------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Oct.  | 1969   | Three Ad ♀♀, a S.Ad. ♀ and a Yr. ♀ were using Hole 24 in mid-October but were not identified. Ad. ♀♀ 178 and 179 were originally tagged with plastic collars which would have been lost by this time.                                   |
| Nov.  | 21     | Ad. ♀ 178 and an Ad. ♀ with a metal tag tear in left ear (later caught and numbered 241) with 6 juveniles were using Hole 24.                                                                                                           |
| Dec.  | 7      | 3 Ad. ♀♀ and 8 juveniles were using Hole 24.                                                                                                                                                                                            |
| "     | 12     | <u>Recaptured</u> 178, 179 and Ad. ♀ 241 (8 juveniles were left in the hole). Each female had 3 functional mammae with the fourth in each case regressed thus indicating an initial complement of three juveniles each.                 |
| "     | 16     | Ad. ♀ 179 found dead, killed by predator probably on 15 Dec.                                                                                                                                                                            |
| "     | 17     | Ad. ♀ 178 and Ad. ♀ 241 and 8 juveniles seen.                                                                                                                                                                                           |
| "     | 24     | Ad. ♀♀ 178 and 241 and only 7 juveniles.                                                                                                                                                                                                |
| Jan.  | 6 1970 | Ad. ♀♀ 178 and 241 and 6 juveniles.                                                                                                                                                                                                     |
| April | 1970   | Group as on 6 January. Only 6 nipples would have been available between 8 juveniles after Ad. ♀ 179 died. It is possible that this may have contributed to the loss of the "extra" 2 juveniles at the end of December or early January. |

The data from this sounder suggest that the adult females were together prior to farrowing in mid-October but their identity was not established. Two of the females, 178 and 241 were together within 3 weeks after farrowing, judging by the size of their juveniles, and were later joined by Ad. ♀ 179 who was with the sounder by 7 December. Thus, even if the females did separate to farrow, they had rejoined to form a large matriarch<sup>al</sup> ~~and~~ sounder within a month of farrowing.

|                       |                                                                                                                                                                                                   |
|-----------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| iii) <u>Ad. ♀ 110</u> | Recaptured on 29 October, 1969 (initial capture 21 Sept. 1967) with 3 Yr. ♂♂. Solitary during November when she farrowed. Exact date of farrowing not established but probably about 10 November. |
|-----------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|

|      |    |                                                                                                                                                                                             |
|------|----|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Nov. | 12 | Ad. ♀ 110 inside hole with 3 Yr. ♂♂ standing about outside hole, yearling males later moved off. (Yr. ♂♂ 237 and 238 identified, i.e. animals which were with her at capture on 29 October) |
| "    | 22 | Heard juveniles squealing as Ad. ♀ 110 left hole. First clear indication that she had young.                                                                                                |
| Dec. | 5  | Ad. ♀ 110 and an untagged adult female emerged from a hole, juveniles presumably remained inside.                                                                                           |
| "    | 9  | Ad. ♀ 110 and Ad. ♀ and 8 juveniles.<br>Groups as above, though possibly less one juvenile, until end of February, 1970.                                                                    |

This example shows Ad. ♀ 110 leading a solitary existence prior to farrowing and only joining, or being joined, by another warthog (apart from her immediate offspring) 3 to 4 weeks after farrowing. The yearling males did not rejoin the sounder and were only seen at her hole once during November.

#### 4. Inter-change between sounders

Only one clear record of an animal changing from one matriarchal sounder to another has been obtained.

|                  |                                                                                                                                                                                                                                                            |
|------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <u>Yr. ♂ 172</u> | Captured 14 February, 1969 with Ad. ♀ 170 and S.Ad. ♀ 171. The entire sounder was not captured but was later found to comprise, during February and March, 2 Ad. ♀♀, 1 S.Ad. ♀, 3 to 4 yearlings and 5 to 6 juveniles. Yr. ♂ 172 did not rejoin the group. |
| March 17         | Located Yr. ♂ 172 with an Ad. ♀, a Yr. ♀ and 3 juveniles. The Ad. female later became Ad. ♀ 184 when she was captured in May, 1969. She was distinguished before capture by a very short tail and a characteristically torn ear.                           |

Ad. ♀ 184 was recaptured with her sounder at the end of October, 1969 and Yr. ♂ 172, then a sub-adult was still with the



sounder. Ad. ♀ 184 did not breed during the 1969 season and she was still accompanied by a sub-adult male, presumably 172, in March, 1970.

The results from field classifications and from observations of known groups are summarised in Fig. 55.

Observations of tagged groups indicate that bonds between mature females, or between females and their female offspring, may be stable and last through mating and breeding cycles. Bonds between females and their male offspring seem to be less durable and males may leave their mothers or matriarchal sounders after they are 12 months old and they certainly leave them by about 30 months of age. Two or more females and their young may join to form large sounders after farrowing.

Major disruption of matriarchal sounders occurs during the breeding season. However clear evidence is available to show that young animals, particularly females, may rejoin their mothers after they have farrowed. Inter-change of young animals between matriarchal sounders appears to be uncommon and matriarchal sounders are probably filial in structure.

Young warthog, yearlings or sub-adults, or both, may remain with an adult female through the breeding season if she does not farrow. Young males in such sounders may leave before the following mating season. The resulting spinster groups, an adult female with a younger female and probably her offspring, are thus a variant of the matriarchal sounder : adult female with sub-adults or yearlings, or both, but no juveniles.

Little information is available on sub-mature heterosexual

groups but these are probably a transitory grouping most common during the breeding or farrowing season. If formed at other times, for example by the death of a sow, they may be fairly stable and last until members become sexually mature.

The presence of bachelor groups in the Sengwa warthog population is clearly established. Bonds between males are less stable and groups of individual males remaining together for more than a few months have not been recorded. Older males tend to be more solitary than younger males. Males may, at any time of the year, temporarily associate with matriarchal sounders. However, even during the mating season such associations do not last more than a day or two.

Social groupings of warthog in the Sengwa Area are thus characterised by three main types of sounder : solitary adult males, bachelor groups and stable matriarchal sounders. Matriarchal sounders are of three main forms : an adult female with juveniles; adult female(s) with juveniles and yearlings; adult female(s) with sub-adults or yearlings, or both, but without juveniles. Matriarchal sounders appear to be mainly filial groupings while associations between males appear to be more temporary and, except in young males, are unlikely to be filial.

## C H A P T E R    V.

S O C I A L    B E H A V I O U R.

Fradrich (1965) studied the behaviour of suids and of warthog in particular. He observed warthog in the field in East Africa and in zoological gardens. I have been able to confirm, on both tame and wild warthog, many of his observations and extend others. Scent marking behaviour in warthog and bushpig is described apparently for the first time. Other forms of communication between individuals are described as well as observations on agonistic, courtship and maternal behaviour of warthog. These topics are pertinent to questions on social organisation and dispersion of the species.

A. C O M M U N I C A T I O N.1. V o c a l i z a t i o n.

According to Fradrich (1965) sounds of suids can be divided into three types, namely grunting, squealing and growling. He found warthog to be less vocal than other suids and to have a more limited range of noises. Warthog are seldom heard in the field but our tame warthog have been surprisingly vocal. The young are particularly so and emit, almost continuously, little chirrups and squeaks which have a remarkably bird-like quality. Many sounds uttered by warthog are not clearly separable to the human ear and one may grade into the other with the possibility of a number of meanings or shades of expression between extremes. There also seems to be the possibility of individual variations of voice and

recognition, e.g. of a mother's call by her young.

Physical analysis of the repertoire of suid sounds does not appear to have been made and the following is a preliminary list of warthog sounds which I am able to recognise.

a) Rhythmic grunts.

i. "Chant de coeur" or rhythmic courtship grunt. Signoret et al.(1961) cited by Hafez (1962) have described regular series of soft grunts emitted by the domestic boar during courtship. Their term of "chant de coeur" seems appropriate and is adopted for the similar courtship noise in warthog. The warthog chant de coeur is a loud, rhythmic, almost explosive grunt which may be audible at a distance of 80 m or more. It is very like the "phut-phut" of a two stroke engine and Fradrich (1965) likened it to the sound of a motor car engine idling. The mouth is slightly open and the lower jaw moves rhythmically as the grunts are emitted.

ii. Location call. Call given by a lactating female to her young when these have become separated from her. The noise is a brief series of grunts very similar to those uttered by the boar in the chant de coeur but a change in pitch may occur through the series of four or five grunts. I have heard this call in response to distress cries by members of a litter and also when the entire litter has become separated from their mother. Hafez (1962) describes a food call, a series of soft grunts, in the domestic pig which serves to bring her litter to suckle. I have not heard such a call in warthog although the soft low call (iv. below) may be comparable.

iii. Greeting call. Again a series of explosive grunts which



may not be distinctive from the previous vocalization. The call has been made when one animal runs up to another in its group which it may not have seen for a while or from which it may have been temporarily separated. Rosemary very frequently used to run up to us making this noise when she had been away for a day or two. Other tame warthog have emitted this call at feeding time when they come running up to the kitchen or to whoever is carrying their plate of mash. Overtones of aggression could be discerned when Grace and Melodie approached one and called in this manner. A possible variant of this call is heard from half-grown or adult animals when they are running around looking for other members of their group. Grunts seem to last longer, with a plaintive note to them.

iv. Soft low call. A series of low, soft grunts occasionally uttered at the entrance of holes by a mother calling her young or an animal looking for its sounder. Possibly a low intensity variant of types 2 or 3.

b) Single grunts, growls or snorts

i. Threat - attack. A harsh growl-cum-grunt, almost a squeal has been heard as a prelude to an attack on humans. I have not heard this noise in an intra-specific conflict.

ii. Warning. A high intensity low pitched "Woooooomph", like a forceful expulsion of air, rather than a vocalization. I have only heard it three times but its warning content is unmistakable. The first occasion was when MacDuff approached Rosemary and her juveniles. I was standing next to Rosemary when she "gathered herself up", issued this low, intense "Wooooomph" and lunged at MacDuff who was about 3 m away. Susan made the noise on

two separate occasions during the first week after she had farrowed and when I approached her and her juveniles too closely in the vicinity of their hole. No attack followed.

iii. Alarm grunt. A short low grunt, almost a snort, which usually precedes flight and is often heard in the field.

c) Squeals.

i. Submissive squeal. A short high pitched squeal emitted at the moment of turning to flee after an agonistic encounter ("head low submissive posture", page 158).

ii. Squealing growl. Long, drawn-out, throaty squeals and growls are given by animals cornered by a conspecific or when they are being pushed by a dominant animal, e.g. emitted by a female head-pushing against a heavier and dominant male. A female, resisting the attentions of a courting male, frequently made these noises which were clearly audible at a distance of 150 m.

iii. Long-loud squeal. This is like the typical squeal of domestic pigs when they are being handled or restrained and also occurs in warthog when they are caught.

iv. Squeaks (discomfort).

(a) Short high pitched little squeaks which are sometimes drawn out into a whimper are frequently emitted by resting animals. If two or more warthog are huddled together each movement by one will elicit squeaks from the disturbed animal which may, if the disturbance is sufficiently severe, approach the squealing growl.

(b) Very young warthog have a clear repetitive "complaining" noise which is a high pitched squeak followed by a throaty "churring" noise; thus "eek - chrrrrrrr, eek - chrrrrrrr". The

noise seems to accompany discomfort such as cold and hunger.

(c) Juvenile animals when separated from their group rush around emitting a high pitched "eek - eek - eek".

Although very preliminary, the above list does suggest a fairly wide variety of vocalizations in warthog and hence the possibility of a corresponding degree of complexity in vocal communication.

## 2. Greeting.

Naso-nasal and naso-anal contact between suids has been reported by Fradrich (1965). Nasal contact between mother and young is important in Sus scrofa L. during the nursing period (Gundlach, 1968). Examination of the anal region by one warthog meeting another seldom occurred in our tame animals. Naso-nasal or naso-oral contact is however frequent. Contact, or greeting, between two animals may be a touching of noses, a sniffing of each others mouth and also occasionally a sniffing of the pre-orbital area (Fig. 56). Sniffing the ground and each other's spoor may occur if a greeting has not lead to further amicable behaviour which may take a variety of forms : rubbing against each other, one placing its chin on the other's back, gentle forehead to forehead pushing and sometimes play-fighting in young animals.

Tame warthog regularly push their snouts against one's legs when first making contact. Sometimes recognition at a distance of even a few paces may not have been established and as a standard practice I put out the back of my hand to establish "nasal" contact when larger animals approach quickly. For example, should I meet Susan away from the camp she may advance towards me in such a

manner that I realise she has recognised me; I then put out a hand, she moves up and presses her nose against it and relaxes. She knows who I am. I may then scratch her briefly and she might rub herself against my leg or press her head, particularly the pre-orbital area, against my leg. The two Scouts who have spent days with her are similarly greeted in the morning. Occasionally they noted, "Susan did not greet me this morning; I do not know why".

It is worth noting the very different greeting shown by Percival, the bushpig. Oral-olfactory contact again seems to be important but before any touching occurs a rather surprising open mouthed panting is shown. This panting was always readily elicited by panting to him with one's mouth about 20 cm away from his. The pant could also be prompted by blowing into his nose. Whenever our dog panted near his face, as when playing with him, he would "greet" the dog with a few pants. The panting also contains a vocal element and sounds rather like a series of hoarse grunts accompanied by a simultaneous expulsion of air. He occasionally greeted bones in this fashion and would greet one through a pole fence if one blew or panted through it. The behaviour was present when we first acquired him at the age of about 6 weeks and was still shown when he was 22 months old.

Dr. R. E. Boltt elicited a greeting from a bushpig in a zoo by panting appropriately - the bushpig was apparently delighted at being addressed in the proper fashion! The behaviour would thus appear to be an endogenous pattern. Percival had no conspecifics with him and it is not known whether physical nasal or oral contact usually follows the panting ceremony.



Greetings in warthog do not appear to be highly ritualised and behaviour which might be described as appeasement behaviour has not been recognised. The behaviour described here does however suggest that olfactory rather than visual clues are important to individual recognition in warthog.

### 3. Grooming.

Mutual grooming is known to occur in warthog (Fradrich, 1965). It most frequently takes the form of drawing hair through the lips or the incisors and the movements are akin to those of grass plucking (Fig. 57). Grooming is often not at all gentle. Tame warthog have occasionally groomed my legs and the process is a painful one since the hair is all but pulled out. Licking with the tip of the tongue also occurs but less frequently than "hair pulling" or combing.

In tame warthog grooming has been observed between the following individuals :

| <u>Groomer</u>    |   | <u>Groomed</u> |
|-------------------|---|----------------|
| Susan             | - | her juveniles  |
| Juveniles         | - | Susan          |
| Mackintosh        | - | Susan          |
| Susan             | - | Mackintosh     |
| Susan's juveniles | - | Mackintosh     |
| Grace and Melodie | - | Mackintosh     |

and between litter mates.

Daily activity records indicate that grooming most frequently occurs at the end of rest periods - a transition from resting to activities such as feeding or moving away from the resting site. Grooming may also be solicited by one animal moving in front of another and lying down. Slight erection of the mane is a

characteristic reaction to being scratched or groomed. The accumulation of nits on warthogs' manes together with hair combing may have some bearing on pilo-erection in this situation (Fig. 57a). Raising of the mane is typical of flight - fight situations. Grooming may last for as long as ten or fifteen minutes but I have not timed grooming sessions. Tame animals will certainly allow one to scratch them for longer than this. Ticks and other ectoparasites may be removed in grooming but the tame animals seldom carried many ecto-parasites and grooming appeared to be more than a toilet activity.

Grooming may occur without any evident solicitation. For example, Susan and Mackintosh had been resting during the middle of the day and I was sitting on the ground near them. Susan woke and moved slowly over towards me, pressed her nose against my leg and proceeded to groom me. Although flattered by her attentions I soon stopped her and she moved off, with Mackintosh following. Short grooming sessions occur a few times each day and may be quite frequent when the animals are in their holes.

The importance of mutual grooming in maintaining social interchange between individuals within a social unit is well recognised (Etkin, 1964) and in warthog may be of some significance in the maintenance of durable social bonds.

#### 4. Scent marking.

Scent marking does not appear to have been described in suids and marking behaviour of both warthog and bushpig is described below.

Pocock (1943) described a pre-orbital gland in Hylochoerus but did not find one in Phacochoerus or in other suid genera. Owen (1868, cited by Pocock, 1943) noted a "naso-maxillary pit between the eye and the snout but rather nearer the eye", in warthog. Carpal, mandibular and eyelid glands have been described in Sus (Frechop, 1955 and Grassé, 1967) and reference is made to the presence of pre-orbital glands in ruminants with Sus, Potamochoerus and Phacochoerus mentioned parenthetically (Frechop, 1955). Fradrich (1965) saw warthog regularly visit favourite rubbing posts, particularly after wallowing. The sides of the body, the neck and, more gently, the area about the eyes, were rubbed on these posts. Fradrich did not equate any of these actions with marking.

Pre-orbital and salivary marking have been observed in warthog and salivary marking has been observed in bushpig. The external appearance of the ant-orbital area of a male warthog is clearly illustrated in Fig. 58. A pit as described by Owen (1868) is apparent but there is also a trough leading from the anterior corner of the eye. The origin of the secretion which causes the moist patch under the eye has not been established but it appears to originate from the eye. A copious milky eye secretion was noted in some captured male warthog, but not in others, after they had been injected with a tranquilizing drug ("Azaperone", Janssen Pharmaceutica). The ant-orbital trough and stained area are more developed and striking in mature male warthog than in females and immature males. This part of the face is rubbed on tree trunks, stumps and other similar objects (Fig. 59 <sup>b</sup> to <sup>d</sup>).

Warthogs also wipe the corners of their mouths on objects

(Fig. 59 a, b) and the resulting smear is probably saliva. Similar marking has also been seen in Percival, the tame bushpig. He was never seen rubbing his eye or pre-orbital area against objects in a way that suggested marking and no moist ant-orbital area was evident up to the age of 22 months. The bushpig marked trees, stumps and fence poles about the camp by wiping the side of his mouth against them. Wet smears were always visible immediately after he had marked. Typically he first sniffed at the pole or tree and then reached up and ran the side of his mouth down it. The movement might be repeated on the same part of the pole or on the opposite side of it. Salivary marking or mouth wiping was frequently followed by vigorous rubbing of his neck, particularly the area immediately behind his ears, against the pole or tree. Percival also had a distinctive, slightly musky body odour which is not apparent in warthog. Vigorous body rubbing may also be a means of depositing scent.

Warthog rub both the mouth, ant-orbital area and sometimes the neck on objects being marked. The mouth-wiping movement of warthog differs from that of the bushpig presumably because of differences in structure of the snout and lips. Warthog twist the head to one side and the inner surface of the lip flange, lying behind the tusks, is wiped against the tree or stump (Fig. 59 a, b). They then move forward and methodically rub the pre-orbital area on the marked object. The neck and sometimes the trunk may also be rubbed. One or other of these patterns may occur in isolation or the sequence may vary. As in bushpig, marking is usually preceded by sniffing and the animal may reach up and place its mark as high as possible



on tree trunks or poles (Fig. 60).

Scent marking behaviour has been observed in both tame and wild warthog. The intensity of the behaviour varies from a perfunctory touch or wipe to a vigorous session of two or three minutes. Ontogeny of the behaviour has not been investigated but it becomes apparent in tame animals before they reach maturity, at 6 to 7 months. Scent marking is often associated with agonistic encounters. It was very evident in MacSweeny during the mating season when he was 20 months old and sexually mature. On his periodic visits to the camp he would move from one marking post to the next, inspecting and then marking each. Marking has been observed at waterholes and in the vicinity of sleeping dens as well as in other parts of the home area. Regularly marked patches on mopane fence poles and some trees in the camp have become noticeably worn from the activities of four generations of tame hogs. Soft-barked trees may be scored by the tusks during mouth-wiping.

Warthog will rub their pre-orbital area against other warthog. Rosemary frequently rubbed her eye against my or my wife's legs after greeting and other tame warthog have also done so. Strange vehicles in the camp may also be marked.

On the few occasions that I have observed the reactions of one animal to the recently placed mark of another the behaviour has been reminiscent of dogs; the mark is inspected and the animal then places its own mark on the post. Reactions of tame hogs to each others marks have been similar.

a) Comparative aspects of scent marking in suids

The giant forest hog, Hylochoerus has a well developed pre-

orbital gland which appears to be separate from the eye (Pocock, 1943). The marking behaviour shown by Potamochoerus and Phacochoerus suggests a possible gradation of development from mouth wiping to pre-orbital gland marking. Potamochoerus marks with its mouth by means of a copious, probably salivary, secretion. Phacochoerus marks with both its mouth and an orbital or pre-orbital secretion. The position of the tusks and shape of the mouth appear to affect the efficacy of mouth wiping in the warthog which seems to deposit less fluid than the bushpig does. It would be interesting to know whether Hylochoerus, in addition to the pre-orbital gland (which it presumably uses in marking) also uses a salivary secretion. The low backward sweep of the tusks suggests that mouth-wiping may be even less readily accomplished by Hylochoerus than by Phacochoerus.

Histological studies of the cranial integumentary glands of African suids do not appear to have been performed.

b) Other forms of scent marking in warthog.

Fradrich (1965) described urine marking by mature male warthog which was accomplished by spraying urine over the fresh urine of mature females. This behaviour has been seen at Sengwa in only two situations. One was a male spraying urine over the recently deposited urine of a female in oestrus and the other was when a male sprayed urine onto a patch of ground from which a block of rock salt had just been moved. This patch of ground was marked twice within half an hour by the same male. I have frequently seen our tame male warthog urinate in their wallows but never the females. Urination occurred in the usual manner as opposed to being forcibly squirted out.

No clear pattern of marking by means of faeces has been observed although there is an indication that warthog will, when passing certain areas, regularly defaecate at them. Two such "lavatories" exist in the Sengwa camp; tame warthog almost always defaecate at these when passing. Young warthog readily learn to use sand boxes provided for them indoors. One generation, even after they became free to roam outdoors, insisted on returning to the site of their original "latrines" inside the house to urinate and defaecate.

Both tame and wild warthog have frequently been observed sniffing the spoor of other warthog, other game species and man. Tame animals have shown they are capable of following spoor trails to locate each other. Superficial examination of warthog feet has not revealed the presence of pedal or carpal glands. Nevertheless the intensity with which warthog have been observed to sniff at strange warthog spoor suggests that some identifying scent may be deposited.

Thus, although behavioural observations of both tame and wild warthog indicate that they are capable of detecting and possibly recognising conspecifics from their spoor and faeces warthog nevertheless mark objects in their environment by mouth wiping, pre-orbital (? orbital) secretions and by neck rubbing. These scent marks are placed at water holes, sleeping dens and at other points in the animal's home area. The precise social function of the marks and of marking behaviour has still to be determined.

## B. AGONISTIC BEHAVIOUR.

Information on agonistic behaviour of warthog is fragmentary and their repertoire of expression incompletely described. Without this information, it is difficult to assess social interactions in the field, except possibly where overt aggression occurs. The following descriptions are based on interactions between tame free ranging animals and an examination of 16 mm film records of some of the agonistic encounters.

### 1. Threat and Submission.

Threat behaviour may vary from a slight, almost inconspicuous, movement of the head towards another animal to a highly stylised lateral or latero-frontal display. I am not yet able to identify in a formal, as opposed to an intuitive, manner the components of more subtle threat postures or movements. That they occur is evidenced by an ability to anticipate more obvious forms of threat or aggressive intention.

Simpson (1964) and Fradrich (1965) noted a lateral threat display in warthog which they illustrated by a single drawing and photograph respectively. The display, more fully illustrated in Fig. 61, is characterised by stiff-legged mincing steps, erect mane, tail arched forward with the tip held against the flank, body curved and head and shoulders held high. The snout points downwards and the head faces the opponent obliquely, perhaps better to display the tusk and warts of one side of the face in profile. The tail may be momentarily straightened or swung out before again being deliberately pressed to the flank.



The example illustrated in Fig. 61 was drawn from cine film of an encounter between Mackintosh and one of Rosemary's orphaned juvenile males (referred to below as RJ male) when both were nearly 8 months old at the end of May, 1969.

Rosemary's three juveniles made one of their occasional visits to the camp at about 0900 hours. Mackintosh was in camp on his own. Susan who invariably chased the juveniles was away. RJ male was walking down the drive-way when Mackintosh saw him. They were approximately 15 m apart and proceeded to walk towards each other with ears pricked forward. When about 10 m apart Mackintosh's mane rose and I started filming. He went over into a lateral threat display and moved obliquely forward for two seconds. Threat reached its highest intensity between 2 and 3 secs. Mackintosh rose to his full height and almost skipped broadside on towards RJ male, (frame 50 and 56). RJ male moved away a step initially (frame 56, Fig. 61) but then lifted his head and shoulders. Mackintosh became hesitant and RJ male moved his body forward (frame 87, Fig. 61). By  $3\frac{1}{2}$  secs, Mackintosh's threat had ebbed and the two hogs moved together cautiously and touched noses shortly after 4 secs (frame 97). After a brief touch of noses their heads were brought into contact and pushing, cautious at first, started at 5 secs. By  $5\frac{1}{2}$  secs. they were pushing vigorously and by 6 secs. Mackintosh had delivered a blow to the side of RJ male's head and was forcing him aside. RJ male began to withdraw by 7 secs. and was in flight two frames later. Mackintosh then chased him and the other two juveniles, a male and a female, away from the vicinity of the house.

Twenty minutes later Rosemary's juveniles had returned and were again in the drive-way. Mackintosh threatened RJ male as before and this time RJ male made a brief submissive gesture when Mackintosh was approximately 3 m from him and ran in the opposite direction to which Mackintosh was moving. Mackintosh gave chase but with less intensity than after the earlier encounter.

Ewer (1968) has drawn the distinction between offensive and defensive threat. Both are illustrated in the example of Mackintosh and RJ male in Fig. 61. Mackintosh's threat from frames 2 to 57 was clearly offensive. However during this time and up to frame 50, RJ male had not shown any clear indication that he was going to withdraw from the encounter; his ears were forward all the time. In frame <sup>6</sup>57, where RJ male showed signs of withdrawal, his posture showed some similarity to that of submission (described later) but his ears were still pricked forward. I interpret this stance

as defensive threat bordering on submission. From this position RJ male went over into a more intense defensive threat by lifting his head and shoulders while remaining slightly back on his haunches (frame 86). As RJ male's defensive threat became more pronounced Mackintosh hesitated and also showed an intermediate between his initial high intensity offensive threat and the defensive threat posture of RJ male. It will be noticed that his ears were back although he was displaying with his tail (frame 86). By frame 92 there was not a great deal of difference between the postures of the two males except for the raised tail of Mackintosh who then further displayed with his tail by wrapping it onto his left flank. After a preliminary nose-touching and rather cautious head-pushing a serious fight developed and Mackintosh, who was on home ground, drove RJ male away. A month later after a prolonged fight Mackintosh was beaten in the second of two encounters by RJ male.

The defensive threat posture shown by RJ male in frame 86 of Fig. 61 has been seen in other conflicts where it has apparently dissuaded would-be attackers from carrying out their threat.

The offensive lateral threat display may be very brief, lasting less than a second, with a body cant to one side and the tail held momentarily against the flank as the animal moves towards its adversary. I have also seen the display last about 10 seconds and cover a distance of nearly 12 m. The animal was moving obliquely forwards at a brisk walking pace. Threat may vary from being lateral and across the front of an adversary to an oblique, almost frontal, display. I have seen the pattern occur momentarily before an animal attacked another from the rear. Vocalization, gnashing

of teeth and such-like have, with one exception to be described later, not been heard to accompany intra-specific threat.

A second inter-, rather than intra-specific, threat pattern has been shown by our tame animals and by penned feral warthog. It is best described as a mock-attack and its main features are illustrated in the following example, taken from MacDuff at about 5 weeks.

"MacDuff faced Bokkie, a tame year old impala standing about 2 m from him on my verandah. MacDuff assumed an upright posture and with mane erect, rushed at the impala with a short sharp squeal. MacDuff's head was held high, his snout well forward and he stopped abruptly about 20 cms from Bokkie's legs. As he stopped he pushed his snout up vigorously three or four times before turning about and walking back to me. A minute later he repeated the sequence. The impala showed no concern, which, considering the size of the warthog, was not surprising."

Adult animals in stockades have rushed at me in an essentially similar manner, at the same time emitting a threat attack grunt (see page 142 under "Vocalizations"). MacSweeny frequently threatened me with a lateral threat display and sometimes a chant de coeur preceded or followed the display. I interpreted this as part of courtship behaviour and MacSweeny, of all the tame warthog we have kept, was probably the most imprinted on humans. He did however once rush at an elderly woman seated on the ground in mock-attack fashion with head held up and an accompanying threat attack grunt. The woman waved an arm at him and stood up and MacSweeny stopped short without touching her. (It was this incident which prompted me to move him to the north of the Research Area page 189, Fig. 75).

Thus MacSweeny showed two forms of threat to humans, lateral display and mock-attack. I have not seen mock-attack in an intraspecific situation. The short rush towards an opponent, combined with a vocal threat, suggests a pattern which may fit into



what Ewer (1958) refers to as Leyhausen's "esperanto of expression". The only time I have heard a threatening noise accompany threat in an intra-specific conflict was when Rosemary lunged at MacDuff as he approached her and her litter the first day she brought them into camp (the young were a month old). Her movements differed from those of mock-attack in that her snout was more vertically inclined, her body was at first obliquely orientated towards MacDuff and no pushing movements of the snout were observed.

I have seen warthog attack each other without any ritualised threat pattern being evident. Fradrich (1965) noted that he only saw threat gestures precede playful fights. The most spectacular threat displays I have seen occurred between Mackintosh and one of Rosemary's juvenile males when both were 8 to 9 months old; these displays also preceded the most evenly matched and intense, prolonged fights I have seen. Brief threat display frequently occurred during play fighting; MacDuff once gave a beautiful demonstration of the lateral threat display at only 6 weeks of age. Attack without threat has occurred in the tame warthog in situations where there was little doubt as to the outcome or where the attacker was a recently parturient female. In both of the following examples the attackers were larger and heavier than their respective opponents.

April, 1968. MacSweeny (18 months old) was wallowing in camp and Rosemary approached him rather cautiously from the rear. She was about 6 m away from the wallow when MacSweeny leapt out and attacked her. She countered his onslaught, withdrew and ran. Rosemary squealed throughout the encounter (squealing growl and finally a submissive squeal).

This sequence was filmed (Fig. 62) from the time of contact between the two animals until Rosemary (on the left in Fig. 62) had made good her escape. The speed of the encounter can be



gauged from the frame counts given with the drawing; the entire sequence took little more than a second.

October, 1968. Rosemary had left her litter in their hole and came trotting into camp for food. MacDuff, then 12 months old, was standing near the kitchen door. Rosemary, when about 5 m from MacDuff, quickened her pace and launched into a direct attack. The only noticeable threat components were a raised mane and "pricked up ears" in both animals. MacDuff parried the attack, gave way and ran off. His left hind leg appeared to have been strained and he limped slightly. The initial head-on contact with Rosemary may have caused the slight injury.

There were undoubtedly signals which heralded these attacks. MacSweeny's demeanour in his wallow was patently aggressive and MacDuff had ample time to move away but seemed inclined to challenge Rosemary. Threat, in the sense that opponents were given the opportunity to withdraw, was however absent from both encounters.

The submissive posture described and illustrated by Simpson (1964) has been seen but usually as a brief component of a more dynamic submissive gesture. The typical submissive posture of artiodactyls is a lowered, outstretched head and neck (Ewer, 1968). The warthog submissive posture is essentially similar and varies from a lowering of the head to a ducking movement, with snout pointed well forward, followed by flight. Ducking and dodging are usually accompanied by a submissive squeal. Gradations from a slightly lowered head to the final submissive gesture of ducking and fleeing are illustrated in Fig. 63.

The encounter was again between Mackintosh (on right in Fig. 63) and RJ male when both were nearly 17 months old. Mackintosh was by this time leading a solitary existence. He had also broken a carpus some two months earlier and this had not fully healed. So, despite his superior weight, he was in no position to fight and

and he had also been beaten by RJ male 8 months earlier.

Mackintosh walked slowly up behind RJ male and the female litter mate accompanying him. RJ male swung about when Mackintosh was about 2 m away and threatened him - Mackintosh stopped. RJ male approached Mackintosh still threatening (frame 1, Fig. 63). The two animals then touched noses (frame 23) for 2 seconds after which Mackintosh began to withdraw and show full submission. RJ male did not follow Mackintosh at all as he trotted off. The encounter took place in the camp and Rosemary's two juveniles had spent about two hours there. The animals had already met and similar encounters had occurred earlier in the morning.

At the start of the encounter Mackintosh's ears were still pricked forward (frame 1, Fig. 63). By frame 11, nearly half a second later, his ears were moving back and thereafter the differences between his posture and that of defensive threat (RJ male, frame 57, Fig. 61) are mainly in the angle of the snout, which is more horizontally inclined in submission, and the backwardly directed ears. The mane is also not erect.

Walther (cited by Ewer, 1968) considered the head low posture of appeasement in various antelope to be derived from the concealment posture of the young animal in response to danger. Ewer considers other evidence to support the view that appeasement postures in many mammals are derived from intention lying down movements rather than from attitudes adopted by the young in approaching the mother to suckle. The full submissive gesture in warthog is not a static display (as it appears to be in antelope) but a ducking movement accompanied by a squeal and dodging to one side, after which the animals trot or run away. This difference, if it is a real difference (for I have not seen full descriptions of the postures and have only observed appeasement in bushbuck where dodging followed by flight was not seen), may be due to differences in the escape pattern shown by respective young. An escape pattern

shown by very young warthog is characterised by an initial dodge followed by a brief lying-low posture before the animal runs (page 183 and illustrated in Fig. 64). The position shown by Mackintosh in frame 78 of Fig. 63 bears a remarkable similarity to that shown in frame 3, Fig. 64, by 3 week old MacSweeny. This similarity only became clear to me some time after I had drawn these sequences so that similarities are not due to any particular selection on my part.

I have not seen warthog lie down in intraspecific threat-submission contexts. Tame warthog, particularly Rosemary and Susan, often broke into huts and sometimes our kitchen in search of food. When cornered indoors and threatened (they were usually beaten for these misdemeanours) they would back into a corner squealing and crouch low with chin and belly almost touching the ground. These animals never attempted to attack in such situations even when 2 years old and weighing more than 140 lbs. They squealed until the way was clear for them to run out of the door.

These observations support Ewer's (1968) view that submissive postures in the artiodactyls are intention movements of lying down, probably derived from juvenile concealment behaviour. A mere lowering of the head in warthog may, because of their very short necks, need to be emphasized by squealing, dodging and at least token flight. Ducking and dodging occur very frequently and even when animals are as much as 4 to 5 m apart. The gesture has, at close quarters, very practical considerations attached to it; the animal remains in a position to parry an attack until the last moment. Flight is then across the front of the aggressor who would have to turn his head sideways to slash with the lower canine

which is the main and only dangerous offensive weapon. By this time the fleeing animal would be out of the way.

## 2. Fighting.

An examination of fighting in warthog is important for two reasons. Firstly, it may provide a fuller understanding of their cranial anatomy and, secondly, it may allow us to judge the extent to which fighting in the species has become stylised. Ewer (1968) examined fighting methods in mammals and considered that of the suids to be incompletely stylised. This conclusion suggests the possibility of intra-male rivalry leading to mortality and a disparate sex ratio. Ewer's (1968) views of suid fighting were based mainly on descriptions by Fradrich (1965) who observed warthog fighting in zoological gardens. Gundlach (1968) studied the ontogeny of fighting in feral European wild boar (animals not in a wholly confined situation) and concluded that fighting in Sus scrofa was more stylised under these conditions than Fradrich had observed. My observations of warthog fighting suggest that the same may be true for warthog.

### a) Fighting in very young warthog.

Fighting in very young warthog bears a remarkable resemblance to that described by Gundlach (1968) for young wild boar. I was unable to observe fighting until the hogs were about 10 to 14 days old, largely because they remain in their holes up until this age. In Sus scrofa fighting was fully co-ordinated at about 4 weeks



while in warthog it appears to take about 2 months.

The major feature of early fighting is its uncoordinated nature (Fig. 65). Animals may strike each other on any part of the body and biting occurs (Fig. 65a). Blows delivered by the head take a variety of forms, the most characteristic being side-swipes in which the bridge of the snout makes contact (Fig. 65d). Lateral swipes in which the side of the snout and the canines make contact and upwards pushing movements (almost "rooting movements") are frequent (Fig. 65c). Animals may stand head to tail, leaning against each other, shoulder to shoulder, and bite or butt each other's flanks (i.e. lateral fighting characteristic of Sus scrofa) (Fig. 65 a, b). Frontal pushing, sometimes while resting on the fore-carpals and the delivering of blows to the head, the characteristic fighting technique of older animals, is apparent even at two to three weeks (Fig. 65d).

MacSweeney (at 2 to 3 weeks) indulged in frontal pushing contests with my fist. His ability to keep his forehead firmly placed against my fist, even when this was drawn rapidly backwards, was astounding. Side-swipes were delivered with remarkable rapidity and his forehead instantly returned to the pushing position in contact with my fist. In this game the side-swipe blows were all delivered with the bridge of the snout and not with the side, where the tusks would have been brought into play.

In December, 1966 I cared for two young bushpig for a fortnight. Their fighting showed similar lack of co-ordination and was again very like that depicted by Gundalch for Sus scrofa; they exhibited a form of "crossed sword fighting" (Ewer, 1958),

which was not seen in young warthog. The animals would whirl around, engaging each others raised and upwardly directed snouts with rapid side blows accompanied by biting.

Frontal fighting in warthog was developed by the age of about two months and biting was no longer apparent in "serious fights". Disoriented fighting, butting at any part of the body and pushing movements such as occur in digging and rooting occurred in spirited play fighting even at 5 or 6 months. Serious fights at this age were characterised by frontal pushing and blows aimed only at the head and possibly neck.

b) Fighting in animals older than 6 months.

Fradrich (1965) describes warthog fighting as frontal attack in which forehead contact is maintained by powerful pushing. Ewer (1968) extends this, possibly on the basis of her work on cranial anatomy and Fradrich's photograph of frontal pushing, to say, "The heads are held symmetrically, with noses pointing downwards and the two are in contact from the forehead down along the length of the snout". Simpson (1964) however described fighting as "... pushing, in which the contact area was confined to the anterior surfaces of the tusks and the snouts", and, "Each attack comprised attempts to get behind the defensive tusks, interspersed with trials of strength where each animal tried to push the other backwards".

Frame-by frame examination of 16 mm film of serious fights shows that full frontal contact as described by Ewer is rare. It does however occur during temporary lulls in the fighting when strenuous pushing is not evident. It often occurs in pushing bouts

which are not fights, as between a male and a female in courtship and between litter mates at a wallow. Contact during serious fights and when pushing is most intense seems to be confined to the anterior snout area (Figs. 62, 66 and 67). The tusks of all animals filmed were still small and I have no information on how the tusks of more mature animals might engage.

Examination of the skull and head structure of warthog shows that the snout is flat and almost as broad as the forehead; it forms a broad flat contact area anterior to the tusks. This is more evident in males than in females. The forehead is slightly concave and contact between two apposed skulls is limited to the brow ridges and the snout between the canines. The skull between the brow ridges is rather thin which is not the case in bushpig and forest hog where it is much more heavily armoured. The skulls of two warthog with large tusks can only be brought into contact from forehead to nose tip sym<sup>m</sup>etrically if the tusks of one skull are placed anteriorly to those of the other. Forehead to forehead contact in males with large tusks also places the head well within the orbit of the other's tusks. Full frontal contact in serious fights between warthog with well-developed tusks seems improbable but conflict between such animals needs to be examined in detail.

Fighting warthog direct and parry blows with remarkable rapidity and agility. Attempts to disengage frontal contact are made all the time for, as soon as one animal can, with advantage, disengage from pushing, he can strike the other. My contests with 3 week old MacSweeny (page 162) suggested that firm frontal contact was not only a pushing contest but also a continual manoeuvring for position.

in which one could both hold ones opponent and judge when it was expedient to strike. The duels were reminiscent of the school-boy game of pushing fists together and trying to strike the opponent on the back of the hand behind the knuckles; only by pushing one's opponent's fist firmly can one anticipate and parry a blow and a delicate balance between pushing too hard or too lightly has to be maintained.

Oblique upward and sideways swipes of the head are characteristic of the fights I have filmed and these can readily be observed in the fighting of younger animals. Blows are delivered with the bridge of the snout (in large mature animals it may be with the blunt upper canines) and the head is twisted towards the opponent accordingly. If the lower canines were to be engaged the head would have to swing laterally and initially be twisted away from the opponent. This, in turn, would place the animal in a position from which it would be unable to regain frontal contact rapidly or to parry an opponent's thrust.

A high frequency of blows in fights between young warthog or those without well-developed tusks might be associated with a lack of suitable anti-slip or locking devices which well developed tusks would provide (Geist, 1966). The fighting of half-grown warthog (Fig. 66) does, however, bring out one important feature, to wit, the "aim" is to strike the opponent about the head and push him off balance rather than to get past the tusks and to attack the flank or belly as Ewer (1958) suggested. I have never seen blows directed to the flank except where animals have been forced into a fence or other obstruction and then blows were with the bridge of



the snout. The lower canines have not been brought into play in any of the fights I have seen and a careful examination of cine film indicates that the mouth is not opened except in the fighting of very young warthog (less than 3 months old). However, if one animal pushed another's head sufficiently far around, so that it was standing almost parallel to it, a lethal blow to the neck or flank would be possible.

The development of tusks and warts shows not only that fighting is frontal (Geist 1966; Ewer, 1958) but also supports the idea that fighting is highly structured. Blows are directed at, and taken on, those parts of the body which are the most protected (Fig. 67). There are rules to the game and one of them is that the opponent is struck on the head and not, as it were, "below the belt". Leakey's hypothesis (Ewer, 1958; Tookey 1959) that warts and tusks are primarily a means of protecting the head from thorns while feeding on succulent grasses in thorn thickets seems, to me, to be highly improbable. I have never observed thorns in the warts and scratches on the upper canines could equally well result from walking through the veld, lying down and wallowing (when tusks come into contact with abrasive grit) and from mature males' habit of thrashing bushes.

Ewer (1958) in discussing warthog warts, points out that they are situated to guard against attack from below. The bony sheath of the upper canines also suggests that the major forces applied to it are from the front and below. The sheath is thickest and best developed on the posterior dorsal angle. The wart along the lower edge of the dentary would serve to cushion blows directed upwards or

sideways against the lower jaw. In the sub-orbital area the zygoma is extended outwards and downwards, is thickened and has the sub-orbital wart resting on it. The wart and projecting zygoma appear to function as cushions to absorb blows of an opponent as well as possibly blocking the movements of an opponent's tusks and so shielding the eye. The sub-orbital warts project forward slightly and side-swipes frequently land on the outer and posterior surfaces of the wart. The high position of the eye not only enables hogs to see further in open country (Ewer, 1958) but also serves to remove it beyond an opponent's tusks. The function of the anterior, supra-oral, warts is primarily to protect the underlying tendons of the masseter muscles and in females protection is afforded by a thick dermal pad (Ewer, 1958). Supra-oral warts and the bridge of the snout were frequently cut and scarred in tame animals after fights. In males the warts may provide an additional anti-slip projection during fighting. The position of the head in lateral display during threat and courtship may serve to show the warts of one side of the head in profile. If so, a display function would have served to emphasize their development as signalling devices in intimidatory displays.

At the end of a fight "there is always a moment of danger when the weaker yields and must turn to make good his escape" (Ewer, 1968). The submissive posture and retreat shown by Rosemary after being attacked by MacSweeny (Fig. 62) is a characteristic form of withdrawal from fight or an attack. As the submissive animal turns to run, the aggressor usually lunges forward at the fleeing animal's side. I have never seen the dominant animal make contact

and, as already mentioned on page 160 , the position of the fleeing animal makes it difficult to deliver a lethal blow. After lunging forward the winner may pursue its rival but by this time it is too late to inflict an injury. Curved horns of wildebeeste are not unlike the upper canines of warthog as offensive weapons. Estes (1969) was impressed by the considerable agility of wildebeeste both while fighting and in disengaging from a fight. He only once saw an animal gore another in the side at the end of a fight and no injury resulted. I have been similarly impressed by the agility and speed at which warthog attack and counter-attack and the ability of out-maneuvred animals to defend themselves. I have not seen a defeated animal tusked while disengaging from a fight. The only battle scars seen have been on the head, although leg injuries may be sustained in pushing (MacDuff vs. Rosemary, page 158 ).

In summary, observations show that elements of fighting common to other suids occur in the uncoordinated fighting of very young warthog. Adult patterns of frontal fighting are however present at an early age. Serious fighting between animals older than six months consists of frontal pushing contests and simultaneous attempts to strike at the opponent's head with the broad flat dorsal surface of the snout or the blunt upper canines. When an advantage has been gained vigorous pushing against the head and neck of the opponent occurs, with the apparent intention of throwing him off balance or perhaps to the ground. Attacks to the body and use of the lower canines have not been observed though presumably an animal thrown to the ground or off balance alongside the victor may be gored with the lower tusks. Positions in which goring may occur have not however

been observed in serious fights. Disengagement from fights shows a characteristic submissive flight pattern which, because it is across the front of the victor, also serves to minimise the risk of injury. Warts serve to cushion blows to the head and their disposition is adapted to fighting techniques; these structures also serve to emphasize that warthog fighting is highly structured. Fighting between fully mature males with large tusks needs to be examined to determine the precise form of frontal contact and the possible role of warts as "blocking" devices.

### 3. Field observations

Aggressive encounters between warthog, apart from the playful fighting of litter mates, have been recorded in the Research Area. These have occurred between the following categories of animal :

- (a) Adult males attacking and chasing younger males and females at water holes.
- (b) Adult males attacking other adult males at warthog holes and at water holes.
- (c) Adult males chasing sub-adult and yearling males when courting oestrous females.
- (d) Adult females chasing other adult females at water holes and at hog holes.
- (e) Adult females chasing younger warthog from holes and elsewhere during the farrowing season.

Contacts were nearly always very brief but chases have sometimes lasted for a few minutes. No prolonged frontal contacts which could be described as fights between males have been seen by myself or my staff. I have seen more subtle encounters but Scouts tended



to record only clear cases of fighting or chasing. These invariably consisted of a very brief frontal contact followed by a chase or of a chase only. Clashes have been most frequently observed at the artesian borehole where there is a small well-used water hole. On some days at the peak of the dry season three chases have been seen there on one day. Fradrich (1965) noted that warthog arriving at water holes often waited until warthog already there had moved off before going to drink and wallow. Similar behaviour has been seen at Sengwa, but not consistently. Some groups will tolerate others sharing the water hole, while others, particularly adult males, will interrupt a wallow to chase any "intruders" off. Mr. B. Ball (pers. comm. 1969) has seen an adult warthog kill a younger animal which approached it while wallowing. As the young animal approached the wallow the adult lunged at it, tossed it into the air and then followed up the attack, finally killing it and eating part of the intestine. The observation was made in the Mana Pools Game Reserve in June, 1968.

During the mating season I have twice seen juvenile warthog with their abdomens slit open and intestines protruding. No other wounds were visible on the animals and my impression was that they had been gored by other warthog, probably courting adult males. Apart from these isolated cases I have no evidence to suggest that intra-specific fighting in warthog is directly responsible for more than the occasional death. Neither have I any record of adult animals being wounded or slashed during the mating season by other warthog. Warthog captured during the rut have not shown fighting scars.

The social basis of agonistic encounters seen in the field is not known; some have undoubtedly been due to inter-male rivalry during the rut, others have been females driving off young animals before the farrowing season (see under "maternal behaviour", page 174 ). Conflict at waterholes, holes and at feeding grounds suggests that some form of territorial behaviour may occur. This question will be discussed in the final discussion. The very brief nature of the encounters which have been observed, particularly those between males, leads to the speculation that dominance relationships amongst warthog living in an area may be fairly well established and that allometric growth of tusks and warts may serve to reduce the frequency of prolonged fighting.

### C. MATING BEHAVIOUR

Courtship has been described by Simpson (1964) and Fradrich (1965). I have seen full courtship, i.e. terminating in copulation, only once in the field. A tame free ranging warthog "courting" humans has been filmed. Game Scouts have observed courtship and mating in the field. Observations on courtship are in general agreement with those of Simpson and Fradrich but variations in the behaviour are apparent and observations from Sengwa are therefore described.

Simpson (1964) depicts the tail of the male as being held horizontally straight out behind the female, in courtship and lateral threat. I have not observed this but have seen the tail wrapped around against the flank as in threat (Fig. 61) or carried in a characteristically bent position (Fig. 68) during courtship. The

male also shows a springy, hip-rolling gait while following the female and the chin is frequently placed on her rump or back. This behaviour presumably serves to bring a receptive female to a stop as it does in the domestic swine (Signoret et al. cited by Hafez, 1962). I have seen an adult male place his chin on a female's back while standing beside her, as opposed to doing so while following from behind. During the same courtship sequence the male frequently attempted to mount from the side (he was a fully mature adult). Bouts of frontal pushing occurred with the female squealing loudly (squealing growl) and the male, when facing her after some of these bouts, placed his chin on top of her outstretched head. Short spells of following by the male were followed by lateral (? intimidatory) displays and frontal pushing. Chant de coeur occurred during following and intermittently at other times.

Copulation is not always preceded by a long courtship walk or by the chant de coeur. In May, 1967 Edson<sup>Ndiamani</sup> saw an adult male and yearling female emerge from a hole and before moving ten paces from the hole the male mounted; copulation lasted 6 minutes. Similarly brief preliminaries have been noted on other occasions when mating occurred after a pair emerged from a hole.

Adult male warthog will visit holes in the early morning during the mating season and join up with oestrus females which might emerge. Young males or bachelor groups have been chased as they emerge by adult males waiting outside or visiting holes. I have found adult males sniffing about well used warthog holes as late as 1000 hours during the mating season and it is probable that they trace and follow up oestrus females from holes. When Susan was

mated in June, 1968 an adult male was waiting outside her hole well before she emerged. Males may sleep with females they are courting but do not always do so. We have only twice captured an adult male with mature females in over 100 captures.

Courting males have been observed chasing younger animals which were accompanying an oestrus female but on other occasions they have taken little or no notice of them. All the courtship and mating observed in the field has been by fully adult males. Sexual behaviour or even interest by yearling males has not been observed in the field. Sub-adult males do attempt to approach oestrus females but each time they have been observed with or near a courting group there has been an older male present or they have been chased off by a fully mature boar. Copulation between Susan and Rosemary's juvenile male (20 months old) occurred in May, 1970 but this was in the staff village where competition from wild males was precluded. The following day Susan was mated by a mature wild boar and the yearling male was not seen with her. Susan was courted again the following month and it is possible that her mating with the yearling was unsuccessful and that the adult male that was with her in May joined her too late.

Evidence from group structure and observations of radio tagged groups, presented in the last chapter, suggests that warthog are polygamous or possibly promiscuous. There is no evidence to suggest that warthog in the Sengwa Area are monogamous or that pair formation occurs during the mating season.



#### D. SOME ASPECTS OF MATERNAL AND JUVENILE BEHAVIOUR.

Observations of two tame free ranging warthog which bred near the author's house are reported. The two animals were Rosemary who was mated on the 13 or 14 April, 1968 and farrowed on the night of the 28 September, 1968 (she met an untimely death 3 months later) and Susan, who was mated on the 14 June, 1969 and farrowed on 21 November, 1969. Both females were mated by wild males and fell pregnant in their second year. Gestation periods were 170 days and 160 days respectively. Susan first showed signs of being in oestrus on the 10 June and although she was seen being mated on the 14 June she may have mated before this. The data from these two females and their litters is compared with published information where possible and with that obtained from wild warthog in the Research Area.

##### 1. Pre-farrowing period

Pregnant females leave their half-grown young or other warthog and farrow, in a hole, on their own (Fradrich, 1965 and Chapter IV). The question arises as to whether the pregnant sow is deserted by her young, whether she merely leaves them (perhaps by moving to a new area) or whether she drives them away. Both Rosemary and Susan farrowed in solitude. Rosemary had been solitary for six weeks before she farrowed : Susan parted from Mackintosh, a yearling male, a few hours before she farrowed. Rosemary farrowed at night or in the early morning; Susan did so during the day. Pre-farrowing behaviour of the two females is described below.

The first signs of antagonism between Rosemary and the two

juveniles accompanying her (Susan and MacDuff) occurred in July, 1968 when Rosemary was seen chasing the two juveniles near camp. At the time the three warthog were sleeping in the pen in camp. At the end of July Rosemary spent three consecutive nights away and was not seen during the intervening days. The two juveniles continued to sleep in the pen.

During August Rosemary was seldom seen and by mid-August was no longer accompanied by Susan and MacDuff. She visited the camp briefly on 19 August. On 5 September she came into camp in the evening, attacked both juveniles and then left. She returned for mash on the evening of 16 September and was closed in the pen with Susan and MacDuff when they were fed. On the evening of 27 September she returned and was again closed in the pen with Susan and MacDuff. She made considerable efforts to get out and was released. I did not see her attempt to chase Susan and MacDuff and they did not avoid her. Rosemary was by this time sleeping in Hole 1 alongside the Gorge (Fig. 5 ), some 200 m from the camp.

Observations on Susan were more detailed and her behaviour differed in some respects from Rosemary's. The first apparent attempt by Susan to drive Mackintosh away occurred at Hole 12 (Fig. 5) on 24 September, 1969 about two months before Susan farrowed on 21 November, 1969.

Susan entered Hole 12 at 1735 hours on 24 September, 1969, followed closely by Mackintosh. During the next 10 min. Mackintosh entered and emerged from the hole four times, complaining almost continuously. Susan appeared to be preventing him from remaining in the hole. Mackintosh rooted briefly near the hole and then at 1750 ran up and reversed rapidly into it. A minute later and after a fearful noise from both animals Mackintosh emerged. Susan could be heard digging, deep in the hole, with her snout. Mackintosh entered the hole again a minute later but immediately emerged. Susan, still digging,

emerged partly and paused to wipe her eye (pre-orbital area) on a small bush at the entrance of the hole before she reversed into it again. This occurred at 1754 by which time Mackintosh was rooting about 15 m away. At 1818 Mackintosh rushed back, swung about as if to reverse into the hole, stopped, stood for a while and then lay down at the entrance with his head resting on his forefeet. He remained thus until 1825 and then slowly manoeuvred back into the hole. He then started shovelling soil out of the hole with his snout. At 1827 I could no longer see his head. Two minutes later he was near the entrance again, still digging. This behaviour continued intermittently until 1833 when I left him lying in the hole with his head at the entrance. He finally spent the night at Hole 12 with Susan.

The following evening the two hogs again went to Hole 12. On arriving at 1807 hours, "Susan struck Mackintosh and he moved. screaming" (C. Maguchu). At 1809 Susan entered. Mackintosh soon followed and lay with his head at the entrance until 1828 when he reversed into the hole. The following night (26 September) the two animals slept at Hole 1 and no conflict occurred. The nights of 27, 28 and 29 September were spent at Hole 3 and no conflict was observed. On 30 September, at Hole 11, conflict occurred again; Mackintosh squealed at the entrance while Susan was behind him in the hole. Similar forms of conflict occurred while entering holes on the 1, 2, 4 and 12 October, but not again until the week before Susan farrowed.

During the five days before Susan farrowed she became increasingly intolerant of Mackintosh and attacked him frequently. On 14 November a "friendly fight" became "serious" and Susan chased Mackintosh for 10 paces. On 18 November Susan struck him several times during the day and once chased him for over 30 metres. By the 20 November Susan attacked him whenever he approached her. From 1650 hours on the 20 November contact with Susan was lost when the recorder fell ill. However at 1800 hours Mackintosh was found on

his own in the camp and at 1845 he moved down to Hole 14 which he entered at 1900 hours. Both hogs emerged from Hole 14 at 0600 hours on 21 November (the day Susan farrowed) but Mackintosh kept a short distance behind Susan. At 0610 hours C. Maguchu noted :

"These two hogs were not grazing together as usual because Susan was not allowing Mackintosh to feed close to her or walk close to her. Mackintosh was ever moving behind her, lonely, at 3 - 7 yards."

Mackintosh was attacked by Susan at 0640, 0700, 0710, 0755 and 0835 hours. Both hogs went to Hole 14 at 0910 and Mackintosh entered first. Susan followed and chased him out (the hole had two entrances); he entered again and was again chased out, after which he moved away. Susan remained in the hole and juveniles could be heard squealing when it was visited at 1630 that afternoon.

Mackintosh returned to the hole and slept the night there (Susan and her juveniles were still there). He was not seen entering the hole but he emerged from it early the following morning. On the night of 22 November he slept in the pen in camp and although he visited Susan's hole on the morning of 23 November he did not sleep there that night. He was ill at ease when near the hole and as P.Mzila described it, "he was wearing frights." On the night of 24 November Mackintosh again slept at Hole 14. On 25 November he slept in the pen and then disappeared for 2 weeks.

Thus both Rosemary and Susan exhibited some intolerance of the juveniles attached to them 6 to 8 weeks before farrowing. Susan showed antagonistic behaviour intermittently for  $2\frac{1}{2}$  weeks, from the 24 September, to 12 October, but did not succeed in driving Mackintosh away. Rosemary last attacked Susan and MacDuff 3 weeks before she farrowed but she had by this time effectively separated



herself from them. Susan's antagonism returned the week before she farrowed but she still failed to drive Mackintosh away. Both females showed antagonistic behaviour towards the half-grown warthog on the day they farrowed and after this.

Fradrich (1965) recorded a female warthog leaving her sounder three weeks before farrowing but he never observed any conflict. Adult female warthog in the Research Area have been seen chasing young warthog during the farrowing season and altercations have occasionally been heard at holes (at dusk) during this time of the year. These observations, together with those of the tame warthog, suggest that the pregnant mother has to actively break the bonds between herself and her half grown young if she is to farrow in isolation. That the break between mother and offspring is not always permanent is illustrated by observations of radio tagged females 182 and 145 described in Chapter IV (pages 128 and 133).

## 2. Nursing - suckling period

The period between birth and weaning can be divided into two phases. The first or hole-centred phase during which the young are left in the hole by the mother and a second phase during which the young always accompany the mother away from the hole and which lasts until they are weaned.

### a) Hole-centred phase. (Phase I)

Periods spent out of the hole each day by Susan and her juveniles during the first 50 days after parturition are shown in Fig. 69. Susan was followed when she left the precincts of her hole so that any time spent out of the hole by her juveniles, in

her absence, would not have been recorded. Rosemary's hole(s) was watched from dawn to dusk each day for two months after she farrowed. The times at which she or her juveniles, or both, emerged and entered the hole were recorded. Rosemary's juveniles only once came right out of the hole while she was away and that was for 6 minutes when they were 12 days old. Juveniles have seldom been seen at holes in the field except when the mother is present.

Transition from Phase I to Phase II occurred at 49 days in Susan's litter (Fig. 69) although at 37 days the young accompanied their mother all day and at 55 days they remained in the hole for 30 minutes while Susan was out. Change from Phase I to II was less clearly defined in Rosemary's litter. At 31 and 32 days of age the juveniles accompanied Rosemary all day. They did so again at 40 to 43 days of age but on 7 of the next 11 days they remained in the hole for periods of between 2 and  $4\frac{1}{2}$  hours while Rosemary was out. (Days on which they remained in the hole were 44, 47, 49, 50, 51, 52 and finally 54.) The 54th day after farrowing was the last on which Rosemary's young remained in the hole while she was away and transition from Phase I to Phase II thus occurred at 55 days. Change from Phase II in Susan's litter, at 49 days, was however not so sharply defined when the total time spent out of the hole each day by the juveniles was compared with that spent out of the hole by Susan (Fig. 70a).

Both Rosemary and Susan changed their holes during Phase I. Rosemary did so 7, 11 and 47 days after farrowing and Susan did so at 20, 21 and 22 days after farrowing.

Fradrich (1965) considered young warthog to be largely independent of the hole after the first week. Child et al. (1968), citing Fradrich (1965), state that, after the first week, young warthog spend all day with the mother. Field observations of radio tagged and untagged hogs, suggest that the age at which juveniles begin to spend all day with their mothers is, in the Sengwa Area, about 6 to 7 weeks. Week-old warthog are however quite active and capable of following their mother away from the hole. This is evident from records of both Rosemary and Susan but in neither instance did the juveniles move far; the longest move before the young were 2 weeks old was about 200 metres.

A following response is shown by young warthog by the time they are a week old, if not before. Warthog approximately two weeks old have shown a clear following response to human foster parents. There is however a delay between the initial appearance of the following response and the time when the young always follow the mother. Factors inducing or causing the young to remain in the hole on some occasions but not on others are not known. Gilbert (1967) noted that fallow deer fawns (Dama dama) initiated the return to their hiding places after nursing. The return of young warthog to their holes after nursing outside appears to be initiated by the young and behaviour by the mother which might induce them to return has not been noted. In the event of danger or of a warning grunt from the mother they do rush into the hole (see also escape response, page 183 ) but this is a different issue.

Movement of the mother away from the hole, without the juveniles, tends to occur only when the young are in the hole.

If, during Phase I a following response to the mother while she moves inside the hole is absent (her shape would be different and a silhouette not always present) then some other mechanism would be required to get the young out of the hole as well as to attract them to her while she is in the hole. Young warthog do emerge when called by the mother with a low, soft, sometimes rhythmically repeated, grunt (see also under "Vocalizations", page 142 ). Such a mechanism, "no exit from hole unless called by mother and follow mother without being called when out of the hole when she can be clearly seen", could account for Phase I behaviour. That is, the young do not always accompany the mother when she leaves the hole, but they are able to follow her during this initial phase should the need arise. These are, however, speculations.

Both females changed holes during Phase I (page 179). The reasons for Rosemary's changes are not known. Susan was forced to move when part of Hole 14 collapsed; it was in an erosion-gulley and became flooded. Susan did visit Hole 7 with her young 8 days after parturition and after a night of rain. This was their first major expedition from the hole and at the time I thought Susan was going to move to Hole 7. For some reason it proved unsatisfactory and she returned to the partially waterlogged Hole 14.

Sanitary conditions could induce changes during the initial hole-centred phase. Young warthog were not seen emerging to defaecate at the hole entrance, as Fradrich (1965) recorded, Susan's hole had two entrances and water flowed through the hole on at least three occasions before she moved. Faeces and urine may not have created a problem as they may have done in the holes



used by Rosemary. It is perhaps noteworthy that both females eventually took up residence in Hole 3a, a two entrance erosion-gulley type hole.

Time spent feeding each day by Susan during the first 3 weeks after parturition was markedly less than at any time before parturition. She and Rosemary spent remarkably little time away from the hole during the first week of nursing. Susan's normal daily feeding regime only reached its former level some weeks after farrowing (Fig. 70b and Fig. 47). Time spent feeding (not including suckling) by the juveniles is also shown in Fig. 70b. Susan's juveniles started feeding on solids when 17 days old but much of this time was spent in exploratory nibbling at food items and soil. The young also ate their mother's freshly dropped faeces. The days on which they ate faeces are shown in Fig. 70b. The onset of feeding coincided with the time they started to emerge from the hole fairly regularly. Geophagia could have started well before this while the animals were still in the hole. The early occurrence of coprophagia may be of importance in the development of digestive processes; it coincided with the warthogs' earliest grazing.

Nursing intervals could not be determined while the animals were in the hole. However during the period 3 weeks to 6 weeks after birth it was approximately 40 mins.. Average daily nursing intervals varied considerably but marked changes in the average interval between suckling were not apparent during Phase I.

The reaction of Phase I juveniles to danger or to the mothers alarm call is marked by a characteristic flight pattern which fades

early in Phase II. When suddenly alarmed, young warthog dodge, fall flat, lie motionless and pressed to the ground for one or two seconds and then flee to their hole or other refuge (Fig. 64).

The crouched position may be shown in response to sudden movements e.g. a dog (known to the animals) jumping over them or to a variety of "foreign" noises such as the harsh grating of a badly fitting door or even a door slamming. I have not seen this reaction in relation to predatory birds but since young warthog are occasionally taken by eagles it may well occur in this situation.

Altmann (1963) states that young wild boar dodge and lie motionless in response to a warning grunt from the mother. No information is given on how long the young remain motionless but it would be interesting to know whether the brief crouch followed by oriented flight is peculiar to warthog and perhaps associated with the young seldom being far from their hole at an age when the pattern is present. The pattern fades when the animals are about two months old and its disappearance coincides roughly with the termination of the hole-centred phase.

b) Group integration phase (Phase II)

Phase II begins when the juveniles accompany their mother for the entire day (i.e. at 6 to 7 weeks) and ends when they are weaned. Susan's juveniles were weaned at 21 weeks. Rosemary was still suckling her young when they were orphaned at nearly 13 weeks.

At the onset of Phase II Susan's juveniles were spending less time feeding than she was. Two weeks later, at 9 weeks, the juveniles were feeding for as long as their mother each day (Fig. 70b).

Roth (1965) observed an inflection in the growth curve of hand-reared warthog at about this age despite no change in diet. Child, Roth and Kerr (1968) consider that although lactation may last three to four months milk is not important to juvenile warthog after about 9 weeks. Nursing intervals and the number of suckling periods per day showed no marked change in Susan's juveniles at this age (Table 29). The frequency of nursing remained high for a further two months and only tailed off sharply during the last week of nursing when the young were 21 weeks old. Unfortunately it is not known how the quantity of milk taken by the juveniles changed.

Child et al. may well be right that suckling is not essential after three months; Rosemary's juveniles survived after being orphaned at this age. However, it does not necessarily follow that prolonged nursing is of no importance, either nutritionally or socially. Ewer (1958) has remarked that prolonged nursing may have an important bearing on the formation of mother-young bonds in social species. She also points out that little is known of the development of digestive efficiency in mammals.

Phase II appears to be an important period in the development of social cohesion in the sounder. The extent to which members of a group act in unison has been taken as a measure of group cohesion. Susan and Mackintosh engaged in the same activities for 85% of the time i.e. the two animals were resting, feeding, drinking etc. simultaneously on 85% of the activity records made at 10 minute intervals. During Phase I Susan and her juveniles were engaged in different activities as frequently as they were doing the same thing (Table 30). By the time the juveniles were 12 weeks old

group cohesion amongst the 5 animals had reached the 85% level. Cohesion amongst the four juveniles alone was even more marked and changed from 70% during the first month (December) to 90% during their fourth month (March) (Table 30). Similar data for other species have not been found so it is not possible to state, in comparative terms, how unified a warthog sounder may be in its activities.



## CHAPTER VI.

HOME RANGE BEHAVIOUR.

Only one study of warthog home range is known to me. Fradrich (1965) observed 5 untagged groups of warthog over a period of 3 months in the Nairobi National Park. The animals lived in an open area of the Park approximately  $1 \text{ km}^2$  in size. He found that the home ranges of 4 groups overlapped considerably while the fifth, a solitary adult female, had an exclusive home range. Fradrich did not see conflict between these groups of warthog and neither did he find any signs of marking or other indications of territorial behaviour. Feeding, drinking, wallowing and resting sites were shared in apparent amity. There was some degree of separation at watering points in that a group arriving at a water hole would wait until the group already there had departed before it would go down to the water. Each group of warthog usually slept in its own hole at night and only occasionally slept in another hole. Fradrich did not see warthog sleeping in holes which had been used by other groups of warthog. Fradrich considered seasonal shifts in the home ranges of warthog unlikely.

A number of authors have suggested seasonal movement and dispersal of warthog from dry season concentration areas to out-lying areas at the onset of the rains. Lamprey (1964) postulated a slight wet season dispersal to account for changes in the density of warthog in his transect area in the Tarangire Game Reserve. Bigourdan (1948) records movements away from the Niger River in West Africa at the onset of the rains, a movement apparently

induced by the flooding of the river. Shortridge (1934) considered that extensive movements of warthog occur in South West Africa in response to seasonal changes in the distribution of water. Child (1968), on the other hand, considers that warthog can live for several months without free water and records that they are resident in parts of Botswana where, during the dry season, there was no surface water for 40 miles.

#### A. WILD WARTHOG

##### 1. Size of home range.

The home ranges of radio-tagged hogs have been measured from base maps on which the locations of groups were plotted (Figs. 71 - 74). The perimeter of each home range was determined by joining the outermost sightings of each group. The smallest home range was  $0.62 \text{ km}^2$  and the largest was  $3.3 \text{ km}^2$  (Table 31). Home ranges were however determined at different times and are based on varying amounts of data (Table 31). The method of plotting home range boundaries is extremely arbitrary and unlikely to be an accurate reflection of home range shape and area (Jewell, 1966). The data on home range size are however intended to show only the order of size of warthog home range in the study area.

##### 2. Adherence to home range.

The movement of warthog out of their home area after capture and their subsequent return was shown by (a) Ad. ♂ 175 who moved to the east of the Sengwa River after being captured at Hole A2

and returned to the home range area shown in Fig. 71 5 days later. (b) Ad.♀ 182 also moved eastwards across the Sengwa River after being recaptured at Hole 76a on the 26 June, 1969. She had returned to her previous home area by the 7 July, 1969 (Fig. 73).

Evidence from the recapture of tagged warthog suggests that animals once established in home ranges adhere to them for long periods if not for life. Twenty four warthog older than 12 months when first tagged have been recaptured on one or more occasions providing a total of 30 recaptures (Table 32). All except four animals, which were in the same group, have been recaptured within 800 metres of their original point of capture after periods of between 2 weeks and 38 months. The four exceptions were Ad. ♀ 184 and members of her sounder. They were recaptured after 6 months at Hole 78, 2.35 km from their original point of capture, at Hole 9, but returned after this to their previous home range (Fig. 72). The movements of this sounder were associated with a fire and will be discussed below.

Ad. ♀ 145 (Chapter IV, page 128 Fig. 73) was originally captured in her home range area in September, 1966. She was subsequently recaptured four times within this area and was still there at the end of 1969.

Warthog have, however, been seen as far as 6 km from their point of capture and release (Fig. 75). Ad. ♀ 15 was captured at Hole 23 and seen on the evening of the same day at Hole 30. Two groups of warthog captured in the Lutope Experimental Area during August, 1969, were seen early the following month at points 4.5 and 5 km respectively from their points of release. These animals

were caught during an intensive capture operation and disturbance in the Lutope Experimental Area was considerable. It is not known whether they returned to the vicinity of their capture.

Only two records of movement greater than 6 km have been obtained. A yearling female (Number <sup>31</sup>~~19~~) tagged at Hole 29 in October, 1966 was recovered 14 months later in the neighbouring controlled hunting area. The warthog was shot by an African hunter and the locality reported was approximately 15 km from Hole 29. A yearling male tagged in the Lutope Experimental Area in August, 1969, as a juvenile (Number 196) was shot in the controlled hunting area a year later and approximately 16 km from where it was tagged.

Jewell (1966) notes that the concept of home range implies "a self imposed restriction to movement". The movements of MacSweeny after he had been released some 16 km from his home area at the Gorge contrasted sharply with the limited movements found in radio-tagged hogs. MacSweeny had an established home range about the Sengwa Gorge and on being evicted was faced with a new and unknown area. It was only after two months of wandering (Fig. 75) that he appears to have "settled down" in the vicinity of the Thaba Mance camp. He was unfortunately killed by a lion in September, 1968 and the extent of the area over which he ranged in that month was not determined. He was however sleeping at the Thaba Mance camp on most nights.

These observations suggest that the concept of home range is applicable to warthog. Although capable of moving over large areas, as evidenced by MacSweeny, animals do tend to live within limited



areas for long periods and it is within these rather confined areas that they normally travel in pursuit of their routine activities.

### 3. Home range in relation to food.

Warthog in the Sengwa Area show clear seasonal changes in diet and mode of feeding (Chapter III). During the cold and dry season of the year they subsist primarily on the rhizomes of two species of perennial grasses, Digitaria milanjiana and Tristachya superba. In the wet season they graze on a wide spectrum of grasses but show a preference for short grasses and certain annuals, e.g. Sporobolus marginatus, Chloris virgata, Urochloa trichopus. Transect results suggested that shifts in home range may occur as a result of seasonal changes in food availability (Chapter II).

Home range data do not provide any evidence of marked shifts in home range with change in season. The interdigitation of vegetation types within the study area is such that both wet and dry season forage are readily available within the home ranges of animals so far observed. However an examination of the precise situations in which radio tagged animals have been found feeding supports the general observation that seasonal shifts in feeding grounds occur (Table 33).

### 4. Home range in relation to water.

Surface water is well distributed in the study area and warthog living on the western edge of the Sengwa Experimental Area would, at the peak of the dry season, have to move only between 2.5 and

3.5 km to water. This situation would however only obtain for a period of about one month in a good year and perhaps two to three months after an unusually poor rainy season. No animals living on the extreme western edge of the study area have been tagged so that the possibility of shifts in home range in relation to changing patterns of water availability cannot yet be examined.

The numbers of warthog drinking at the artesian borehole (Fig. 4) show marked seasonal changes. Few animals use this water hole from November through to July but, by mid-September, as many as 100 warthog may visit it in a day. Many of these animals may come from the south-western part of the Sengwa Experimental Area.

#### 5. Effects of fire.

Transect data showed clear changes in warthog density associated with local burning. Evidence is available, from observation of tagged animals, that warthog may move or shift their home ranges temporarily to take advantage of the flush of green grass which follows a dry season burn.

In September, 1969 the southern part of the Sengwa Experimental Area burned for the first time in five years. The burn was almost entirely confined to the Brachystegia woodland where, in previous seasons, warthog were seldom seen. By the end of September, 1969 and a fortnight after the fire, there was a very noticeable increase in the numbers of warthog seen along the road from the southern game fence to the artesian borehole. Ad. ♀ 184, Ad. ♀ 171 and Ad. ♂ 189 moved south into this burnt area and the vicinity of the

artesian borehole. Ad. ♀ 232 was, during November, moving from holes near the Sengwa River to the burnt area daily. These animals did not, so far as is known, frequent the burnt area after December.

6. Home range in relation to holes.

The following aspects of warthog behaviour in relation to holes have already been established in Chapter III,

- i. Warthog use a number of holes and do not use the same hole for long periods.
- ii. There are many more holes available to warthog in the area than are used by them on any one night.
- iii. Very few holes are in continuous use for long periods of time and the highest use index obtained was approximately 70%.
- iv. More than one sounder may use a hole but they seldom, if ever, do so on the same night. If this does occur the hole is generally a large and complex one and the two sounders using it may sleep in different parts of the hole.
- v. Conflict between sounders has been observed at holes (Chapter V).
- vi. Adult male warthog may not always sleep in holes at night.

Radio-tagged animals have been contacted in the late afternoon (peak feeding time) and followed to their holes or they have been located feeding and then located again later, once they have entered their holes. These observations show that warthog may move from one end of their home range to another in order to enter a hole. They do not necessarily enter the hole nearest the point at which they may be feeding in the late afternoon and may even pass by holes



which they have used on other occasions.

The factors determining a warthog's choice of hole on any particular day are not known. Their behaviour between the end of intensive feeding and entering a hole suggests they may "decide" well in advance where they are going to sleep. The demeanour of a warthog heading for its hole is very different from that of an animal moving between feeding areas or going to water. Susan, in February, 1970, provided a very clear illustration of an "intention to sleep in a particular hole". The artificial hole in the warthog pen in the Sengwa camp had fallen into disuse and early in February it was opened, cleaned, sprayed with insecticide to destroy an infestation of fowl mites and re-roofed. Shortly after this Susan inspected the hole during the day and she and her juveniles slept in the hole that night. The pen was then used to hold a bushbuck and access to the hole was closed. After not having used the hole for some nights Susan arrived one evening and tried to force her way into the pen, even digging near the hole entrance. She was chased off and went to Hole 9 which is approximately 80 m from the pen. After a few minutes in Hole 9 she emerged and again tried to force her way into the pen before finally retiring to Hole 3. The behaviour of going to a particular hole rather than trying the nearest hole available would presuppose a freehold on particular holes by a sounder or by a few sounders.

#### 7. Patterns of hole use and home range groupings.

The holes used by tagged individuals and sounders have been examined to see which holes were shared and by which groups. The



data suggested a "clan" system of hole use and home range groupings may obtain amongst warthog occupying the Sengwa Experimental Area. A clan is defined here simply as being composed of at least two, but generally more, sounders which share a number of holes and whose home ranges are more or less co-extensive. .

Clans were initially delineated by arranging holes in groups according to area and from my general impressions of the pattern of hole use. Individual hogs or sounders were then assigned to a clan on the basis of the hole at which they were first captured. The clans were then "tested" by plotting the holes which tagged groups subsequently used and home range data was superimposed on this. The data are summarised in Table 34 which shows the holes at which hogs were initially captured and those they subsequently used. Holes shared within and between each of the four clans recognised are shown in Fig. 76 and the points at which radio tagged matriarchal sounders have been seen are shown in Fig. 77. Initial groupings, chosen on the basis of area, were A, A-B, B, B-C, C, C-D and D. These six preliminary groups were then reduced to four (A, B, C and D) and further animals were captured and radio-tagged in an effort to break down the hypothesis.

The data for hole use cover 42 months, 36 sounders (116 tagged animals) and a total of 343 observations of tagged animals using holes. Remarkably few holes have been shared between clans: 7 as opposed to 23 within clan areas (Fig. 76). Home ranges of radio tagged matriarchal sounders within each clan show a similar pattern in their degree of overlap (Fig. 77). Sounders within a clan tended to show more <sup>or less</sup> <sub>^</sub> co-extensive <sup>x</sup> home ranges which overlapped

very little with those from neighbouring clans. For example in Clan C (Fig. 77) the home range of Ad. ♀ 182 lies almost entirely within that of Ad. ♀ 145 but there is little overlap between these home ranges and those of Ad. ♀♀ 104, 158, 171 and 184, all of which again show considerable overlap and constitute Clan B. Boundaries between clans were drawn where least overlap occurred and where holes were shared, and serve merely as guide lines rather than as clearly defined and identifiable boundaries in the field.

Once the initial pattern had emerged I attempted to radio-tag sounders which might be living on the boundaries of clan areas in an attempt to disrupt the pattern which had been observed. Four artificial holes (A3 to A6, Fig. 76 and 35) were also constructed on what were then considered to be clan boundaries. Ad. ♀ 104 was captured at Artificial Hole A3, Ad. ♀ 240 was captured at Artificial Hole A4 and Ad. ♀ 110 was captured at Hole 38 on the boundary between Clan C and D.

The home range and holes used by Ad. ♀ 104, whose identity was unknown until she was captured at Hole A3 (former boundary between Clan A and Clan B), fitted more closely with those of Ad. ♀♀ 158, 171 and 184 (Figs. 72 and 7<sup>7</sup><sub>6</sub>) than the previously delineated Clan A. The home ranges of Ad. ♀♀ 232 and 239 (Clan A, Figs. 74 and 77) also indicated that the boundary between Clan areas A and B was in the vicinity of Artificial Hole A1 rather than A3 and A4 (Fig. 76). The two matriarchal sounders caught in Clan A, Ad. ♀♀ 232 and 239, subsequently joined to form a single sounder after both had lost their litters and some two months after they had been tagged.

Ad. ♀ 240, captured at Artificial Hole A4 on the boundary between B and C did not completely come within the Clan B or Clan C areas. Her home range during the first month after capture was split and both of the areas she frequented (Fig. 73) were near the boundaries of Clan C. She moved back and forth between these two areas three times before taking up more permanent residence in the southern sector of her home range, near the area in which she had been captured (Fig. 73). She was a young adult female who had not been caught before and it is possible that construction of two artificial holes, A5 and A6, gave her a foothold in the area between Clan B and C which was previously devoid of good holes. Unlike the data from Ad. ♀♀ 104, 232 and 239, those from 240 suggest that home ranges of warthog may be a continuum of overlapping home ranges rather than a series of clans within the Sengwa Experimental Area. Ad. ♀ 240 was accompanied by two sub-adult females (156 and 157) originally caught in Clan B area at Hole 7 in October, 1968. The mother of these two animals was injured in capture and had to be destroyed, leaving them orphaned. This suggests that Ad. ♀ 240 had affiliations with Clan B. The two sub-adult females had however left her by mid-January, 1970 and since there were no further records of their movements it is not known whether or not they returned to Clan B.

The data from Clan D are inadequate but Ad. ♀ 110 has not been recorded in Clan C area since she was tagged in October, 1969. She was caught at Hole 21 within the Clan C area two years earlier but was then in the company of an Ad. ♂ and a second Ad. ♀ who was in oestrus.

A further sounder was tagged within the Clan C area in December, 1969. One of the animals was Ad. ♀ 178, known to be a Clan C hog who had been tagged with a plastic collar 7 months earlier. She was accompanied by Ad. ♀ 179 (who was with her when previously caught) and Ad. ♀ 241 who had been tagged in the Clan C area in October, 1966 but she had lost her ear tags and was either warthog number 30 or number 32. The home range of this sounder was small during December, 1969 to February 1970 and situated in the north eastern corner of Clan C area; it did not overlap with the home ranges of Ad. ♀ 182. Ad. ♀ 145 was still in the area at this time but her radio collar was not transmitting.

Therefore, although data from the 8 additional warthog tagged at the end of 1969 provided support for the existence of clans in the Sengwa Experimental Area the evidence was not unequivocal.

The home ranges of adult males and their use of holes does not fit the clans derived from matriarchal sounders very clearly. Earlier evidence (page 105) suggested that fully mature males were more independent of holes than matriarchal sounders and for this reason they may be only loosely attached to clan groupings.

Information on adult males is meagre. Ad. ♂ 161 on whom most home range data are available fits into Clan B quite satisfactorily (Fig. 78). Of the two adult males caught in Clan C holes (Ad. ♂♂ 11 and 42) there is only one clear record of entry into another hole and this was when Ad. ♂ 42 was captured at Hole 21 in the Clan C area. One adult male, Ad. ♂ 2, was captured in a Clan D hole but there are no further records of him entering holes. Shortly after capture he was however seen in the Clan C area but this may have



been temporary displacement. Ad. ♂ 41<sup>a</sup> was captured at Hole 22 (Clan D hole) as a sub-adult of about 28 months in February, 1967. He was seen once again in 1967 in Clan D area. During 1969 (by which time he had lost his collar but was identified by distinctive ear notches resulting from metal tags) he was seen at the main holes in Clan C area and also consorted with two radio-tagged females in Clan C (Ad. ♀♀ 145 and 183, see also pages 128 and 133).

The three adult males radio-tagged during 1969 were all captured at Artificial Hole A2 (Fig. 76 & 78). This hole was built in November 1968 and although within the Clan C area its status is not clear.

(i) Ad. ♂ 175 was captured at Hole A2 - 3 (Artificial Holes A1 and A2 each comprised three holes spaced about 15 m apart; page 95 and Fig. 40a) on 25 March, 1969 and was tracked until 20 April, 1969 when he was killed by a lion. There are no records of him entering holes and his observed home range was entirely within the Clan C area.

(ii) Ad. ♂ 176 was captured at Hole A2 - 1 on 20 April, 1969 together with Yr. ♂ 177. The animals separated after capture. Ad. ♂ 176 was tracked until early June when his transmitter failed. He was recorded entering two Clan C holes, 20 and 42, in May, and June respectively. He was also recorded entering Hole 8d in Clan B area (Fig. 71) where he was seen with an adult female on three consecutive nights. His identification was not however positive.

(iii) Ad. ♂ 189 was captured at Hole A2 - 3 on 13 June, 1969 and was tracked until the end of June. From the few contacts made during June his home range appeared to be on the boundary of Clan

B and C. He was subsequently seen in September, 1969, at the artesian borehole (Fig. 4) and in December to the north of Clan C area (Fig. 78). At the time he was captured each of the three holes comprising artificial Hole A2 were being used by male warthog and conflict between them was recorded.

The information for Ad. ♂ 161 was obtained mainly during the dry season while that on Ad. ♂♂ 175, 176 and 189 was obtained just before and during the mating season. The mating season may result in considerable disruption or reshuffling of male home ranges and this may account for the home range of Ad. ♂ 161 fitting into the clans while the data for the other three radio-tagged males is unclear.

#### 8. Movements of sounders with overlapping home ranges.

Attempts during 1969 to obtain simultaneous records of the movements of a few sounders whose home ranges overlapped were thwarted by short transmitter life and a lack of antennas which would allow accurate radio fixes to be obtained at frequent intervals throughout the day. However, the limited data which <sup>are</sup> ~~is~~ available from the use of portable tracking stations (page 26 and Fig. 9) ~~does~~ indicate that sounders whose home ranges overlap may retain a space/time separation so that direct contact is infrequent. A typical example of radio fixes obtained on three groups within a home range group during an afternoon and the following morning is shown in Fig. 79. The areas covered by the three groups did not overlap during the tracking period.

When homing in on radio-tagged animals, I often tuned in to

other tagged animals in the vicinity or moved from one contacted group to the next. Contact between sounders was seldom seen and they were very seldom found within a 100 m of each other.

B. TAME FREE-RANGING WARTHOG.

Home ranges of tame warthog during late 1968 and early 1969 were determined by mapping points which they were known to have visited (Fig. 80). The observations show that after Rosemary (who farrowed at the end of September 1968) parted from Susan and MacDuff the two yearling animals did not move away from their earlier home range and remained within that of Rosemary and her juveniles.

Detailed home range data for Susan and Mackintosh from May to November 1969, for Susan and her litter from 21 November 1969 until June, 1970 and some data for Mackintosh during January to March, 1970, were obtained while recording daily patterns of activities. Localities, to the nearest 25 x 25 yard square, were recorded every ten minutes during the day for periods of 12 to 30 (or 31) days each month (Table 2).

Home range size in the tame animals was generally smaller but within the range of home-range size recorded for wild animals (Table 31). Home range data for Susan and Mackintosh from May to November are summarised in Fig. 8. The time spent in different parts of the home range differed considerably. Some 42% of their time was spent in only 5 % of the home range area. This area comprised the camp, the cook's village and the main village. It is not surprising that these were favourite areas for they were places

of safety with good shade, water and near the author's house where they received some food each day. Records of feeding do however show that little time was spent scavenging for scraps and the animals did graze and root about these centres of activity. Their main feeding areas were, however, away from the immediate vicinity of the camp and villages. Their behaviour, despite the great concentration of time spent about human dwellings does show certain features recorded for many other mammals, viz. core areas, shifts in home range boundary and a certain area, larger than the core areas, which was common ground throughout the five month period (Fig. 82).

Susan's home range was markedly smaller during the week before she farrowed than during the previous five months (Fig. 82 & 83). Changes in her home range during nursing are shown in Fig. 83. The gradual expansion of this with decreasing dependence of her juveniles on their hole is apparent. Mackintosh, who became solitary after Susan farrowed, extended his home range and although he still moved over much of the home range occupied by Susan (Fig. 83) his centres of activity differed from hers. He avoided the immediate vicinity of her hole and the two sounders seldom met. MacDuff and Susan also showed similar shifts once they became separated from Rosemary. MacDuff moved further afield near the mating season of 1968. He was seen in the Sengwa Experimental Area, 7 km from the Gorge, a year later. Mackintosh also moved further afield during the mating season but full data on his movements could not be obtained because he repeatedly eluded his observers. He was seen about 2 km west of the Gorge in October, 1970 in the company of Rosemary's juvenile male.



Tame female warthog have shown little inclination to move away from the Gorge and their rather limited home range areas. Susan did occasionally make brief (a few hours) exploratory trips out of the home range areas shown in Fig. 83. During June 1970 and before she was courted for the second time she moved about 700 m north of the area mapped in Fig. 83 but returned to her normal home range the same day. Rosemary's juvenile female at 2 years had farrowed and was still living in the vicinity of the Gorge during October, 1970. She occupied the hole (Hole 3a) in which she had lived for most of her first 3 months.

Thus although the tame warthog home range data must be treated with a certain amount of caution, it does indicate that warthog are likely to have core areas within their home ranges. They are unlikely to be as marked in wild animals as they were in the tame animals. The data also show that boundaries are likely to be shifting rather than fixed and that home ranges are not "patrolled" in any set manner. Persistence of tame females within their ranges conforms with data obtained from wild animals. Information on the home range behaviour of wild males is meagre but the behaviour of tame male warthog suggests that it is the males that are the dispersive element of the population.

C H A P T E R 7.DISCUSSIONA. GENERAL.

Advances in any branch of science are governed not only by its conceptual framework but also by the techniques which can be applied to gather relevant information. This study covers a broad field and a variety of techniques have<sup>s</sup> been employed. Distribution and abundance have been studied by the use of permanent transects; population structure has been examined from field classifications; movements and home range behaviour have been studied by tagging warthog and using radio-tracking techniques. Hand-reared free-ranging animals have been used to provide information on a variety of aspects of warthog biology.

Transects such as those used here have been used by Lamprey (1963 and 1964) and by Jarman (1968) both of whom were studying ecological problems relating to a wide variety of game animals. The transect system at Sengwa was also used in a wider ecological study of game-tsetse relationships although only those results appertaining to warthog have been presented here. High expenditure in effort and staff which the transects demand (Table 3) would not have been justified in a single species study. The wooded savanna areas of Africa present considerable problems in sampling game populations; aerial counts are satisfactory only for the largest mammals. During 1965, road strip counts (Dasmann and Mossman, 1962) and adaptations of this technique were also used but the results were highly variable and would have entailed just as great a sampling

effort as has been expended on the transect system. Attempts to evaluate game populations by recording spoor on swept paths were not successful although distribution of spoor activity on transects provided useful data which confirmed, in most instances, the distribution pattern shown by sightings. Major problems in recording spoor were very high recorder variability and the fact that estimates of numbers of animals crossing the transects and numbers of sectors which had been crossed (inhabited) could not be related to animal number. At best the data provided only an index of relative abundance with respect to place and time; the technique may have applications where game populations are highly disturbed and animals seldom seen. Variations in soil type and the distribution of game paths also influence the results. The transects themselves did not become game paths except occasionally for elephant.

During three months in 1965 the entire boundary of the Sengwa Research Area was patrolled every 48 hours and spoor crossings of all animals moving in and out of the area were recorded in an attempt to discover whether any substantial game movements were occurring from the neighbouring hunting areas. The records were highly variable and only very large-scale movements could have been adduced from the data (no trends were, for example, apparent in elephant and buffalo crossings, much less for species such as kudu and warthog).

High day to day and month to month variability for densities calculated from sightings along transects emphasizes the crudity of such field techniques and the need for large numbers of frequently patrolled transects to provide useful information.

The use of field age and sex classifications to provide

information on population structure has already been discussed in Chapter II, section C. The technique is limited largely to species which exhibit marked seasonal breeding. In long term field studies the technique has the advantage of not disturbing the population by removal of animals such as is usually necessary for accurate aging from skeletal material. Attempts to derive life tables from age ratios (Caughley, 1967) or from skulls recovered in the area have not yet been made. Aging criteria for warthog up to 48 months have been developed (Child, Sowls and Mitchell, 1965) but none appear to have been derived for older animals.

Radio-tracking is a recent technique and apart from Harthoorn et al. (1970) who telemetered body temperatures from partially confined animals, results obtained by using this technique on African mammals have not yet been published. Press reports indicate that it is now being widely used in Africa. It is a powerful technique which, when used in conjunction with telemetred physiological data from feral animals, has considerable possibilities for furthering our understanding of the relationships between large mammals and their environment. This study shows that, despite Hanks' (1969) pessimism, radio tracking can be used effectively in remote areas to yield biologically valuable information. Even within the framework of the comparatively unsophisticated equipment I have used, radio-tracking offers the prospect of a more rigorous statement of habitat preferences than can be obtained from transect sampling techniques. Long-term monitoring of individuals on a carefully designed sampling programme can provide data on the duration for which animals occupy different habitats. Remote telemetering of position, combined with



direct observation of tagged animals can provide information on how animals are using the different habitats and micro-habitats within the areas they occupy. The level of sophistication of equipment need not be high. The technique is a particularly valuable one for the wooded savanna areas where it is otherwise difficult to keep track of particular animals for long and it may provide more direct information than transect sampling techniques. The use of the technique in obtaining more reliable information on home ranges than can be obtained by conventional tags has already been discussed (page 25).

Tame hand-reared~~d~~ animals have been extensively used in ethological studies but seldom in ecological work and Field (1968<sup>a</sup>) describes their use in feeding studies of large African ungulates. Animals used in this study were not confined during the day after 3 - 4 weeks and seldom ever at night after the age of c. 7 months. They were reared in groups and since they established home ranges in the vicinity of the Research Station animals of different ages were available for observation. Tame animals have consequently been used to provide information on a wide variety of topics; much of this information was, under the conditions at Sengwa, otherwise unobtainable. This study shows the value of such animals as a complementary source of data for ecological and behavioural field studies. There is no doubt that some aspects of their behaviour were influenced by the conditions in which they lived. Where this has appeared to be the case I have said so. Comparison between information from tame and feral animals, where it was possible, revealed a high degree of similarity and I consider their use, in

the absence of similar information from wild animals, to be justified and, indeed, illuminating. Of major importance is the close contact one can establish with tame, free-ranging animals and the added insight this can give to the way in which they live. Tame animals provide guide lines and reveal questions which can subsequently be investigated in the field.

#### B. DENSITY, DISTRIBUTION AND HABITAT REQUIREMENTS.

A full understanding of warthog habitat requirements requires detailed information on the way in which the animals live in a variety of environments and particularly in marginal areas where limiting factors might be more clearly defined. The Sengwa Area is favourable warthog habitat and densities recorded in optimal habitats are nearly as high as any reported from elsewhere. Published data on warthog density are summarised in Table 35. Although the data in Table 35 are not strictly comparable, a variety of techniques having been used, they do indicate that a density of c. 15 warthog per  $\text{km}^2$  is high. The highest mean seasonal density recorded in the Sengwa Research Area was 12.3 warthog/ $\text{km}^2$  in vleis areas in C.mopane woodland. Local seasonal densities of as high as 37 warthog/ $\text{km}^2$  were however recorded and in some habitats, in some seasons, no warthog were seen.

Although this study has been confined to a single area it throws some light on warthog distribution and habitat requirements. The transect data confirm the general statements of earlier authors (page 35) that warthog inhabit lightly wooded areas and tend to avoid dense woodland and thickets. An examination of density in relation

to finer divisions of vegetation structure fails to reveal any clear correlation between physiognomy and warthog density. The more important factor appears to be the extent to which the vegetation is uniform or broken and variable. Thus large tracts (5 or more  $\text{km}^2$ ) of uniform habitat such as the Sengwa flood plain <sup>g</sup>Grassland, flat areas of Brachystegia woodland not dissected by drainages, large deciduous thickets and the Baikiaea woodland habitat, with its understorey of Baphia, exhibit low warthog densities. Those habitats <sup>flat or</sup>very variable in physiognomy, such as Acacia communities on alluvial soils, C.mopane areas well dissected with drainages and vleis and the complex of C.mopane-Combretum-Tristachya W.B.G. between the Sengwa and Lutope Rivers (Fig. 4 and Appendix <sup>1</sup>Fig. 1) carry high densities.

In viewing distribution in relation to habitat it is easy to divide the vegetation into blocks which seem, to our eyes, to be essentially reasonable. There is however no reason why a warthog (or any large mammal) should view his domain in the same way. Possibly more important, although more difficult, to analyse is the disposition of habitats and micro-habitats within the compass of the individual's range. It may be that for this reason that, although a rather general picture of density in relation to habitat, such as I have drawn in Fig. 16 and on page 41, can be recognised, it breaks down when examined too closely. This point is well illustrated by an examination of the variations in density within C.mopane woodland habitat (page 44). This perhaps is to be expected from the results of broad survey techniques and shows, on the one hand, their advantage in providing a general overall view and, on the other hand, their

limitations in not providing a clear view of more specific habitat requirements. It is to the behaviour of individuals that one must turn for the latter.

Observations that warthog are selective grazers (Ewer, 1958) have been confirmed. The animals show a preference for grazing on short pastures to which their height, snout length and habit of frequently kneeling when grazing (callosities on their carpals are evident in the foetus) seem admirably adapted. They do however crop taller grass up to a height of about 50 cms. No quantitative observations of the feeding efficiency or feeding rate in relation to sward structure have however been made. Arnold (1964) provides evidence that feeding efficiency in sheep may vary with grassland structure and it is to be expected that animals are adapted anatomically and behaviourally to deal with particular types of vegetation. Departures from the vegetation for which it is most suited, both in terms of structure and species composition, may result in a drop in feeding efficiency.

Despite a specialized mode of grazing warthog are able to feed efficiently in two other major ways. In the Sengwa Area they feed extensively on the inflorescences of certain grasses when these are towards the end of the rains and then turn their attention to rooting for rhizomes of perennial grasses on which they feed almost exclusively for 6 months of the year. A reconsideration of Ewer's (1958) examination of their cranial anatomy reveals that, despite specializations for grazing, warthog have retained the suid propensity to dig efficiently with their rhinarium. In hard dry soils they were seen to be more efficient at uncovering rhizomes than was a bushpig.



It thus seems unlikely that rooting by warthog is an emergency mechanism and Child's (1968) view that they are using the most nutritive food available to them during the dry season may well be correct. No information is however available on the nutritive value of rhizomes used by warthog. The rhizomes they utilize are denied to other large herbivores which lack appropriate anatomical specializations. Warthog in the Sengwa Research Area have been found rooting for Tristachya superba and Digitaria milanjiana before the end of the rains and while green fodder is still available; rhizomes may be more nutritious for warthog than the green fodder which the animals can find at the end of the rains and during the dry season. Neither tame nor wild warthog sought out green grass near rivers during the dry season. Warthog continued to root even when green grass following dry season burns was available and despite making extensive use of post-burning flushes when these occurred.

The feeding behaviour, anatomical adaptations and food preferences of warthog in the Sengwa Area suggest two main habitat requirements: (a) short grass pastures of palatable species (it seems these must be green rather than dry as little or no use of dry fodder has been noted in the Sengwa Area and no clear references were found in the literature to their grazing dry grass), (b) perennial grassland containing suitable rhizomes. In the Sengwa Area these are medium height grasslands about a metre high.

In the two high density habitats (Fig. 16), C.mopane vlei (including the vlei edge) and Acacia communities on alluvial soils, both requirements are met throughout the year. In C.mopane-Combretum-Tristachya W.B.G. habitat large quantities of rhizomes are available during the dry season but the grassland does not provide suitable

food during the wet season. Wet season requirements are found in the surrounding and adjacent C.mopane woodland areas (Fig. 4). In addition, consistent seasonal changes in habitat density were demonstrated by the transect data from this area (Fig. 18). Home ranges of animals living in this area were about 1 km<sup>2</sup> in extent and incorporated both wet season (C.mopane woodland) and dry season (C.mopane-Combretum-Tristachya) food requirements. Here the influence of vegetation mosaics on density is most clearly apparent for neither habitat on its own would support as high a density throughout the year.

Observations of home range behaviour indicate a strong attachment to particular sites. Fradrich (1965) also considered warthog to be very local and not to move seasonally. There are reports in the literature (Shortridge, 1934; Bigourdan, 1948) of warthog moving seasonally to take advantage of differences in water and (presumably) food distribution. Child (1968) however reports that warthog remain all year in certain areas despite a lack of water in the dry season. There is some evidence of very local shifts (page 191) of home range in the Sengwa Area in response to flushes of green grass following dry season grass fires. Extensive movements of warthog have not yet been critically established by tagging animals and results of this work, together with that of Fradrich (1965) and Child (1968), suggest that a year-round attachment to particular areas is more likely, particularly in female warthog. Such attachments would, in part, explain the failure of warthog to use and invade large areas of uniform vegetation which provide favourable conditions for only part of the year, e.g. Brachystegia woodland, where holes occur and

rhizomes of Tristachya are abundant but little used.

The question arises as to why warthog should be very localised in their movements, failing to move long, or even moderately long, distances between habitats providing wet season food requirements on the one hand and dry season requirements on the other. The answer may lie in their dependence on holes both for refuge from low temperature at night (Sowls and Phelps, 1966) and as a refuge from predators. Predation may provide a sufficiently great selection pressure to make it important for warthog to know the precise location of holes within their ranges and, perhaps more important, to have particular refuges which are almost always open to them. Soils which make for durable holes may thus be important; in sandveld areas of the Sengwa Research Area holes, although numerous, tend to be less durable and therefore necessitate more frequent inspection. There are limits to the area with which an animal can become thoroughly and confidently familiar. A balance must be struck between metabolic requirements and the area over which an animal can move with surety and familiarity. For a herbivore a smaller, very thoroughly known area may be more efficiently exploited than a larger, less well known area, both in terms of individual well-being and in terms of survival.

Earlier evidence (page 90) indicated that holes per se did not influence warthog distribution in the Sengwa Research Area but that particular types of hole were important (page 96). Large erosion type holes were most important and their distribution was associated with drainage patterns and soils which also provided favourable feeding conditions for warthog (page 100). Thus

environmental effects on density are seen as being an interaction between spatial disposition of contrasting food requirements and the limitation placed on movement by the need for particular types of hole and the need to know both where all the refuges are and which of them are open and available for use in emergencies at any particular time. It is to be expected that social influences will also play a role in modifying distribution and density patterns in relation to particular environmental features. This problem is taken up in the next section.

The above views suggest that holes, and warthogs' dependence on them, may play an even more definite role in governing warthog distribution than does food. Apart from the need to know which factors govern a warthog's choice of hole we need to understand why, in the first place, warthogs, as large herbivores, have taken to living in holes. Sowls and Phelps (1966) have shown that body temperatures in young warthog may differ by as much as  $3.9^{\circ}\text{C}$ . between early morning, when it is lowest, and late afternoon, when it is highest. Temperature fluctuation in young bushpig under similar conditions was less than  $1.1^{\circ}\text{C}$ . Young warthog are known to die when not provided with additional warmth at night and animals as old as 8 months may die on cold nights when denied access to suitable holes (page 105). These observations do not however explain why body temperature in warthog should vary so greatly and why, if it is due to their lack of a dense hairy coat as Sowls and Phelps suggest, warthog should be comparatively bare skinned. I suggested earlier that warthog cranial anatomy reflected adaptations to feeding in seasonally dry and arid habitats - areas which are also



characterised by marked diurnal fluctuation in temperature. It seems possible that lack of thermal stability might be an adaptation to such conditions if its primary function is one of water conservation. A possible solution to the problem of water conservation could be to forego strict physiological regulation of body temperature and consequent water loss at high and low temperatures and place a greater reliance on behavioural means of thermoregulation. Warthog show marked sensitivity to ambient temperature (Chapter III, section C) ~~§~~ and behaviour such as resting in the shade and wallowing when day temperatures are high, basking and huddling together when day temperatures are low, and sleeping in holes at night most probably serve a thermo-regulatory function. Such a function has still to be critically established.

The speculative nature of these considerations serves to direct attention to the need for information on three inter-related physiological problems, water metabolism, nutrition and thermoregulation, the resolution of which are required before we can fully understand the relationships between warthog and their environment.

#### C. SOCIAL STRUCTURE AND DISPERSION.

In summary the social structure of warthog in the Sengwa Area is characterised by three main types of sounder : matriarchal sounders, bachelor groups and solitary adult males. Spinster groups occurred but were infrequent and are considered to be a form of matriarchal sounder. Hetero-sexual (sub mature) sounders and solitary adult females were transient social phases associated with

disruption of the family unit during the farrowing season. The most durable social bonds seem to be those between females. Matriarchal sounders when composed of more than a female and her immediate offspring are probably extended families or kinship groups.

Social structure shows some seasonal changes which are probably a consequence of seasonal breeding. Field observations of tagged groups show that males do not form stable pairs with females during the rutting season and that mating is polygamous or promiscuous. During the rut males remain with a matriarchal sounder only during the time females are in oestrus although at other times of the year they may join them briefly. Pregnant females drive off their young of the previous breeding<sup>season</sup> before they farrow; these young animals generally form transient hetero-sexual sounders which may later rejoin them but they do not always do so. Instances of females, together with their young, joining to form large familial sounders of 8 to 16 warthog have been recorded. Large sounders tend to fragment during the dry season and before and during the farrowing season. Attachment of young males to matriarchal sounders wanes after about 18 months and males form bachelor groups although some may remain attached to matriarchal sounders, even if only loosely, until they are c. 30 months old.

Warthog are altricial and the young do not regularly accompany the mother when she leaves the hole until they are about 6 weeks old. Home ranges of nursing mothers are correspondingly reduced at this stage. Group integration (cohesion) is well advanced before the young are weaned and lactation may be prolonged beyond the point at which it is essential to the nutritive well-being of the young. Sounders

comprising mother and young form a closely integrated social unit until the following farrowing season.

Group structure of warthog in the Sengwa Area appears to be very similar to that described by Gundlach (1968) for Sus scrofa. Fradrich (1965) considered adult males to be part of the family unit in warthog and this condition may obtain in parts of the animals' range where breeding is less seasonally distinct. Bigourdan (1948) however noted bachelor groups in a warthog population where a single annual breeding season was not evident and further information of warthog group structure is required from other parts of its range.

Home range observations showed that females may adhere to particular areas for long periods, if not for life. Information on males, although meagre, suggested that they may move more widely than females. Home ranges were found to overlap considerably and territoriality (in the sense of exclusive possession and defense of parts of the home range) was not apparent. Core areas were evident in tame free-ranging warthog but observations of feral animals were not sufficiently detailed to show whether core areas exist under completely natural conditions. There is little doubt that the concept of home range as it normally applies to mammals (Jewell, 1966) is applicable to warthog. Stoddart (1970) refers to an animals "range" and considers reference to "home" to have little meaning since it is difficult to define and apply in the field. Stoddart follows Dunnet's (1956) definition of an individual's range as "that area occupied and traversed by an established individual in the course of its normal activities. The individual must be established in the sense that it is no longer transient, but has settled down more or

less permanently in a local population". Jewell (1966) defines home range as "the area over which an animal normally travels in pursuit of its routine activities." The qualification of "range" by "home" seems to adequately cover Dunnet's rider that the individual must be established as part of a local population. Jewell draws attention to the need to qualify home ranges in terms of time: this has not been attempted in the present study because data are <sup>as</sup> yet too fragmentary. The information so far available on warthog home range behaviour does not justify any extension of the rather broad concept of home range as defined by Jewell (1966). Of greater interest is the possibility of "clans" existing in the Sengwa warthog population.

#### 1. Clan system of hole use and home range groupings.

Patterns of hole use by tagged animals and the home ranges of matriarchal sounders suggested that warthog in the Sengwa Experimental Area may be organised into clans or home range groups (Figs. 76 and 77 and Table 34). Hunter (1964) described the formation of home range groups within a flock of sheep restricted to a 350 acre pasture. Home range groups were composed of groups of related sheep which restricted their movements to different parts of the pasture. Four home range groups within the pasture were readily distinguished and numbered between 20 and 52 sheep. Grubb and Jewell (1966) described home range groups in feral sheep living on Soay Island. Laws (1970) recognised discrete unit populations of elephant in East Africa which number between 2000 and 8000 animals. He has also shown that the basic social unit in elephant is a small matriarchal group of about 6 animals. Laws (1970) further postulates the



the occurrence of clans (an intermediate population unit between the family group and discrete population units) comprising 200 to 500 animals and which he recognised on the basis of spatial distributions within populations.

Sengwa warthog, in common with sheep and elephant, show a predominantly matriarchal family unit with males being solitary or forming bachelor groups. Home range observations of tame free-ranging animals suggested that younger animals, after leaving their mother (or being driven off by her), may form home ranges which are more or less co-extensive with their former range and that of their mother (Fig. 83). Sub-division of matriarchal sounders such as between a sow and her maturing or mature female off-spring, could result in a pattern of co-extensive home ranges such as were observed in the Sengwa Experimental Area (Fig. 77).

The answer to the crucial question of whether or not clans are a social reality rests on the type of interactions that may occur between groups within clan areas and between groups from neighbouring clan areas.

a). Social and group interactions.

Interactions between clans. No encounters between known individuals or sounders from adjacent clans have been observed. One clear example of conflict at a hole occurred when Ad. ♀ 15 (Clan D and captured at Hole 23; Fig. 75) was seen, the evening after being tagged, trying to enter Hole 30 (Clan A) but an adult female already occupying the hole emerged and chased her away. A month later Ad. ♀ 15 was back in Clan D area and using Hole 27b some 300 m from the hole at which

she was initially captured. Although such an encounter could occur between animals living within the same Clan area, Hole 30 was a large hole and discrete sounders from the same clan have on other occasions been observed using the same hole on the same night. However, as was mentioned earlier (page 98) it has not been possible to establish whether on such occasions the sounders slept in the same part of the hole or not.

Circumstantial evidence for the existence of clans may be adduced from the behaviour of animals disturbed by capture. Many newly tagged animals have moved out of the defined clan areas but have shortly returned to the vicinity of their capture. No clear examples of mature animals permanently moving their home ranges after tagging have been recorded although there are two records of long range movements by immature animals into the neighbouring depopulated hunting areas (Fig. 75). Apart from one record of a sub-adult male (S.Ad. ♂ 220, Fig. 75) being seen in Clan D area a month after capture there are no records of movement between the Lutope and Sengwa Experimental Areas even though over 100 animals have been tagged in each area. The centres of the two Experimental Areas are some 5 km apart. Although of a largely negative nature the above evidence lends further support to the hypothesis that fairly discrete population units occur within the Sengwa Area.

Interactions within clans. Mature females and their young have been observed to join together to form large familial groups (Chapter IV) which persist through the wet season and fragment between the mating season and the following farrowing season. Interchange of young individuals between one matriarchal sounder and another or between

matriarchal sounders and bachelor groups has only been recorded three times. Two of the changes occurred within clan areas while in the third two orphaned females apparently temporarily joined an adult female whose status was not clearly established (Ad. ♀ 240, page 196).

Simultaneous records of movements within a clan area indicated that at any one time animals are probably well spaced within their respective clan areas. Meetings between tagged groups (except between males and matriarchal sounders during the rut) have not been seen while homing in on tagged groups or while following them. Tagged animals have occasionally been found within 100 m of each other and unmarked sounders have been seen in close proximity (50 m) of known groups. On occasion two apparently discrete groups have been found resting together. Animals observed on the burnt Sengwa flood plain over several afternoons in September, 1967, kept apart although during the course of an afternoon the areas over which they moved frequently overlapped. These data suggest that sounders within a clan area are largely independent and although sounders may amalgamate after farrowing there is no evidence of any co-operative organisation.

Agonistic encounters observed between individuals and sounders in the field (Chapter V) must be accommodated within any general hypothesis about spacing systems in the population. MacBride (1969) in a study of jungle fowl has shown the degree of complexity that occurs in spatial organisation when hierarchies and territory (in the form of portable space) are both present within so clearly recognisable a social entity as a flock of fowl. Agonistic encounters between warthog have been observed most frequently at

small water holes. This is to be expected from a situation where, given daily peaks in drinking and wallowing activity, sounders are most likely to meet. The single record I have of conflict between two tagged animals from different sounders was made at a water hole in Clan B area (R.Ngwarai, 27 September, 1969). Ad. ♀ 171 accompanied by 3 juvenile ♀♀ was drinking at the pan when Ad. ♀ 158 (also Clan B) together with a Yr. ♂ and a Yr. ♀ approached the pan. Ad. ♀ 171 chased Ad. ♀ 158 about the pan for some 5 minutes before Ad. ♀ 158 left. Ad. ♀ 171 drank again and then moved off.

Records of conflict at water holes (between untagged animals) show that adult males may drive off younger males and sometimes adult females. Adult females sometimes drive off younger animals of either sex and occasionally other adult females. The observations suggest that some form of hierarchical organisation occurs between groups (or between dominant animals from these groups) using these water holes. Solitary adult males are sometimes intolerant of other warthog (even adult females) in feeding areas. Such intolerance has however been observed only occasionally and when animals approached to within c. 20 m of the feeding adult male. Fradrich (1965) noted that groups arriving at a waterhole would wait until warthog already there had departed before going down to water. Conflict between groups of tame warthog was frequent and probably emphasised by the feeding regime. Dominance - subordination relationships were apparent and it seems reasonable to postulate the existence of a form of hierarchical organisation, which need not be a linear one, between animals and sounders sharing a common area.

Scent marking has been described in warthog (Chapter V) and



although its social function has yet to be established it may well serve to order the movements of largely independent but possibly related sounders within the postulated clan areas. Ewer (1968) discusses the functions of scent marking and points out that it can serve as a means of informing neighbours of each others movements and presence. Martin (1968) further notes that although scent marking behaviour has often been taken to imply territoriality its function in this context has been clearly demonstrated in only one or two instances.

b) Hole tenure.

Warthog when followed to holes in the evening were found to go to particular, one felt almost "predetermined" holes, rather than to the nearest available hole. This behaviour seems to indicate that sounders may have a freehold on particular holes. Patterns of hole use by tagged animals (Table 34 and Fig. 76 ) also suggest that although warthog use a number of holes and that particular holes may be used by different sounders at different times, some form of tenure exists. The adaptive advantages of such a system are not difficult to imagine; the chances of being caught by a predator while searching for a vacant and suitable hole are probably greater than if entry, by right of tenure, is unimpeded. There are many cues to which warthog may be responding as they move to their holes, and of which human observers are unaware. The scent trails of other animals moving through the area and in the vicinity of holes may be particularly important. I have seen warthog approach an already occupied hole, with the obvious intention of entering, only to stop and sniff the

ground some yards from the hole and then move off. At some holes animals have been seen following a distinct route (over a distance of up to 100 m) to the entrance. A hog knowing the hole, and the route, would be able to read the signs of probable occupation without having to approach the hole if it crossed such a path. Hole use may thus operate simply on a "first come, first served" basis. Warthog often inspect holes during the day and in moving about their range obtain information on holes being used. On some occasions when Susan changed her hole, the new hole had been inspected earlier in the day. It seems probable that if a group uses a hole on one night their scent will "keep it open" for them for the following night. If they move to a new hole the vacated hole can be taken up by another group which may or may not have inspected it earlier in the day. Such a system would not however provide the basis for the formation of clans or for the dispersion pattern of home ranges and hole use observed in the Sengwa Experimental Area.

In Chapter III (page 102) I suggested that holes might be classified in terms of how they are used by the population. Data on intensity of hole use (Fig. 41) showed centres of activity in so far as holes which were well used tended to be far apart and were also large and durable; it was further suggested that an element of tradition might surround their frequent use by many sounders. Since warthog of both sexes are likely to be attached to their mothers for 12 to 18 months (females for longer) such a suggestion is feasible. Holes form fixed and often persistent structures in the environment and since warthog do not construct their own holes these may provide the basis for patterns of dispersion. The distribution pattern of

intensity of hole use fits fairly well with the observed clan distribution (Fig. 41 and Figs. 76 and 77). The clans have been delineated on the basis of distribution patterns rather than on the basis of social interactions. It seems probable that they arise from the matriarchal organisation of the sounder and the strong attachment to home range areas in which animals have spent the first year or more of their lives. In sheep such attachment of young to home ranges and to dams results in a loosely knit, but recognisable home range group (Hunter, 1964, and Grubb and Jewell, 1966). In warthog the need for animals to retire to holes at night places limitations on the size of the group; the number which can fit into a hole is restricted and the formation of large sounders is rare (Tables 24 and 25). This fact may partly account for the largely independent nature of family units within the postulated clans and scent marking behaviour and hierarchies may further serve to avoid undue competition for favourable holes within clan areas.

Little is known of the home range behaviour of solitary males and bachelor groups and their role within warthog societies or within the clan is not clear. Mature males are more independent of holes than are young warthog and family groups and this may permit them greater freedom of movement. Ewer (1968) has drawn attention to the manner in which the primary function of territory in large herbivores has become linked with sexual selection and considers that societies in these animals "represent solutions to the problem of how to preserve the advantages conferred by male aggression and at the same time avoid its potentially deleterious effects". Three main solutions are apparent : one is based on territory where males are precluded

from pursuing younger males beyond the limits of their territory, another is the abandonment of spatial territories in favour of defense of females, while a third is the development of stylised fighting and rank order within a herd (Ewer 1968). The present limited information on behaviour of male warthog does not yet allow us to see how far sexual selection may have influenced warthog social structure.

c) Clan concept and warthog dispersion.

I have used the term "clan" in a sense similar to that in which Grubb and Jewell (1966) used the term "home range group". Grubb and Jewell suggested that their model of home range groups for Soay sheep might prove useful for other ungulates. Although the existence of clans as social units in the Sengwa warthog population has not been clearly established the model provides a very useful working hypothesis and one which has already provided the basis for some field experimentation. The extent to which clans in the Sengwa Experimental Area are governed by the disposition of suitable holes is, in conjunction with radio tracking techniques, open to experimental investigation by the simple expedients of blocking and constructing holes. The concept of clans also provides a useful bridge between behavioural and ecological studies. Clans appear to be an intermediate condition between solitary territorial organisation and fully fledged herd structure. The former type of social organisation tends to occur in smaller ungulates occupying uniform woodland or forest habitats while large herds are characteristic of open plains (Jarman, 1968). Small herds and family groups tend to occupy more broken habitats. I have argued that mosaics of suitable savanna



vegetation are an important requirement for warthog which because of their need to live in holes are predominantly local in their movement patterns.

A territorial organisation (where home range and territory are co-extensive) would result either in one group or individual claiming much of a clan area, with a consequent reduction in population density, or parcelling a clan area into territories some of which would not provide adequate resources to meet varying seasonal requirements and may not provide an adequate choice of suitable holes. Herd formation or the formation of large groups is precluded in warthog by their need to sleep in holes. The social system envisaged in the Sengwa Area allows for a stable society of largely independent small groups in which, within each clan area, a suitable mosaic of vegetation types, a variety of holes and possibly more reliable water resources are available to meet the contrasting seasonal requirements of its individuals. The system can be viewed as a pooling of resources between a number of possibly related groups. This prospect of warthog social structure reflects one way in which mammals have succeeded in "retaining the advantages accruing from social life without forfeiting those resulting from being territorial" (Ewer, 1968).

The identification of clans and an examination of their structure, their size and the area they encompass may provide a fruitful meeting ground between behavioural and ecological studies, a subject recently discussed by Crook (1970). Clans are likely to vary in size (number of individuals and area) and, by focusing attention on these units within a population and the ecology of the

areas they occupy, it may be possible to investigate more directly the complex interactions and inter-relationships between environmental resources and social behaviour and the manner in which each may influence dispersion and density.

## 2. Population regulation.

An early aim of this work was to see how far Wynne Edwards' (1962) ideas on population regulation through social behaviour and dispersion might be applied to warthog in the Sengwa Area. The alternative view point of Lack (1954 and 1966) was that populations were controlled directly by density dependent environmental factors, particularly food. Wynne Edwards considered food to be the ultimate, rather than proximate, controlling factor but held that populations, through socially mediated mortality and checks on population growth, kept their numbers below the level at which they might over-exploit their food resources.

Warthog density in the transect area fluctuated within fairly narrow limits during the course of this study (Fig. 12). An initial decline in density was ascribed to environmental factors, fire and drought, which may have resulted in an acute shortage of food. This initial decline does not appear to have been density dependent; it had a major effect on juvenile survival. As Child (1968) points out, such direct environmental reductions of population density can be expected in dry savanna areas where rainfall is often erratic. Warthog density increased during 1967 and 1968 and levelled off in 1969 suggesting that density dependent mechanisms were curtailing further population growth.

Observations of warthog diet, and distribution and abundance of food indicated that, in a normal wet season, food was plentiful and widespread, while during the dry season warthog diet was restricted largely to the rhizomes of two species of grass. Food as a limiting factor is thus most likely to operate during and towards the end of the dry season. Quantities of rhizomes available to warthog in Clan C area of the Sengwa Experimental Area (Fig. 77 and Fig. 34) were found to be very high and far more food was available than the local population could use. The estimated weights of rhizomes, 3 - 5 tons per ha, do not appear to be excessively high as Stoddart and Smith (1955) report  $4\frac{1}{2}$  tons (? Imperial) dry weight of grass roots per acre in prairie grassland. Holes in the area are plentiful and there is clearly no absolute shortage of holes, for few are used more than 70% of the time and most are in use less than 30% of the time. The implication of these observations was that socially mediated mechanisms were preventing further increases in warthog density. Breeding success in the warthog population declined as population density increased (Fig. 22) (and was) due possibly to a decreased birth rate or to increased juvenile mortality or both. Changes in sounder structure were observed and young animals tended to remain attached to matriarchal sounders after their first year. Proportion of yearlings/adult recruited into the sub-adult class increased (Fig. 22) and sex ratio also changed; the proportion of males, particularly young males, increased.

Though these data strongly suggested that population density was being governed by social factors, two important environmental factors, predation and disease, were not however studied. Lions are the main

predators of warthog in the Sengwa Area and warthog, in terms of numbers of kills found, form the main prey of this predator. The effects of predation on warthog numbers in the Sengwa Area are not known. Even if data were available to show that predation was checking further population growth it would still be necessary to distinguish the extent to which mortality was socially induced, e.g. by young animals being denied access to suitable holes or being driven into new areas where they would more readily fall prey to predators. Similar considerations apply to the role of disease in checking population growth. Field observations of mortality due to disease are hampered by sick and injured warthog retiring to holes in which they may die. Dispersal of young warthog has not been specifically studied and until information on this topic and causes of mortality have been investigated it will not be possible to propose in any critical manner how population number of warthog in the Sengwa Area is regulated.



SUMMARY.

The data on which this dissertation is based were obtained in the Sengwa Research Area, Rhodesia, between 1965 and early 1970.

The Sengwa Research Area and intensive study areas within it are described in Chapter I while a full description and map of the vegetation are appended. Methods used in the study included a system of permanent transects totalling 60,000 yards which were traversed almost daily for five years. Groups of warthog encountered in the field were aged and sexed and the data provided the basis for an analysis of population and group structure. Extended observations were made of many mapped and numbered warthog holes. Three "generations" of hand-reared but free-ranging warthogs provided complementary behavioural data unobtainable in the field. More than 240 warthog were captured and tagged. Radio-tracking techniques were introduced in September, 1968.

Chapter II provides data on abundance and distribution of warthog in the transect area and population data derived from field age and sex classifications. Warthog density declined early in 1966 after widespread fires and delayed rains. Density increased towards the end of 1967 and during 1968 but showed no further increase during 1969. A wet season dispersal of warthog from the study area was not evident.

Although warthog occurred in all habitats, densities were highest in vleis in C.mopane woodland areas and Acacia riparian communities on alluvial soils. Lowest densities occurred in Combretum thickets and Baikaiea woodland on deep sandy soils. Consistent seasonal

changes in warthog density occurred in some habitats and areas and were associated with seasonal changes in availability of food. Localised dry season grass fires resulted in marked local increases in warthog density. Densities in different parts of the same habitat differed considerably but the causes of these variations are poorly understood.

Population structure is described in terms of ratios which represent the numbers of immature animals (juveniles and yearlings) relative to the adult population. The collection of such data and their validity are examined. Breeding success was low when density declined during 1965 - 1966 season but was high after a subsequent favourable season (1966 - 1967). Breeding success in the following two seasons declined despite apparently equable seasons and was apparently associated with an increase in population density over this period. Recruitment of yearlings into the adult class showed an upward trend after the 1966 - 1967 season. This result suggested that environmental and social influences act differently on the juvenile and yearling components of the population.

Sex ratio in the Sengwa population changed during the period of study. It approached parity when population density was highest and was approximately 1 ♂♂ : 2 ♀♀ when density was lowest. The sex ratio in juveniles at the end of their first year did not differ significantly from parity. In adults (36 months +) it was approximately 1 ♂♂ : 2 ♀♀. Annual changes in sex ratio were mainly due to changes in the proportions of males and females in yearling and sub-adult animals. Sex ratio data from other sources are summarised and discussed, as is the problem of bias in field records

of sex ratio. It is concluded that sex ratio in warthog populations may vary from about 1 ♂♂ : 2 ♀♀ to 1 ♂♂ : 1 ♀♀. A higher incidence of mortality in mature males may result from their solitary habit and from not always sleeping in holes at night. Mortality attributable to inter-male rivalry was not recorded in the Sengwa Area.

The third chapter deals with the major environmental factors of food, holes and water and climate, in so far as it affects daily activities and the use of holes. Warthog are primarily graminivorous although animals are occasionally eaten. Clear seasonal changes in diet and mode of feeding occurred. Warthog grazed mainly on short annual and some perennial grasses during the rains, ate flowering heads of grasses when these sere towards the end of the rains and subsisted on the rhizomes of a few perennial grasses during the dry months. Feeding, particularly rhinarium digging, seen in tame warthog and bushpig is described and observations related to cranial anatomy made. In addition to showing specialised grazing warthog were, in contrast to bushpig, highly efficient at rooting in hard, seasonally dry soils for grass rhizomes. I suggest that this feature has allowed warthog to invade and compete successfully with ruminants in the seasonally dry savannas of Africa. The availability of food and its distribution in the Research Area are described. Food is plentiful and widely available during a normal rainy season but may be scarce after widespread burns and if rains are unduly delayed. Although the dry season diet is restricted largely to the rhizomes of Digitaria milaniana and Tristachya superba, these occurred in large quantities (2 - 5 tons per ha) in favourable areas and there was no evidence to suggest an absolute shortage of food in the study



area or that the food resource was being over-utilised.

Holes are more numerous than warthog in the Sengwa Area and no evidence was found to suggest that warthog excavate their own holes in the field although they did modify existing holes. Three main types of hole were used, namely caves, antbear diggings and subterranean erosion-gulley holes. Of these, erosion-gulley holes were used most frequently. Artificial holes constructed in the field were readily used by warthog. Few holes were used more than 70% of the time and warthog frequently changed holes. Particular holes may be used by a number of sounders at different times. Well-used holes tended to be widely spaced and the distribution pattern of hole-use is discussed in relation to warthog density and food availability. The possibility that holes may be classified in terms of how they are used by the population is briefly discussed. Ectoparasites and other mammals in holes do not appear to affect the frequency with which particular holes are used.

Although most animals enter holes before dark and emerge at about sunrise, adult males may remain out of holes until well after dark and may not enter at all on some nights. Carrying and scraping grass into holes has been observed during the cold season but not before parturition or during the farrowing season. Holes are used as refuges from the rain but warthog were not found to seek refuge in them from the mid-day heat. Warthog may remain in a hole for as long as 36 hours after humans or lions have waited outside.

Daily patterns of activity of tame, free-ranging animals were characterised by morning and evening activity with a period of rest in the middle of the day. Although drinking occurred at all times of



the day it was most frequent between 0700 - 0900 hours and 1400 - 1700 hours during the dry season. Wallowing during the dry season occurred most frequently between 1400 - 1500 hours and seldom occurred when ambient temperature was below 80°F. Similar data were obtained for the wet season but peaks were less marked. Daily activity showed some degree of temperature dependence and the possibility of behavioural thermo-regulation in warthog is apparent. Measurements of body temperature in relation to ambient temperature and behaviour are however required.

Age and sex composition of warthog groups are described from large numbers of field classifications, and changes in composition of known groups are outlined. Sounders varied in size from 1 to 16 animals. Solitary animals were the most frequent; almost 70% of groups seen constituted 5 animals or less and most of the population occurred in groups of 4, 5 and 6 animals. Sounders of 6 or more warthog were most frequent during the rainy season and lowest at the end of the dry season at the onset of farrowing. Sounder types derived from an analysis of field classifications are outlined and then examined in relation to observations on the structure of known tagged groups. Warthog group structure in the Sengwa Area is characterised by three main types of sounder : solitary adult males, bachelor sounders and matriarchal sounders which are probably filial groups.

Changes in the incidence of sounder types occurred during the study period and were related to changes in population structure. Increased density, lower breeding success and higher recruitment of yearlings into the adult class were associated with a higher

incidence of matriarchal sounders containing sub-adults and yearlings of both sexes in addition to juveniles. This suggested a prolonged attachment of mother and offspring at higher densities. The incidence of sounders containing both adult males and adult females was low even during the mating season. No evidence for pair formation during the mating season was found.

Aspects of communication between warthog and some features of agonistic, mating and maternal behaviour were studied. Scent marking in warthog and bushpig is described, apparently for the first time. Both species show what is probably salivary marking by wiping the side of the mouth on objects. Warthog also show a form of pre-orbital marking. A tame bushpig did not show pre-orbital marking behaviour. Other possible forms of scent marking by warthog are considered.

Threat displays and submission are described and illustrated. Fighting in very young and older warthog was examined. Warts function as protective devices in fighting and the degree to which warthog fighting is stylised is discussed. Field observations of conflict between warthog are summarised.

Courtship behaviour in warthog varies and males may initially locate females by visiting holes in the early morning. Field observations suggest that mating is restricted largely to fully mature males (42 months +). Age at sexual maturity in male warthog appears to vary and is discussed briefly. Courting males in the Sengwa Area joined matriarchal sounders for one to three days while females were in oestrus and then left. Mating was polygamous or promiscuous.

Two tame free-ranging warthog produced litters and observations of these animals indicated that expectant mothers drove off younger half-grown warthog attached to them before they farrowed. Young warthog accompanied their mothers away from the hole regularly only after they were about 50 days old. Offspring of one female showed coprophagia<sup>y</sup> once they started grazing at between 3 and 4 weeks of age. Although they were weaned at 21 weeks they were feeding for as long as their mother each day by the time they were 63 days old. Development of group cohesion is described.

The home ranges of 15 radio-tagged warthog ranged from 65 to 330 hectares and average home range size was 115 hectares. Females, once established in a home range, adhere to these for long periods, if not for life. Home range behaviour in relation to food, holes and water is examined. Shifts of home range in response to the flush of green grass following dry season burns were observed. Home ranges of adult males overlapped as did those of matriarchal sounders. The occurrence of "clans" or home range groups in the study area is postulated on the basis of patterns of hole use and dispersion of more or less co-extensive home ranges. Tame, free-ranging warthog showed "core areas" within their home ranges, a larger area which was used in all months and a peripheral area and outer boundary which varied from month to month over five months. Home range of a female was greatly reduced during the first six weeks following parturition.

The main techniques used in this study are reviewed briefly and the advantages of radio tracking and use of tame free ranging animals in behavioural and ecological field studies outlined. Habitat requirements of warthog are discussed and it is argued that

warthogs' dependence on holes places limitations on their movements; a seasonally variable diet makes mosaics of suitable wet and dry season habitat an important requirement. Attention is directed to the need for physiological studies on thermo-regulation, water balance and nutrition to understand why warthog have become so dependent on holes. Main features of warthog social structure are outlined and evidence for the existence of clans or home range groups is examined. Clans appear to be partially determined by the dispersion of holes and, although the existence of clans as social entities is not established, the concept provides a useful framework within which to relate warthog social organisation to their habitat requirements. Evidence of behavioural regulation of warthog populations in the Sengwa Area is no more than suggestive; ~~and~~ crucial information on factors governing mortality and changes in reproductive rate is not available.



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APPENDIX 1A preliminary classification of the vegetation and a  
vegetation map of the Sengwa Research Area.

The general climatic, topographic and vegetational features of the Sengwa Research Area have already been outlined in Chapter I. Early attempts to interpret the ecology of game species in the area in terms of broad vegetation types were not successful. It thus seemed desirable to examine and map the vegetation of the area in some detail. Vegetation of the Research Area was first mapped by G. Davison in 1965 who recognised 10 vegetation types but no description or definition of the vegetation types accompanied the map (drawn at 1 : 400,000 and from the 1958, 1 : 40,000 aerial photography).

1. The vegetation map

The typing and mapping of vegetation units in the area has been carried out by myself. Collections of the grasses (by myself) and of the trees and shrubs (by N. Jacobsen and A. Lind) have been made for the area. Specimens of all plants collected have been sent to the National Herbarium in Salisbury for identification by Mr. R. Drummond (trees and shrubs) and Mr. B. Simon (grasses). Duplicate specimens of identified material have been retained at Sengwa.

<sup>The</sup>  
~~In~~ 1965, 1 : 25,000 aerial photography was used, in conjunction with ground checking, to demarcate vegetation types. The base map on a scale of 1 : 50,000 was traced from preliminary sheets of the area on this scale which were published by the Surveyor General, Salisbury. The Tsetse Control Branch of the Department of Veterinary

Services kindly allowed me to use their mapping facilities to transfer information from 1 : 25,000 aerial photographs to the base map. The vegetation map was completed in March, 1968.

## 2. Classification of vegetation types.

Recent classifications of the vegetation of Rhodesia have been made by Rattray (1962) and by Wild and Grandvaux Barbosa (1968). Rattray discusses physiognomic criteria for this country as well as a floristic classification. I have attempted to apply Rattray's classification to the vegetation of the Sengwa Area but with limited success. This, as might be expected, was largely due to the smaller units recognised here and of which many would fall under one of Rattray's types. Similar difficulties apply to the use, locally, of Wild and Grandvaux Barbosa's (1968) classification which embraces the Flora Zambesiaca region (Mocambique, Rhodesia and Zambia). Vincent and Thomas (1965) produced a broad and useful description of the vegetation of the Sebungwe region and the Sengwa Area falls into their natural region IIIc. Their work has also been referred to in the present study.

### a) Physiognomic Classification.

I have based the physiognomic classification of vegetation here on the system proposed by Pratt et al. (1967) for East African Rangeland. This system grew out of a dissatisfaction with the Yangambi criteria which the authors considered to have little application to the rangeland (grazing areas) of East Africa. Rattray (1962) also considered the Yangambi classification to be

inadequate for vegetation in the lower rainfall areas of Rhodesia and accordingly modified and extended it. The system proposed by Pratt et al. is well suited to typing the vegetation in limited areas in some detail. The criteria are well defined and an objective basis for their application is given. The categories are based largely on the percentage canopy cover of trees and/or shrubs, which can be estimated from aerial photographs, and the height of dominant grass species.

Pratt et al. recognised five basic physiognomic types which may occur in mosaic or be superimposed. These are defined as follows:

1. Woodland (W)                      A stand of trees up to 40 ft. in height with an open or continuous but not interlaced canopy, sometimes with shrubs interspersed and a canopy cover of more than 20%. Grasses and herbs dominate the ground cover. Woodland Thicket (Wt) may be recognised and is an extreme form where trees form a dense stand through which man and ungulates can only pass with extreme difficulty.
2. Bushland (B)                      Any assemblage of woody plants mostly of shrubby habit, having a canopy of more than 20% with the shrub canopy less than 20 ft. high, with occasional emergents. Bushland thicket (Bt) may be recognised and is a dense stand through which man and ungulate can only pass with difficulty.
3. Grassland (G)                      Land dominated by grasses and occasionally other herbs, sometimes with widely scattered or grouped trees and shrubs, the canopy cover of which does not exceed 2%.

Classified by reference to : (i) Height - (Giant - greater than 10 ft. tall; Tall - between 5 and 10 ft. tall; Medium height - between 20 ins. and 5 ft. tall; Short - less than 20 ins. tall). (ii) Genera of dominant grasses. (iii) Degree of swampiness (iv) Dominance of annual grasses or other herbs.

- |                             |                                                                                                                       |
|-----------------------------|-----------------------------------------------------------------------------------------------------------------------|
| 4. Bushed-Grassland<br>(BG) | Grassland with scattered or grouped shrubs, the shrubs always conspicuous but having a canopy cover of less than 20%. |
| 5. Wooded-Grassland<br>(WG) | Grassland with scattered or grouped trees, the trees always conspicuous, but having a canopy cover of less than 20%.  |

Combinations of the above types are possible and in these instances the canopy cover is taken as the sum of the two separate components, for example :

Woodland + Bushland (W+B) - canopy cover of 40% or greater.

Wooded Grassland + Bush Grassland (WG + BG) - canopy cover exceeds 20%.

Wooded and Bushed Grassland (WBG) - canopy cover less than 20%.

b) Floristic Classification.

The vegetation types recognised for the purpose of the map given here are largely variants of the basic associations mentioned in the introduction and shown in Fig. 2. These are briefly as follows :

- (a) Brachystegia woodland types
- (b) Colophospermum mopane woodland types
- (c) Acacia communities on alluvial soils



- (d) Combretum sp. woodland or thicket associations and Baikiaea Woodland which occur on gentle scarp slopes and on deep sandy soils
- (e) Grassland/mopane scrub on heavy black self ploughing soils and
- (f) Grasslands on alluvial soils or sands - Sengwa flood plain.

Each of the physiognomic types occurring within these broad communities is qualified by the dominant trees, shrubs or grasses, or combinations of these. The types recognised here are therefore based almost entirely on features which can be observed directly, rather than inferred, from the vegetation.

Features other than the immediate appearance and dominant species of a plant community can, of course, be used to define the community. The influence of soil, climate, biotic factors, a knowledge of climax communities for the area in relation to the foregoing factors and also of the successional stages reached in various types would be required for an ecologically meaningful classification of the plant communities in the area. Since ecological relationships between the vegetation and the environment in this area have not been established such a classification, no matter how desirable, is not possible.

It should, however, be pointed out that the dominants, sub-dominants and main associates within each type described here have been selected purely on subjective impressions gained in the course of field checks at different times of the year. Some types are better known than others. The method used has severe limitations but is the only one practicable at the moment. Statistical methods of analysis have been developed to provide the basis for an objective classification of plant communities. Grunow (1967) applied such techniques to the vegetation of a bushveld farm in the Transvaal.

The map of the main plant communities which resulted from his analysis contrasted markedly with one produced on the subjective criteria of classification<sup>used</sup> here.

Grass species and authors are listed in Appendix 2, while those of trees and shrubs are listed at the end of this Appendix.

### 3. Description of the vegetation types.

#### 1. River-fringing woodland (Drainage-line woodland).

Physiognomically, this type varies between a tall well-grown but more dense stand of trees of the vegetation through which the river passes to a closed stratified type approaching forest. The former generally applies to Colophospermum mopane drainage lines while the latter occurs along the Kove River. The vegetation fringe of the Kove has not yet been adequately examined. In parts, the Acacia/Grewia woodland and bushland type (Type 5) of the Lutope River might be classified as a forest type (see under Type 5).

#### 2. Brachystegia boehmii - Julbernardia mixed woodland.

This is a tall, fairly open woodland occurring on sandy soils (Kalahari sands or forest sandstone series). It dominates the elevated regions of the Research Area above the escarpment. The grass cover is continuous but sparse and of medium height. Relative dominance of B.boehmii or J.globiflora varies. Shrubs occur but are generally infrequent except in isolated areas where they may form an understorey, subjected to frequent fires.

Associates : Trees - Afzelia quanzensis occurs at lower levels, B.spiciformis, Diplorhynchus condylocarpon,

Diospyros quiloensis (on ant-hills),  
Erythrophleum africanum, Monotes glaber,  
Pericopsis angolensis, Pseudolachnostylis  
maprouneifolia.

Shrubs - Baphia massiaensis sub sp. obovata, Bauhinia  
 sp., Commiphora mossambicense.

Grasses - Aristida vestita, Chloridion cammeronii,  
Loudetia flavida, Pogonarthria squarrosa,  
Schizachyrium jeffreysii, Tristachya superba.

### 3. Baikiaea plurijuga woodland.

Limited to deep sandy soils on eastern slopes of Samapakwa hills and to a pocket on the northern escarpment. The woodland is very mixed and fire damage to older trees evident. Shrubs well interspersed in understorey in most parts and woodland gives impression of giving way to surrounding thicket types.

Associates : Trees - Burkea africana, Commiphora sp. (? karibensis)

Shrubs - Baphia massaiensis, Combretum elaeagnoides

Grasses - ?

### 4. Colophospermum mopane woodland.

C.mopane is the dominant woody species of the area and forms a co-dominant or associate in many of the plant communities in the area. As a vegetation type, mopane woodland covers more than 50% of the Research Area. It shows considerable variation as a type, both in respect to the associated woody species, which are nearly always few, and also in its physiognomy and grass cover. A number of sub-types have been tentatively recognised but the validity and extent of some of these has not been adequately examined. For the

most part the type is limited to the basin and to clay soils. Extensive areas may be water-logged during the rainy season.

The typical C.mopane woodland of the area is composed of tall (30 ft. +) straight and fairly closely spaced trees with little perennial grass cover. Where the perennials occur these are generally Aristida sp., Enteropogon or Heteropogon.

- Associates : Trees - Adansonia digitata, Balanites aegyptiaca, Erythroxylon zambesiaceum.
- Shrubs - Commiphora africana, Grewia sp. (v. occasionally).
- Grasses - Aristida borumensis, A.curvata, A.hordacea, A. leucophaea, A.pilgeri, A.rhiniochloa, Bothriochloa radicans, Brachyachne patentiflora, Chloris virgata, Digitaria milaniana, Echinochloa colonum, Enteropogon sp., Eragrostis sp., Heteropogon contortus, Setaria sphacelata, Sorghum versicolor, Sporobolus sp. (particularly the annual S.panicoides), Urochloa trichopus.

Apart, however, from the Aristida sp. and in some parts H.contortus, the distribution of other perennial species is very patchy. The annuals, C.virgata and S.panicoides, are widespread.

#### 4a. C.mopane type - open woodland on undulating ground.

A more open type of woodland with fairly well developed grass composed mainly of Heteropogon contortus and Aristida sp. It occurs to the west of the Lutope River on the undulating, dissected ground rising to the foothills of the Samapakwa. Exposures of mudstones



(derived from Madumabisa shales) are frequent and black clay soils which are derived from them tend to crack during the dry season.

4b. C.mopane type - Cathedral mopane.

Characterised by very tall, well grown C.mopane trees of 50 ft. or more in height and a well developed short grass cover of Chloris virgata, Sporobolus marginatus (or S.albomarginatus), Eriochloa macclounii, Sporobolus panicoides.

4c. C.mopane type - Eroded and hard pan areas.

Grass cover in this type is generally sparse and composed primarily of Sporobolus marginatus, Chloris virgata, Urochloa trichopus and species such as Aristida rhinochloa, Brachyachne patentiflora and Setaria pallide-fusca.

5. Acacia tortilis-Grewia woodland and bushland.

This is a very clear though heterogeneous community in which a more open type is recognised (No. 10). It occurs on dark alluvial deposits of what must at one time have been the flood-plain of the Lutope River. This is indicated by the distinct terrace separating the alluvial soils from the surrounding mopane clays. The river has since cut down to a level well below that of the plain, which is no longer flooded. Trees of most species are larger here than elsewhere in the area. A striking feature is the very similar size, and possibly age, of the large and mature A.tortilis trees which reach a height of c. 60 ft. Regeneration of this species is only evident in one isolated patch. The evergreen species, Trichelia emetica, is found in small dense stands of very mixed vegetation. These areas, which may in the past have been more extensive, are akin to the

Trichelia type, medium altitude riparian forest of Rattray.

The alluvial areas are heavily utilised by many species of game in the dry season. The animals trample down the grass and smaller shrubs creating a very open aspect. Towards the end of the rains the grass cover, chiefly Panicum maximum, is high and dense. Grewia sp. and C.mossambicense dominate the shrubby stratum.

- Associates : Trees - A.albida, A.nigrescens, Erythroxylon, Capassa violaceae, Combretum imberbe, C.zeyheri, C.ghasalense, Kigelia pinnata, Pericopsis africana, Piliostigma thonningii, Diospyros mespiliformis, D.senensis, Trichelia emetica, Ziziphus mucronata.
- Shrubs - Acacia fleckii, Capparis tomentosa (on anthills), Combretum mossambicense, Combretum obovatum, Dichrostachys cinerea, Grewia sp.
- Creepers - Strophanthus sp., Fockea sp.
- Grasses - Dactyloctenium, Digitaria milaniana, Setaria sp., Panicum maximum, Urochloa pullulans.

6. C.mopane-A.nigrescens-Ximenia woodland and bushland.

A tall woodland (30 ft. +) with closely growing mopane <sup>f</sup>orming the dominant species but well interspersed with A.nigrescens. The canopy is in parts almost closed. There is a conspicuous but not well-developed growth of shrubs except in localised patches. The type might be better described as bush-woodland. Soils appear to be dark grey and similar to those in mopane woodland. The grass layer is continuous but often sparse.

- Associates : Trees - Albizia sp., B.boehmii (occasional), Combretum apiculatum, C.hereroense,

C.ghasalense, Diospyros mespiliiformis,  
D.quiloensis (on anthills).

Shrubs - Erythroxylon, Euclea sp., Ximenia americana,  
X.caffra.

Grasses - Enteropogon sp., Eragrostis rotifer,  
Heteropogon contortus. Also Sorghum  
versicolor and Aristida sp. in parts.

7. Mixed Combretum-C.mopane-Erythroxylon woodland and bushland.

This is a very heterogeneous and ill-defined type showing elements of mopane woodland, Combretum thickets and Brachystegia-Julbernardia woodland. It occurs on sandy loams and Combretum trees predominate on the areas of increasing slope. B.boehmii only occurs in parts and in the flatter areas. The woodland canopy is ill-defined in height and a shrubby understory is evident. The medium height grass cover is well-defined.

Associates : Trees - Afzelia quanzensis, Combretum apiculatum,  
C.ghasalense, Commiphora mollis, Dalbergia melanoxylon, Diplorhynchus condylocarpon,  
Erythrophleum africanum, Julbernardia globiflora, Kirkia acuminata, Strychnos stuhlmannii, Terminalia sericea, Diospyros quiloensis.

Shrubs - Grewia monticola, Combretum elaeagnoides,  
Baphia massaiensis, Popowia sp., Bauhinia  
sp.

Grasses - Brachiaria brizantha, Digitaria sp.  
Eragrostis rotifer, E.superba, Heteropogon contortus.

8. Commiphora-Combretum wooded bushland.

Very similar in species composition and aspect to Combretum



thicket type but more open and less extensive. In parts, e.g. eastern escarpment north of Manyoni Tsetse Camp, Commiphora and the wooded complement may predominate. Confined to sandy soils. Tree height generally less than 30 ft. and shrubby layer approximately 15 ft. Grasses generally poorly developed and of medium height.

Associates : Trees - Commiphora karibensis, C.mollis are dominant. Other trees include Combretum apiculatum, Croton sp., Crossopteryx febrifuga, Diospyros guiloensis, Kirkia acuminata, Strychnos stuhlmannii.

Shrubs - Combretum elaeagnoides, Dichrostachys cinerea, Popowia obovata and also coppicing C.apiculatum.

Grasses - Dactyloctenium sp., Heteropogon, Eragrostis, Digitaria ternata.

9. Combretum-Terminalia-Eragrostis wooded grassland and bushed grassland (on tallus slopes).

Generally low stature of trees (15 - 20 ft.) with shrubs formed mainly of fire-damaged and coppicing Combretum species. Varies in physiognomy from W.G. + B.G. to W.B.G. Dominant tree species are Combretum apiculatum and Terminalia sericea.

Associates : Trees - C.ghasalense, C.hereroense, Crossopteryx febrifuga, Commiphora mollis, Kirkia acuminata.

Shrubs -

Grasses - Eragrostis sp. (?rotifer), Loudetia flavida, Danthoniopsis minor, Schmidtia pappophoroides.

10. Acacia tortilis-Grewia-Panicum wooded grassland and bushed grassland.

This is a physiognomic variant of Type 4, It is more open and



the grasses assume greater dominance. Grewia is often not as evident and may be superseded in parts by C.mossambicense. The dominant tree is more conspicuously A.tortilis and Trichelia emetica is less abundant than in Type 4. The grass cover is more varied and includes Hyparrhenia sp., Setaria and Andropogon. Urochloa pullulans may assume local dominance, as may Setaria sphacelata in depressions.

11. Brachystegia boehmii-Combretum sp.-Hyparrhenia wooded grassland + bushed grassland, with C.mopane.

A diverse assemblage of large, scattered or clumped trees with various shrubs and fire-damaged, coppicing Combretum sp. (chiefly C.ghazalense). The cover is variable; Hyparrhenia dominates in most parts but seldom forms a dense pure sward. The soil is pale red to grey and may be described as sandy loam. C.mopane predominates in parts.

- Associates : Trees - Afzelia quanzensis, Combretum apiculatum, C.ghazalense, Diospyros mespiliformis (on ant hills with Acacia nigrescens), Erythrophleum africanum, Erythroxylon sp., Kirkia acuminata, Pseudolachnostylis maprouenifolia, Strychnos innocua.
- Shrubs - C.ghazalense, C.mossambicense (occasional), Grewia monticola, also Acacia fleckii and Bauhinia sp.
- Grasses - Aristida pilgeri, Digitaria milaniana, Hyparrhenia sp., Tristachya superba, Urochloa bolbodes (patchy distribution).

12. Julbernardia-Vellosia wooded and bushed grassland on pebble beds.

Possibly this is an edaphic sub-type of Brachystegia-Julbernardia woodland. It occurs on eroded slopes characterised by conglomeritic pebbles. Trees are generally stunted on the slopes but not at the bottom of gulleys and depressions. The grass cover is for the most part very sparse and discontinuous.

Associates : Trees - Brachystegia boehmii on the fringes, B.tamarindoides, occasional Pterocarpus angolensis, Pseudolachnostylis maprouenifolia, Terminalia randii.

Shrubs - Almost entirely Vellosia sp.

Grasses - Danthoniopsis minor, Loudetia flavida, Rhynchelytrum sp., (? Eragrostis denudata). L.flavida is the most widespread.

13. C.mopane-Combretum-Tristachya grassland (wooded + bushed grassland). (Tristachya-Hyparrhenia medium height; grassland with mopane and Combretum).

Of limited distribution in the area and occurring on pale red loams with interdigitating stands of C.mopane-A.nigrescens-Ximenia W.B. Scattered and generally poorly developed mopane trees occur with Combretum apiculatum and C.hereroense. In parts B.boehmii (sometimes large) also occur. Shrubs are for the most part fire-damaged, coppicing trees (chiefly Combretum ghazalense).

Associates : Trees - Pericopsis angolensis, occasional Capassa violaceae, and Crossopteryx febrifuga which is common and usually shows signs of fire-damage.

Shrubs - Arundinae sp., Hyphenae sp.

Grasses - Andropogon gayanus, Aristida pilgeri,  
Brachiaria brizantha, Digitaria milanjana,  
Elyonurus trappnelli, Eragrostis superba,  
E. rotifer, Heteropogon contortus, Pogonarthria  
squarrosa, Schizachyrium sp., Sporobolus  
festivus.

14. Setaria medium height grassland with Acacia-Combretum (wooded and bushed grassland).

A part of the Acacia communities growing on rich alluvial soils. This type occurs mainly on the edges of the Lutope flood plain terrace and in the depressions or drainage lines generally occurring there. In parts these areas may become water-logged during the height of the rainy season. Andropogon, Digitaria, Heteropogon contortus, Hyparrhenia or Urochloa pullulans may, individually or in groups, form dominants or co-dominants in some areas. Trees are generally tall (40 to 60 ft.) (almost entirely Acacia tortilis or A. albida) giving the type a "parkland" appearance. Anthills, as in the two previous types, on the alluviums are dominated by Capparis tomentosa bushes. The physiognomy tends towards grassland within some of the areas mapped under this type. These would, if differentiated, fall under type 22.

- Associates : Trees - Acacia albida, A. nigrescens, A. sieberiana,  
Capassa violaceae, Combretum imberbe.
- Shrubs - Combretum mossambicense, occasional Grewia  
flavescens, Dichrostachys cinerea, Capparis  
tomentosa.
- Grasses - Andropogon gayanus, Brachiaria brizantha,  
Bothriochloa insculpta, Dicanthium pappilosum,  
Digitaria milanjana, Heteropogon contortus,

Hyparrhenia rufa, Setaria eylesii,  
S.sphacelata, Sporobolus pyramidalis,  
Urochloa pullulans. Echinochloa colonum  
 occurs in depressions where surface water  
 accumulates and stands during the rains.

15. Tall Hyparrhenia grassland with Acacia albida (wooded grassland)

Restricted to the sandy flood plain terrace of the Manyoni River.  
 The species composition of the grassland has not been adequately  
 examined. Panicum occurs beneath the tall and very well grown  
Acacias which often exceed 60 ft. in height. In more sandy parts the  
 grassland gives way to Aristida sp. and to Schmidtia pappophoroides.  
 Local clumps of trees may form woodland covering a few acres.

Associates : Trees - Acacia sieberiana, A.tortilis, Capassa  
violaceae, Combretum imberbe.

Shrubs - occasional Combretum mossambicense.

Grasses. - Andropogon sp., Aristida sp., Hyparrhenia  
 sp., Heteropogon contortus?, S.pappophoroides,  
Phragmites communis (in parts along the edge  
 of the water-course).

16. Tall Hyparrhenia-Terminalia wooded grassland.

Very similar in appearance to the previous type but lacking,  
 apart from occasional trees, the Acacia species.

Associates : Trees - which may be considered co-dominant with  
 tall (30 ft. +) well-grown specimens of  
Terminalia sericea, Capassa violaceae,  
Combretum imberbe, Peltophorum africanum and  
Piliostigma thonningii.

Grasses - As for type 14



17. Commiphora-Combretum wooded bushland thicket.

Composed primarily of Combretaceous shrubs which form a dense shrubby layer generally up to a height of about 12 - 15 ft. Emergents are of a variety of species of which Commiphora karibensis is the most characteristic. The impenetrability of these thickets is not such that they would fully qualify as thickets under the definition given by Pratt et al. The thickets are maintained in a more open condition than they might otherwise be by the extensive movement of elephant within them. The grass cover is generally poorly developed, discontinuous and confined largely to annual species.

Associates : Trees - Azelia quanzensis, Burkea africana, Combretum apiculatum, Commiphora mollis, Diospyros quiloensis, Entandophragma, Kirkia acuminata, Stercula africana, Strychnos sp., Pterocarpus antenussii.

Shrubs - Acacia ataxacantha, A.cinerea, Combretum celastroides, C.elaeagnoides, Bauhinia sp.

Grasses - Alloteropsis cimcinia, Dactyloctenium sp., Digitaria ternata, Panicum sp., Perotis patens, Urochloa trichopus.

18. Baikiaea-Baphia wooded bushland thicket.

Occurs on sandy soils, interspersed with Baikiaea woodland. Shrubby layer generally low (up to 8 ft.) and dominated by Baphia massaiensis. Emergents, mainly Baikiaea, may be very scattered in parts. Grass cover is poor and primarily composed of annuals. Many Combretaceous shrubs, primarily C.elaeagnoides and C.celastroides interspersed with Baphia.

19. Dichrostachys cinerea bushland thicket.

Only a single large stand of bushland thicket has been mapped but other limited stands ( $\frac{1}{2}$  to 1 acre) occur on the Lutope alluvial soils. Shrubs up to 12 ft. in thickets, but generally lower. In area mapped, the stand is dense and impenetrable, except along paths opened by elephant. Occasional emergent A. tortilis. The grass cover is poor but dominated by Dactyloctenium and Panicum.

20. Short Sporobolus grassland with mopane scrub.

Very limited occurrence within the Research Area and confined to seasonally water-logged areas within the Brachystegia woodland area. Requires further examination.

21. Medium height Setaria grassland with mopane on heavy clay soils.

The colloquial name for this type is "sidaga", which refers to the heavy self-ploughing black clay which may become water-logged during the rainy season. Although limited to the western part of the Research Area, extensive areas occur to the north-west of the Sengwa Research Area. The type is described by Vincent and Thomas who draw attention to the multitude of herbs which occur and are interspersed with the grass. C. mopane trees occur in occasional patches near the fringes, but stunted mopane are scattered in the grassland.

Associates : Grasses - Setaria sphacelata, Sorghum versicolor (Vincent and Thomas record Ischaemum brachyatherum, Andropogon sp. and Urochloa sp. as being the major species on a sidaga further west).

22. Sengwa flood plain grassland

The flood plain is a true flood plain in the sense that it is regularly inundated. It appears to have been the result of changes in the meanderings of the Sengwa River over a broad peneplain. The grass cover is consequently very variable and ranges from sparse, predominantly Aristida communities on sandy deposits to rank stands of Hyparrhenia-Andropogon where soils are more fully developed. Parts of the flood plain are being invaded (?) by bushes, chiefly Terminalia and Acacia fleckii. Occasional large Combretum, Piliostigma or Kigelia occur.

Associates : Grasses - Aristida stipitata, A. vestita, Bothriochloa, Brachiaria brizantha, Cymbopogon excavatus, Digitaria sp., Eragrostis sp., Heteropogon contortus, Hyparrhenia sp., Imperata cylindrica, Miscanthidium, Phragmites communis, Panicum sp., Setaria sp., Schizachyrium jeffreysii, Sorghum halepense, Stipagrostis uniplumis, Schmidtia pappophoroides, Tristachya superba.

23. Tall Setaria-Andropogon grassland on alluvial soils.

A tall dense grassland with a composition very similar to that of type 13, but including species which grow in moister soils such as Echinochloa pyramidalis, Eriochloa macclounii, Sporobolus pyramidalis, Setaria eylesii.

24. Sporobolus-Chloris short saline grassland.

Limited to a small area and associated with mopane woodland. Salinity of soil indicated by presence of salt licks and diggings by

game animals. Grasses in depressions tend to be taller (up to 5 ft.) and of more mixed composition.

Associates : Trees - Occasional Colophospermum mopane and Hyphenae.  
 Shrubs - Hyphenae (occasionally)  
 Grasses - Chloris virgata, Digitaria setivalva,  
Eragrostis viscosa, Sporobolus marginatus.  
 In depressions one finds Andropogon sp.,  
Brachiaria, Echinochloa, Hyparrhenia,  
Setaria, Sporobolus pyramidalis.

25. Drainage line grassland in C.mopane.

In parts, resembles the grassland type 20 (medium height Setaria grassland with mopane scrub) though generally differs in that soils are for the most part not deeply cracked when dry - a feature characteristic of self-ploughing soils.

Dominant grasses are Setaria, with Andropogon and Digitaria milanjiana. There is, however, considerable variation in the drainage line grassland in different parts of the area, and these have not been distinguished in the present map.

Seasonally inundated areas, such as pans, in the mopane are not mappable on the scale used. These areas are often characterised by Oryza barthii, Echinochloa and Eriochloa species.



Alphabetical List of trees and shrubs.

- Acacia albida* Del.  
     *ataxacantha* DC.  
     *fleckii* Schinz.  
     *nigrescens* Oliv.  
     *sieberiana* DC. var. *woodii* (Burt Davy) Keay & Brennan.  
     *tortilis* (Forsk.)
- Adansonia digitata* L.
- Baikiaea plurijuga* Harms
- Balanites aegyptiaca* L. (Del.)
- Euphorbia massaiensis* Taub. subsp. *obovata* (Schinz.) Brummitt.
- Brachystegia boehmii* Taub.  
     *spiciformis* Benth.  
     *tamarindoides*
- Burkea africana* Hook.
- Capassa violaceae* Klotzsch (*Lonocarpus capassa* Rolfe).
- Capparis tomentosa* Lam.
- Combretum apiculatum* Sond.  
     *celastroides* Welw. ex Laws.  
     *elaeagnoides* Klotzsch.  
     *ghasalense* Engl. & Diels  
     *hereroense* Schinz.  
     *imberbe*  
     *mossambicense* (Klotzsch.) Engl.  
     *obovatum* F.Hoffm.  
     *zeyheri* Sond.
- Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Leon.

*Commiphora africana* (A.Rich.) Engl. var *africana*  
                   *karibensis* H. Wild  
                   *mollis* (Oliv.) Engl.  
                   *mossambicensis* (Klotzsch) Engl.  
                   *ngogensis* Engl.

*Crossopteryx febrifuga* (Afzel. ex g. Don)

*Dalbergia melanoxylon* Guill & Hutch.

*Dichrostachys cinerea* (L.) Wight & Arn.

*Diospyros mespiliformis* Hochst. ex A. DC.  
                   *quiloensis* (Hiern.)  
                   *senensis* Klotzsch.

*Diplorhynchus condylocarpon* (Muell. Arg.) Pich.

*Entandophragma caudatum* Sprague.

*Erythrophleum africanum* (Welw. ex Benth.) Harms.

*Erythroxyton zambesiaceum* Robson.

*Euclea divinorum* Hiern.

*Grewia flavescens* Juss. var. *flavescens*  
                   *flavescens* Juss. var. *olukondae* (Schinz) Wild.  
                   *monticola* Sond.  
                   *pachycalyx* K.Schum.  
                   *subspathulata* N.E.Br.

*Hexalobus monopetalus* (A.Rich.) Eng. & Diels var. *obovatus* Brennan.

*Hyphenae*

*Julbernardia globiflora* (Benth.) Troupin.

*Kigelia pinnata* (Jacq.) DC.

*Kirkia acuminata* Oliv.

*Monotes glaber* Sprague

*Peltophorum africanum* Sond.

*Pericopsis angolensis*

*Piliostigma thonningii* (Schumach.)

*Popowia obovata* (Benth.) Engl. & Diels.

*Pseudolachnostylis maprouneifolia* Pax.

*Pterocarpus antenusii* (Taub) Harms.  
*angolensis* D.C.

*Strophanthus kombe* Oliv.

*nicholsonii* Holmes.

*Strychnos innocua* Del. subsp. *dysophylla* (Benth.) Verdoorn.

*spinosa* Lam.

*stuhlmannii* Gilg.

*Terminalia prunioides* Laws.

*randii* Bak. f.

*sericea* Burch

*Vellosia humilis*

*Ziziphus mucronata* Willd.

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APPENDIX 2.Species list of grasses collected in  
the Research Area.

Species of grass on which warthog have been recorded feeding in the Research Area are indicated by the letters "l", "r" or "s" which signify which part of the plant is eaten :

- l = leaves and shoots
- r = roots and rhizomes etc.
- s = seeds and flowering heads

Those species which occur in the Sengwa area and on which warthog have been recorded feeding elsewhere are also indicated as follows

- K = Kruger National Park (Anonymous, 1960)
- T = Tanganyika (Lamprey, 1963)
- N = Natal (Anonymous, 1962)
- Z = Zambia (Mitchell, 1963)

Where the designated area is written in parenthesis, it signifies that other species within the genus have been recorded as warthog food in that country.

Species list of grasses

|              |                                             | Record<br>from<br>Sengwa | Record<br>from<br>elsewhere |
|--------------|---------------------------------------------|--------------------------|-----------------------------|
| Alloteropsis | cimcinia (L.) stapf                         |                          |                             |
| Andropogon   | amplectens Ness.                            |                          |                             |
|              | gayanus Kunth var.<br>squamulatus (Hochst.) |                          |                             |
|              | schinzii Hack.                              |                          |                             |
|              | schirensis Hochst.                          |                          |                             |

|              |                                                       | Record<br>from<br>Sengwa | Record<br>from<br>elsewhere |
|--------------|-------------------------------------------------------|--------------------------|-----------------------------|
| Aristida     | borumensis Henr.                                      |                          | (T)                         |
|              | curvata (Nees) Trin &<br>Rupr.                        | 1                        | (T)                         |
|              | hordacea Kunth                                        |                          |                             |
|              | leucophaea Henr.                                      |                          |                             |
|              | stipitata Hack var. graci-<br>flora (Vilg.) de Winter |                          |                             |
|              | pilgeri Henr.                                         |                          |                             |
|              | rhiniochloa Hochst.                                   | 1                        | (T)                         |
|              | vestita Thunb.                                        |                          |                             |
| Bewsia       | biflora (Hack.) Goossens                              |                          |                             |
| Bothriochloa | insculpta (Hochst.) A.Camus                           |                          | T, K                        |
|              | radicans (Lehm.) A.Camus                              |                          |                             |
| Brachiaria   | brizantha (Hochst.) Stapf                             | 1                        |                             |
|              | eruciformis (J.E.Smith)<br>Griseb.                    | 1                        | (Z)                         |
|              | grossa Stapf                                          | 1                        |                             |
|              | nigropedata (Munro ex<br>Hiern) Stapf                 | 1                        | K                           |
|              |                                                       |                          |                             |
| Brachyachne  | patentiflora (Stent and<br>Rattray) C.E.Hubbard       | 1                        |                             |
| Chloridion   | cameronii Stapf                                       |                          |                             |
| Chloris      | gayana Kunth                                          | ?                        | Z                           |
|              | virgata Swartz                                        | 1, s                     | Z, T                        |
| Cymbopogon   | excavatus (Hochst.) Stapf                             |                          |                             |
| Cynodon      | dactylon (L) Pers.                                    | 1                        | Z, T, K                     |

|                |                                             | Record<br>from<br>Sengwa | Record<br>from<br>elsewhere |
|----------------|---------------------------------------------|--------------------------|-----------------------------|
| Dactyloctenium | aegypticum (L.) Beauv.                      |                          |                             |
|                | giganteum Fisher and<br>Schweickerdt        | 1, s                     |                             |
| Danthoniopsis  | minor Stapf and Hubb                        |                          |                             |
| Dichanthium    | papillosum (Hochst.)<br>Stapf               |                          |                             |
| Digitaria      | brazzae (Franch.) Stapf                     |                          | Z, (K)                      |
|                | milanjiana (Rendle)<br>Stapf                | 1, r                     | Z, T                        |
|                | nemoralis Heur.                             |                          |                             |
|                | perrottetii (Kunth)<br>Stapf                |                          |                             |
|                | setivalva Stent                             |                          |                             |
|                | ternata (Hochst.) Stapf                     |                          |                             |
| Echinochloa    | colonum (L.) Link                           | 1, r                     | (Z)                         |
|                | pyramidalis (Lam.) Hitch-<br>cock and Chase | 1, r                     |                             |
| Elyonurus      | trappnelli C.E.Hubbard                      |                          |                             |
| Elytrophorus   | globularis Hack.                            |                          |                             |
| Enteropogon    | sp.                                         |                          |                             |
| Eragrostis     | atrovirens (Desf.) Trip.<br>ex Stend        |                          |                             |
|                | biflora Hack.                               |                          |                             |
|                | cilianensis (All.) Lutati                   |                          |                             |
|                | denudata Hack.                              |                          |                             |
|                | rigidior Pilg.                              | 1                        |                             |
|                | rotifer Rendle                              | 1                        |                             |
|                | superba Peyr.                               | 1                        | T                           |
|                | viscosa (Retz.) Trin.                       |                          |                             |
|                | species                                     | 1, s                     |                             |

|               |                                                            | Record<br>from<br>Sengwa | Record<br>from<br>elsewhere |
|---------------|------------------------------------------------------------|--------------------------|-----------------------------|
| Eriochloa     | macclounii Stapf                                           |                          |                             |
| Eulalia       | geniculata Stapf                                           |                          |                             |
| Hackelochloa  | granularis (L.) O.Ktze                                     |                          |                             |
| Heteropogon   | contortus (L.) Beauv. ex<br>Roem. and Schult.              | r                        | T                           |
|               | melanocarpus (Ell.) Benth.                                 |                          |                             |
| Hyparrhenia   | dissoluta (Nees ex Stend)<br>C.E.Hubbard ex Hutch.         |                          |                             |
|               | filipendula (Hochst.)<br>Stapf                             |                          | Z                           |
|               | filipendula (Hochst.)<br>Stapf var. pilosa (Hack)<br>Stapf |                          |                             |
|               | rufa (Nees) Stapf                                          | r?                       |                             |
|               | sp. near dichroa (Stend.)<br>Stapf                         |                          |                             |
| Imperata      | cylindrica (L.) Beauv.                                     |                          |                             |
| Leersia       | hexandra Swartz                                            | ?                        |                             |
| Loudetia      | flavida (Stapf) C.E.<br>Hubbard                            |                          |                             |
| Leptocarydion | vulpiastrum (De Not.)<br>Stapf                             |                          |                             |
| Melinis       | ambigua Hack.                                              |                          |                             |
| Oryza         | barthii A. Chev.                                           | r                        | Z                           |



|               |                                                  | Record<br>from<br>Sengwa | Record<br>from<br>elsewhere |
|---------------|--------------------------------------------------|--------------------------|-----------------------------|
| Panicum       | atrosanguineum Hochst. ex<br>A. Rich             |                          |                             |
|               | dregeanum Nees                                   |                          |                             |
|               | laevifolium Hack.                                | ?                        |                             |
|               | maximum Jacq.                                    | 1                        | Z, T, K                     |
| Perotis       | patens Gandoger                                  |                          |                             |
| Petrina       | pruinosa (C.E. Hubbard)<br>Phipps                |                          |                             |
| Phragmites    | species                                          |                          |                             |
| Pogonarthria  | squarrosa (Licht.) Pilg.                         |                          |                             |
| Rhynchelytrum | bellespicatum (Rendle)<br>Stapf and C.E. Hubbard |                          |                             |
|               | repens (Willd.) C.E.<br>Hubbard                  |                          |                             |
|               | villosum (Parl) Chiov.                           |                          |                             |
| Rottboellia   | exaltata L.                                      |                          |                             |
| Sacciolepis   | africana C.E. Hubbard &<br>Snowden               | 1, f, s                  |                             |
|               | transbarbata Stapf                               |                          |                             |
| Schizachyrium | inclusum Stent.                                  |                          |                             |
|               | jeffreysii (Hack.) Stapf                         | 1                        |                             |
| Schmidtia     | pappophoroides Steud.                            | 1                        | (K)                         |
| Sehima        | ischaemoides Forsk.                              |                          |                             |
| Setaria       | angustifolia Stapf                               | ?                        |                             |
|               | eylesii Stapf & Hubbard                          | ?                        |                             |
|               | homonyma (Steud.) Chiov.                         |                          |                             |

|              |                                                                 | Record<br>from<br>Sengwa | Record<br>from<br>elsewhere |
|--------------|-----------------------------------------------------------------|--------------------------|-----------------------------|
| Setaria      | pallide-fusca (Schumach.)<br>Stapf & C.E. Hubbard               | 1, f                     | Z                           |
|              | sphacelata (Schumach.)<br>Stapf. & C.E. Hubbard ex<br>M.B. Moss | r, 1                     | T                           |
| Sorghum      | halepense (L.) Pers.                                            |                          |                             |
|              | versicolor Anderss.                                             | s                        |                             |
| Sporobolus   | albomarginatus Stent &<br>Rattray                               | 1                        |                             |
|              | angustifolius De Wild<br>(or Stapf)                             | 1                        |                             |
|              | festivus Hochst. ex A.<br>Richie                                | 1                        | Z                           |
|              | marginatus Hochst. ex A<br>Richie                               | 1                        | T                           |
|              | panicoides A. Richie                                            | 1                        |                             |
|              | pyramidalis Beauv.                                              |                          | Z                           |
| Stipagrostis | uniplumis (Lichst.) de<br>Winter var. uniplumis                 |                          |                             |
| Trichoneura  | grandiglumis (Nees) Ekman                                       |                          |                             |
| Tristachya   | superba (De Not.)<br>Schweinf. and Aschers                      | r, 1                     | Z                           |
| Urochloa     | bolbodes (Steud.) Stapf                                         | 1                        |                             |
|              | pullulans Stapf                                                 | 1                        |                             |
|              | trichopus (Hochst.) Stapf                                       | 1                        | T                           |

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APPENDIX 3.Age and sex classification of warthog in the field.

Studies of population and sounder structure of warthog in the Sengwa Area have been based mainly on age and sex classification of animals in the field. The criteria on which classifications were based are described below and their reliability is discussed. The system used at Sengwa was initially adapted from published data of Child, Sowls and Mitchell (1965) and Roth (1965) on warthog growth. Both authors have proposed field aging criteria for warthog and Roth (1965) described development of sexual dimorphism.

Child et al. provide body measurements of 110 animals shot during October and November in the Nagupande Area (60 km west of Sengwa) and note that shoulder height and length of head + body provide the clearest means of distinguishing between juveniles, yearlings and animals older than 24 months. They also suggest that tusk size may be used to distinguish between 2 year old males and those older than 36 months in the field.

Roth measured growth of captive warthog and examined body measurements of wild warthog to propose the following criteria for field age classifications :

1. Body size in relation to the accompanying sow.
2. Ratio of body length to body weight.
3. Development of warts and tusks.
4. General physical appearance.

Roth defined 6 field age classes in warthog. The categories cut across year classes and because warthog are seasonal breeders in



Rhodesia some of his classes are not represented in the population throughout the year. Consistent application of his scheme was difficult in practice. In order to obtain large samples of classifications in the Sengwa Research Area a simpler system which could be readily used by Game Scouts was developed.

Field classification used in the Sengwa Area.

1. Age Classification.

Four age classes have been recognised :

1. Juveniles - warthog up to 12 months old
2. Yearlings - 12 to 24 months old
3. Sub-adults - 24 to 36 months old
4. Adults - older than 36 months

The breeding season of warthog is spread over a period of approximately 3 months in the Sengwa Area, from October to December. Since it is impossible to distinguish between 10 and 13 month old animals or between 22 and 25 month old animals (i.e. animals born in the same season but which by definition fall into different age classes) in the field an arbitrary birth date is taken. This is 1 October each year, when all animals of a particular year class are deemed to pass into the next age class. For example warthog born the previous October (11 months old) and those born in December of the same breeding season (9 months old) all pass through to the yearling age class on 1 October.

The following main criteria are used to distinguish age classes

1. Body dimensions; should<sup>er</sup> height and length of head + body.
2. Development of tusks and warts.

3. General physical appearance; shape of back, development of withers, hind quarters and heaviness of head.

A more precise statement of these criteria for each age class over three periods within the annual cycle is given in Table 1 and illustrated in Fig. 1.)

## 2. Sex classification.

Sexual dimorphism is shown in the following characters :

1. Supra-oral warts are present in males but absent in females.
2. Infra-orbital warts are well developed in males older than 24 months but poorly developed even in very old females.
3. Tusk shape and size. This is a very variable character which has to be used with discrimination and in conjunction with other characters. Ewer (1958) has drawn attention to the tendency of males to have out-flaring tusks while females have more tightly curved, inward pointing tusks.
4. Testes. A darkly pigmented scrotal sac in males.
5. Penal button. Evident in males.
6. Nipples. Evident only in females which have farrowed and suckled.

Classifying an animal as a female on the basis of an apparent absence of one or two male characters, such as 1, 2, 4 and 5 above, is avoided.

## Terminology

Age classes defined here follow the generally accepted practice of distinguishing between year classes in a species with a well

defined breeding season. The terms used here (juvenile, yearling, sub-adult and adult) denote stages of growth which can be distinguished in the field rather than stages of sexual maturity. Warthog reach sexual maturity before physical development is complete. Females are sexually mature at 18 months while they are still yearlings and males in Rhodesia become sexually mature at 30 months (Child, Roth and Kerr, 1968). Male and female warthog in Uganda reach sexual maturity at 18 to 20 months (Clough, 1969). Tame free-ranging male warthog reared at Sengwa have become sexually mature by 18 months. A male born to one of the tame females and not artificially reared copulated with an oestrus female at 20 months. Age at sexual maturity may differ in different populations and does not appear to be resolved for male warthog. It is relatively easy to extract the numbers of sexually mature and immature animals from classifications based on year classes or growth stages. The reverse operation of extracting year classes or age classes from data originally recorded as "mature" and "immature" is obviously not possible.

#### Validity of classes and field criteria.

Aging animals in the field can be a highly subjective procedure. It is therefore necessary to examine whether the differences between age classes are sufficient to allow confident classification in the field. Because warthog in Rhodesia have a short breeding season, age classes are more distinct than in a species with an extended breeding season. The short breeding season means that at any time of the year a distinction has to be made between animals differing by at least 9 months in age. Sexual and individual variations in

growth may affect the reliability of such distinctions which also become more difficult as growth rate declines in older animals (Figs. 2 & 3).

Head and body lengths and weight of warthog at different times of the year (Figs. 2 & 3) indicate that differences between the age classes are greatest during the October to December period and least during the May to September period. During October to December it is possible to distinguish between four age classes on the basis of body dimensions expressed by length of head + body and general physical appearance expressed by weight. Similar curves are obtained for measurements of head size and neck circumference. Length of head + body and shoulder height (Child et al. 1965) are valid criteria for distinguishing juveniles from older age groups at all times. Juvenile lengths, heights and weights show no overlap with those of yearlings (Figs. 2 & 3 and Child et al., 1965). Yearling males are generally distinguishable from sub-adult and adult males by these criteria. However, by June, differences in body size between yearlings of both sexes and adult females are not as marked and recourse to other criteria (tusk and wart development - see below) is necessary. Yearling males at 22 months (August - September) are as long as adult females and nearly as heavy. Similarly, by February the distinction between sub-adults (30 months) and adults (42+ months) cannot be made with any confidence. The distinction between 22 month old and 34 month old females i.e. between yearlings and sub-adults from May to September, is also unreliable.

The development of tusks and warts provides the most useful basis for classifying animals older than 18 months when used in



conjunction with body size and particularly during the May to September period. Tusk and wart development also enable solitary animals and groups of one age class to be classified effectively. Tusks are generally not visible at all in juveniles and only become obvious, in the field, in animals older than 24 months. This feature allows juveniles on their own, when 10 to 12 months old, to be identified. It also allows yearlings to be distinguished, in conjunction with body size, from adult and sub-adult females between May and September. Distinction between adult and sub-adult females by tusk size is not reliable (Child et al. 1965). The usefulness of tusk size for distinguishing sub-adult and adult males was noted by Child et al. and is supported by our experience at Sengwa.

Infra-orbital warts of adult females protrude about 1.5 to 2.5 cm from the zygomatic arch on which they are anchored, while in adult males they protrude from 6 to 10 cm, in sub-adult males 4 to 5 cm and in yearling males 2 to 3.5 cm. Infra-orbital warts of juvenile males may, by the time they are ten months old, protrude as much as in adult females. They are thus a useful character in distinguishing between adult females and sub-adult and yearling males, as well as between males of various ages. The front or supra-oral warts of juvenile males protrude about 1 cm by the time the animals are 10 months old. A year later they are about 2 to 2.5 cm long and in adult males 3 or more centimetres.

Wart growth may however be variable. Tame male warthog reared at Sengwa all had very much larger warts than feral males of comparable age. Tame animals were also larger and heavier and had shown signs of sexual maturity between 12 and 15 months of age. MacSweeney at

20 months weighed 185 lbs. as opposed to a mean weight of 100 lbs. for wild warthog of similar age. In physical appearance and development of warts he resembled an adult male. The tusks of tame males did not, however, protrude beyond the upper lip any more than in wild males of the same age. Changes in the development of warts and tusks are indicated in Fig. 1. Drawings are based on photographs. Details of upper canine growth can be found in Child *et al.* (1965).

Sexual dimorphism has been described by Roth (1965). The main features are illustrated in Fig. 1 and are listed above. The distinction between the sexes in the field is not always easy and, for females, depends largely on the absence of certain features present in males. Errors are particularly likely in immature animals. In mature animals large females with prominent tusks are readily classified as males by the uninitiated and particularly if they are accompanied by a younger but still adult female. Tusk size alone is not a valid criterion for distinguishing between sexes.

#### Summary and conclusions.

1. Field aging criteria for warthog in the Sengwa Area of Rhodesia are described and discussed. A short breeding season and patterns of growth allow three age classes of warthog to be distinguished in the field throughout the year. These are juveniles (up to 12 months old), yearlings (12 to 24 months old) and animals older than 24 months.

2. Four age classes, juveniles, yearlings, sub-adults (24 to 36 months) and adults (36 months and older) can be distinguished during the breeding season, from October to December. From January to

September body size as a criterion for distinguishing between yearling, sub-adult and adult animals becomes increasingly unreliable. Sub-adult females become indistinguishable from adult females on all criteria and recourse to head and tusk development becomes necessary to distinguish yearlings from adult and sub-adult females.

3. Tusk development and general physical appearance generally make recognition of sub-adult males possible for most of the year. However, if sub-adults are to be distinguished in field classifications, it is also necessary to sex animals because differences in size between the sexes are apparent by 24 months of age.

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APPENDIX 4.Techniques used in the capture and tagging of warthog in  
Sengwa Research Area.

Capturing and tagging animals is usually necessary in field studies of their social behaviour, home range and movement. Recognising numbers of untagged individuals is difficult in wooded savannas of Southern Africa because game animals can seldom be viewed clearly for long periods. Immobilizing drugs have greatly facilitated capture of larger game animals both for marking and translocation (Hagarthorn, 1965). Use of drugs is, however, not always feasible or desirable. In certain types of country and with certain species more direct, old-fashioned techniques may be more successful. Details of these methods are seldom reported in the scientific literature despite the need for their development and refinement.

This paper reports on a method of capturing warthog at their holes and on a variety of tags used on warthog over a period of three years. Warthog, because they wallow frequently and sleep in holes place considerable strain on tags attached to them. Experience gained from warthog may be useful in developing reliable and durable tags for other species.

A. CAPTURE

The method is based on warthogs' habit of sleeping in holes at night. A tunnel-shaped net is placed over the entrance of an occupied warthog hole before dawn and when warthog bolt from the hole they rush into the tunnel and become entangled in the net. A team



of 10 to 15 men, waiting near the hole converges on the catch immediately. Animals are pinned down, bound and then removed from the net to be weighed, measured and tagged; they are released simultaneously, as a group. Over 250 warthog have been captured by this method. No tranquillizing or other drugs have been used on captured animals destined for immediate release. None of the catching team have, apart from an occasional scratch or bruise, been injured.

The tunnel-shaped net (Fig. 1) is made from a game capture net of 6 mm ( $\frac{1}{4}$  ins.) hemp rope with a mesh size of 15 cm (6 ins.) from knot to knot; the net is 2 m deep by 20 to 25 m long. The net is folded in half (2 x 10 - 12 m) to provide a double layer of net which is then fixed over 4 metal hoops to produce a cylinder approximately 4 m long and 140 cm in diameter and open at one end. Hoops are made from 16 mm ( $\frac{5}{8}$  ins.) reinforcing iron which is covered by 19 mm ( $\frac{3}{4}$  ins) p.v.c. garden hose and they are bound to the net with rope. Although only three hoops are required to support the net, a fourth hoop fixed about 40 cm from the open end of the net makes it easier to anchor the net and to maintain a wide opening to the tunnel.

Despite a double thickness of net warthog occasionally break through the tunnel. An additional net, 25 m long by 2 m deep is therefore draped over and around the cylindrical net once the latter is in place.

Other requirements are 6 metal tent pegs 30 to 40 cm long; 10 or more 3 m lengths of 5 - 6 mm ( $\frac{1}{4}$  ins) cotton rope, each with a spliced eye for binding the animals' legs and 6 snout ropes of 12 mm ( $\frac{1}{2}$  ins) hemp rope each about 3 to 4 m long. Cotton ropes

used for tying legs can be used as snout ropes for juvenile warthog.

Initial attempts to catch warthog at their holes failed and this was largely due to ignorance of warthog behaviour in relation to holes. The types of hole used by warthog and aspects of their behaviour in relation to holes have been described in Chapter 3, Section B of this thesis.

Holes being used by warthog are located and then watched in the evening by a pair of observers who station themselves in suitable trees 40 - 100 m from the holes. Holes are watched from 2 hours before sunset until it would be too dark to see a warthog. Observers wait until dark because warthog sometimes enter holes and then later emerge. Attempts to catch, even at well used holes, without seeing warthog enter have invariably failed. A necessary preliminary to capture is searching an area for holes, inspecting these and, at some multiple entrance holes, blocking all but one or two entrances or possible exits. Blocking supernumerary entrances and possible but unused exits does not disturb animals for long. Smaller antbear type holes should be examined with a torch; some are too short to effect capture because the animals sleeping in them lie at the entrance.

Warthog emerge from their holes at about sunrise. When disturbed they may do so at any time of the night. We attempted to block holes at or slightly before dawn or first light. During 1966 nets were placed between 0200 and 0400 hours but this was found to be unnecessary. Approaching the hole immediately before blocking it with poles or placing the net over the entrance is probably the most critical stage of capture. A well co-ordinated and concerted effort

is vital. At least one man must be able to lead the team onto the hole swiftly and surely. Hesitation and searching for the hole entrance in the semi-dark, in all but the larger types of hole, causes hogs to bolt before the hole can be blocked.

Holes with small entrances or the smaller types of hole (e.g. antbear holes) are best blocked first with poles; 4 to 6 men, each carrying a 2 m pole with a maximum diameter of about 15 cm, rush up to the hole from about 5 m and thrust the poles well into the entrance. Additional poles can be pushed in later if necessary. The net is placed over the entrance and anchored before the poles are withdrawn. At erosion-gulley holes or holes with large entrances the net is placed directly over the entrance. Five men can effectively rush onto a hole with the net (Fig. 2) and extend it so that, if warthog do emerge immediately, they run into the tunnel.

Once in place the net is anchored by means of logs and tent pegs which hold the front hoop. Simultaneously the outer net is run around the cylindrical net and the ends are arranged so as to ensure that, if the front hoop of the tunnel is pulled away from the hole entrance, the resulting gap is closed by the outer net.

If, when the nets have been set and the poles withdrawn, the hogs do not emerge the catching team waits quietly near the hole. The wait can be anything from a few minutes to more than twenty four hours. Attempts to induce trapped warthog to bolt from their holes are sometimes successful but more often inhibit emergence. The methods tried include stamping over the chamber of the hole, rattling logs in any additional entrances, poking long sticks into the hole and smoking them out.



Members of a warthog group generally bolt from the hole together. The struggling mass in the nets must be rapidly pinned down to avoid animals injuring one another. Fortunately the tusks of older hogs tend to become entangled in the net. A noose (sometimes 2 in adult males) is fitted around the snout of each animal as soon as possible. When dealing with animals older than 15 months this snout rope is held firmly by one man until the hog is released. After the tusks have been effectively immobilized the legs are bound and animals are removed from the net. Adult sows usually require 3 or 4 men and adult males 4 or 5 men to hold them during measuring and tagging. One man can usually handle a juvenile once it has been tied.

Captured hogs are released simultaneously. They are first lined up facing in the same direction at intervals of 2 to 3 metres. All ropes are then removed. Animals' heads are held firmly against the ground, the jaws are clamped by holding them well behind the canines and a knee is pressed against the neck (Fig. 3). The catch is released after a count-down, at which everyone jumps backwards and clear of the animals. Some hogs lash out sideways as they run off and it is important to those holding animals to move back and away from the hogs unimpeded. Adequate spacing between hogs is also essential; trouser seats have been ripped on stepping back towards an adjacent hog. None of the animals handled has shown any inclination to turn and attack after being released.

### Results

Effectiveness of the technique can be evaluated from the following data :



1. Successful capture days as a percentage of total days on which capture was attempted. Mobilizing a team for capture involves transport and man hour costs and this datum is thus of value.
2. Percentage success per hole at which capture was attempted.
3. Number of warthog caught per hole.
4. The number of animals which escaped or remained in holes, or both, at which an otherwise successful capture was effected. (Table 3)
5. Number of warthog destroyed as a result of injuries sustained in capture. (Table 3)
6. Duration of pre-emergence waits at holes and of handling captured groups. (Table 2)

Results are summarised in Tables 1 to 3.

Records of pre-emergence waits and of handling warthog in 1966 are incomplete and have been omitted from Table <sup>2</sup>1. The 1969 results have been divided into those captures made during out normal tagging programme and those made during a 24 day period in August, 1969.

Between June, 1966 and August, 1969, 257 warthog were captured. During these three years capture was attempted on 100 days, of which 69 were successful, with an average of 3.7 warthog being caught per successful capture day. On some days attempts were made to catch at more than one hole and success per hole attempted was 66%. The greatest single catch was ten animals and eleven hogs have been caught at three holes on one day.

The durations of pre-emergence waits are given only for successful catches. Catches have occasionally been abandoned when the wait has been too long (ten hours in one instance). Long waits

have also been made at holes which finally proved to be empty.

The August, 1969 capture operation was performed in the Lutope Experimental Area and the aim of the operation was to test the capture technique as a possible means of removing the entire warthog population from the 4 square mile Experimental Area at a future date. A capture team of twenty four men was used. The larger team allowed more holes to be watched and more capture attempts to be made. The lower capture success per hole is probably a reflection of attempts to block nearly all occupied holes each morning. Only 15 capture days were realised during the 24 day operation. Two days were taken up by extraneous matters but on the remaining 7 days no warthog were seen entering holes the previous evenings. The number of holes which can be watched each evening can thus effectively limit the rate of capture by this method.

In August, 1970 two teams each of 18 men captured (and removed) 70 warthog from the Lutope Area in 25 days; 63 of these warthog were removed from a 4 square mile enclosure.

#### B. TAGS

Warthog were tagged in order to study their home range behaviour in limited parts of the Sengwa Research Area. Tags had to be durable and allow individual animals to be identified in the field. Design for easy recognition and recording by numerous assistants was also important.

The following tags were used :

##### 1. Ear tags

- a) "Ketchum tamperproof" cattle ear tags
- b) Plastic rotating ear tags manufactured by Dalton Supplies Ltd.

2. Ear notches
3. Shoulder harnesses
4. Collars

1. Ear tags.

Neither type of ear tag has proved satisfactory. Of 43 animals tagged with Ketchum metal ear tags, 11 are known to have lost the tags and 3 to have retained them (one after a month, one after 7 months and one after 4 years). Although 30% of the hogs tagged with Ketchum ear tags have been recaptured, 77% of these had lost their tags within periods varying from 3 months to 3 years.

The retention of rotating plastic ear tags appears to have been better. Of the 150 animals tagged with plastic tags (many also received a metal tag), 33 have been recaptured or recovered. Of these 18 or 54% had lost their tags.

Recovered tags have shown tooth marks and they have become brittle. Tame animals have been seen chewing one another's collars and they also nibble at wrist watches and rings, behaviour which suggests that ear tags may be destroyed or torn out by conspecifics.

2. Ear punches

Ear punches designed for domestic stock have been used to notch warthog ears. A "V" shaped punch has been used on juveniles and a "U" shaped punch on older animals. The "U" removes more of the ear

than the "V" and for certain notching combinations is unsuitable for small ears. Warthog ears allow four distinct notching positions. By using a 1, 2, 4, 7 system commonly used in edge-punched card index systems and by using one ear to denote tens and the other units, numbers from 1 to 99 can be punched on ears. Hundreds can be denoted by a hole punched into the centre of the pinna.

More than 100 warthog have been marked<sup>6</sup> by ear notches. Both ear and punch are swabbed with alcohol before notching. Notches often bleed profusely but heal rapidly. Clearly defined notches have been seen on animals recaptured between 3 and 12 months later. Hogs tagged at ten months old have shown more pronounced but clearly defined notches a year later. Although warthog ears sometimes show tears these are seldom deep or likely to be confused with a punch mark.

Ear notches can be read in the field and under favourable conditions, using field glasses, it is possible to read the coded number at 50 to 80 m. Notches have often been glimpsed as animals are moving away through the bush indicating a tagged animal which can then be followed (to obtain a clearer view of the ears) and identified. The position in which a wary or cautious warthog holds its ears, together with the absence of hair on the edges, facilitates observation of these marks.

Warthog have been caught which have lost a large part or the whole of the pinna. Such losses would clearly lead to "tag losses" but our results indicate that obliteration or deformation of notches is unlikely to exceed 5%.



### 3. Shoulder harnesses.

Twelve shoulder harnesses (Fig. 4) were fitted to warthog in 1966. Harnesses were made from 6 mm ( $\frac{1}{4}$  ins.) braided nylon rope which was threaded through the edges of two flashes. Flashes were of heavy duty "Wydmark Pluvial" (a rayon fabric impregnated with p.v.c.) stitched over a core of celluloid. The longest record of a harness remaining on a warthog was 2 months. Of the four harnesses found in the field, three were intact while the fourth had a broken rope. How the animals shed the intact harness is difficult to visualize but as they were found near warthog hole entrances they may have been removed inside the holes. A slightly different harness was used with more success on peccaries by Bigler (1966).

### 4. Collars.

Apart from a rigid radio collar described elsewhere (Appendix 5) two types of collar have been used on warthog. A fairly durable collar of pluvial sewn over a celluloid core (Pienaar, pers. comm. 1966; Hanks, 1969) and a temporary tag for immature animals made from p.v.c. tennis court marker, 25 mm wide and 1.5 to 2 mm thick. Pluvial collars were 50 mm wide and by using a variety of patterns and red, white, black, yellow and green cloth, 25 distinct collars were made. Symbols were painted on temporary plastic collars using a p.v.c. cloth lacquer. Similar collars were used on kangaroos by Ealey and Dunnet (1956) and I have used their system of symbols.

Twenty five pluvial collars were placed on warthog. Six animals are known to have lost their collars, the earliest after four months when the collar was found in the field. The longest

retention was 27 months but the collar was unrecognisable in the field after about 8 months and had to be washed before it could be identified on removal. The celluloid core had fallen out, most of the p.v.c. had peeled and it was badly frayed. Two other collars have been removed in a similar condition, one after 18 months, the other after 25 months. Resightings indicate that the effective life of these collars is about seven months. After this period wear and tear obscures the colours and patterns on which identification depends. Little mud adheres to the collars before the p.v.c. coating is damaged.

Temporary plastic collars were developed primarily as an adjunct to radio tagging. The collars are cheap (10c. per collar) and unlike the pluviae or radio collars, can be fitted to immature animals without risk of the animal outgrowing its collar since they would tear off before seriously constricting the neck. Collars are fastened with a  $\frac{1}{2}$  ins. verandah bolt and washers, the weight of which causes the joint always to hang beneath the neck. Symbols are duplicated, one set appearing on either side of the neck. A stripe of a different colour from the symbols painted on the nape allows the orientation of the collar to be checked. Symbols are 34 mm wide and 39 mm high and read from top to bottom (dorsal to ventral). They can be distinguished with the naked eye at 25 to 30 m and with binoculars (8 x 30) at about 100 m.

Of 57 temporary p.v.c. collars fitted between July, 1968 and August 1969, 24 had been recovered by the end of 1969. All but one were retrieved in the field. The longest record of a collar remaining on a warthog has been 5 months but average longevity

is likely to be between two and three months. Although this is short, the collars have been extremely useful in instances where one of the animals of a group has been radio tagged. These collars have provided useful information on group composition and a high rate of recovery has provided additional information on movement.

### C. DISCUSSION

The tagging systems described here proved inadequate for a detailed study of the home range and movement of warthog. This inadequacy is ascribed to factors inherent in the study area and in warthog rather than to the shortcomings of the tags. Contact with tagged animals was too infrequent and due mainly to well developed tree, shrub and grass cover. The highest number of observations of an animal tagged with a pluviac collar was 30 made over a period of nine months. One-third of them occurred at one warthog hole over three weeks. Resightings were pathetically low despite a field staff of up to 10 observers working 15 to 25 days each month in a study area of about 25 km<sup>2</sup>.

Contact between an observer and a tagged animal depends largely on chance encounters. Observers' movements through the study area are seldom random and with few resightings a distorted picture of an animal's home range can easily emerge. Because the location of resightings depends so greatly on the observer's route, home range limits are likely to be highly unreliable unless the number of resightings is large.

Detailed information on a few animals, rather than meagre information on a large number of animals, was required. The only

method which promised to meet this requirement was that of radio tracking.

Hanks (1969) has drawn attention to the difficulties of using telemetry equipment in Africa. Not the least of these is the cost involved. The choice between the use of conventional collars and ear tags on the one hand and radio techniques on the other depends largely on the type of information required. Hanks (1969) has rightly pointed out that the use of telemetry in situations where conventional techniques would apply is an extravagance. However experience in the Sengwa Research Area has shown that the continued use of an inappropriate technique, however well tried and conventional, can be as great an extravagance.

Trials made with the various tags described above have paved the way for the development of a reliable and durable radio collar (Appendix 5).

Of the conventional tagging systems used on warthog that of ear notching appears to provide the most durable mark.

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APPENDIX 5.A radio collar for warthog.Introduction.

The successful use of radio tracking techniques in studies of larger African mammals requires, inter alia, the development of reliable and durable transmitters. Two important factors determining the success of radio collars are their range and their longevity. Range is primarily a problem for the electronics design engineer and involves the selection of a suitable frequency and the design of effective receivers, antennas and transmitter circuits. The longevity of a particular transmitter is controlled by its current drain, the size and type of the battery pack and also, very largely, by the manner in which the transmitter has been constructed, encapsulated and attached to the animal.

Radio collars for warthog have to be ruggedly constructed to withstand the considerable wear and tear that results from the animals habits of (a) sleeping in holes, (b) grooming each other, (c) frequent wallowing and (d) scratching and rubbing themselves against such objects as tree trunks and stumps - activities which usually follow a wallow. Warthog are thus well suited to test the durability and reliability of radio collar design and construction.

This report describes the construction of a radio collar which has been used successfully on warthog in the Sengwa region of Rhodesia. The performance of these transmitters and their battery requirements are discussed and the tracking system is described briefly.

### Transmitter circuit

The circuit used in these transmitters is essentially the same as that described by Tester et al. (1964) for use on deer. Transmitters differ from those of Tester in the type and polarity of the transistor used in the circuit and in the use of a broad copper strip for the loop antenna instead of 22 g. stranded wire. The circuit diagram is shown in Fig. 1. Transmitter frequency was between 48.5 and 48.7 MHz. The frequency interval between transmitters was 10KHz within the above band.

### Collar construction.

The transmitter and loop transmitting antenna are built onto a collar of transmission belting 3.8 cm wide by 3.5 mm thick. The belting is cut to a length of 84 cm for adult male collars and 70 - 71 cm for adult female warthog. The ends of the collar are joined by a  $\frac{1}{4}$  ins. verandah bolt which passes through the overlapping belting and copper strip. A strip of 26 g. copper, 2.5 cm wide is fixed to the belting with the aid of  $\frac{1}{8}$  ins. stainless steel pop rivets. The collar is opened and is only partly curved while fitting the copper strip. This ensures a tight fit between the loop and belting when the collar is closed and it also provides additional rigidity to the collar.

The collar, with loop attached, is then fashioned into a roughly elliptical shape with the joint of the collar to one side. Once the collar is fitted the joint lies on the side of the animal's neck. It is situated in this position rather than at the nape of the neck because it is easier to seal when on the neck of a recumbent animal

### 3.

and the possibility of chaffing the nape of the animal's neck is reduced.

Once the loop has been fitted to the collar the base mounting for the transmitter components are attached in the following way : Two holes are drilled through the collar to enable a piece of peg board to be attached to it. The loop is then cut between the drilled holes and a section of about 3 mm is removed. A piece of insulating peg board (38 mm x 18 mm) is then bolted over the cut ends of the loop using 8 B.A. bolts. Two tag strips are then fixed to the collar on either side of the peg board. One strip has three and the other two terminals. Only one terminal on each strip is connected to the loop. The connection is made by bolting the tag to the collar and then soldering the joint between tag and loop. This arrangement provides a fairly firm base for the transmitter which can now be assembled.

#### Transmitter assembly.

The component layout for the transmitter is shown in Fig. 1. Components are assembled in the following order :  $C_1$  is soldered to the positive and negative terminals. The leads are insulated and the component lies flat against the base of the transmitter.  $R_1$  is then soldered into position and the leads are similarly insulated. The Crystal,  $C_2$ ,  $R_2$ , the transistor and  $C_3$  are fitted and soldered in that order.

The transmitter can now be tested by connecting up a set of batteries with a 5K ohm variable resistor in the circuit. The latter allows one to check the minimum voltage at which the transmitter

will oscillate; this should be in the region of 2.2 volts. Current drain and pulse rate can be adjusted by connecting in different values of  $R_2$  and  $C_2$ . The value of  $C_3$  is adjusted to provide maximum output. The latter adjustment is carried out with the collar around one's leg and is finally checked in the field on the neck of the animal to be tagged before the collar is completely sealed.

Current drain in transmitters fitted with a BC 129 transistor has usually been about 0.8 to 1.0 ma. with values of  $R_2$  in excess of 270 K. The transmitters usually stopped oscillating at currents of less than 0.75 ma. even with lower values of  $R_2$ . By using 2N2369 transistors it is possible to reduce the current drain to less than 0.4 ma. Transmitters fitted with this transistor were generally adjusted to operate at a current drain of 0.5 to 0.65 ma. Field tests indicated that these transmitters provided a better signal than those using BC 129 transistors despite the lower current drain. Pulse rate in the collars used here has been between 1 and 2.5 pulses per second.

#### Encapsulation.

The following materials are used to encapsulate the transmitter and collar :

- a) Beeswax for the transmitter.
- b) Dental Acrylic for encasing the wax-potted transmitter and the battery pack. ("Stellon" self polymerizing rapid repair material, produced by Amalgamated Dental Company Ltd., South Africa.)
- c) "Vidaflex" ribbon and "Araldite" for enclosing the collar as well as the encapsulated transmitter and battery pack.



"Vidaflex" is a glass fibre type material and  
"Araldite" an epoxy resin.

The transmitter is first walled off with insulation or masking tape before molten beeswax, which has been allowed to cool to just above its solidification temperature, is poured into the transmitter. Beeswax has been used because of its inert properties and because the components can readily be removed from the wax should a collar be recovered. Components embedded in an epoxy resin or in acrylic would be extremely difficult to salvage. Damage to components resulting from sometimes high polymerizing temperatures of Acrylics and epoxy resins is also avoided.

After embedding the components in beeswax a pair of batteries, connected in parallel, is taped to the collar on either side of the transmitter. The battery leads for switching the transmitter on are twisted together over the transmitter; this area of the collar is not sealed until final fitting in the field. Gaps around the batteries are plugged with cotton wool smeared with molten wax. The acrylic is then mixed and spread over the battery units, the inside of the collar in this region and the sides of the transmitter. This operation is rather like icing a cake except that the acrylic polymerizes rapidly and becomes very fluid just before it sets; a spatula or similar instrument is used to work the material. I find it necessary to carry out the operation in stages. Bonding between separate sections is complete. The acrylic generates considerable heat while it is setting and it is desirable to provide a heat sink or place the unit in a refrigerator. An excess of heat can damage the batteries. However, by using old batteries for all but the last stages of acrylic encapsulation the risk of overheating can be

reduced (Fig. 2). The section immediately over the transmitter, where  $C_3$  is situated, is not sealed with acrylic until the collar is fitted in the field.

#### Fitting the collar.

The collar is eased over the head of a bound and recumbent warthog and the joint bolted. Pulse rate and signal strength are checked both audibly and with the assistance of a meter on the receiver which is at hand but not fitted with an antenna. If the signal is satisfactory the collar is removed again; if not, various values of  $C_3$  are touched into the circuit until the best signal is obtained. A battery-powered 6 v soldering iron is used to remove and replace the capacitors. When the transmitter is finally tuned the collar is removed from the animal's neck, the battery leads are soldered and insulated and the transmitter is sealed with acrylic. This section of the transmitter is then bound with vidaflex and araldite, followed by plastic insulation tape. The latter serves to protect the araldite/vidaflex seal until it is dry. Care should be taken to remove any araldite which seeps out between the windings of insulation tape. If the latter is not done, dirt adheres to the collar, particularly on the inner part, and may build up into a large mud pack which can constrict the animal's neck (Fig. 3). The collar is then placed on the animal's neck, bolted and the loop soldered. The joint is sealed with vidaflex and araldite and the sticky area is covered with a good wrapping of plastic insulation tape. Any residue of araldite is readily removed with a swab of cotton wool dipped into alcohol.

Performance.

At the time of writing (April, 1970) a transmitter life in the field of 150 days has been realised and transmitters are still working. The durability of radio collars described here has not yet been fully tested. However, those collars which have been recovered after a period of six months have shown remarkably little wear. The collars are considered to be sufficiently rugged to last 12 months which is probably as great as the working life of batteries which are currently available.

Batteries and transmitter life.

The first set of 10 collars fitted to warthog in 1969 were each powered with 4 Eveready ZM 9 mercury batteries. The capacity of ZM 9 mercury batteries is rated at 2,400 ma. The calculated life of these transmitters was in excess of 12 months. The greatest transmitter life experienced was only 40 days. A test transmitter running in the laboratory provided a life of 42 days. Transmitters powered with RM 401 H batteries and which were fitted to warthog in 1968 provided a similar transmitter life, as did one transmitter fitted with RM 3 H batteries.

One ~~transmitter~~ transmitter powered with Mallory RM 502 R batteries transmitted, in the field, for 78 days. The capacity of these batteries is the same or similar to that of the ~~ZM~~ ZM 9 batteries. The collar was later recovered, fresh batteries were connected to the circuit and the transmitter functioned immediately.

Nine transmitters, powered with Mallory ZM 12 batteries and constructed as has been described here, were fitted to warthog



between October, 1969 and January, 1970. Of these one failed the day it was put onto a warthog. This collar was recovered a month later and one of the batteries was found to be completely dead. (this particular transmitter had only two batteries which were connected in series). The failure was probably due to a faulty cell. Of the remaining eight transmitters, seven are still transmitting well with the longest still working after 150 days. The eighth transmitter started transmitting intermittently after 110 days. The fault is thus electrical or mechanical and not due to battery failure.

Kuechle (1967) states that standard mercury cells are unreliable after about 42 days and recommends the use of cells specially designed for low drain operation if a transmitter life of greater than 42 days is required. The Eveready cells which I have used are standard mercury cells. On testing the voltage of batteries recovered shortly after transmitter failure I frequently found that one pair of cells produced a normal voltage reading of about 1.3 v. while the other pair showed a potential as high as 1.1 v. but with the polarity of the cells reversed. This polarity reversal suggests a breakdown in the cells rather than that the power in the batteries was exhausted. Mallory ZM 12 batteries have an improved barrier between the anode and cathode which makes for a longer effective life at low drains (Kuechle, 1967).

Mercury cells can be damaged by overheating. This can occur while soldering leads to batteries or when potting them. Heat damage may have occurred in the single case of battery failure which was experienced with ZM 12 batteries. To minimize the possibility of



damage to cells while soldering leads to them, I have adopted the practice of leaving batteries in a deep-freeze for a few hours prior to soldering. Precautions against overheating batteries while encapsulating them have been described above.

Reliability and durability.

A fuller evaluation of these radio collars will have to await the recovery of the series of eight transmitters which are currently on warthog. These collars were, however, built on the basis of experience gained from 17 radio collars which were attached to warthog between September, 1969 and June, 1969. 11 of the 17 collars have been recovered; 7 were removed on recapture of the tagged animals, 2 were recovered from predator kills and 2 which had been shed were picked up. These collars differed from those described above only in the type of loop material used and in the loop-tuning capacitor. The method of encapsulating the transmitter and collar was the same.

The following causes of transmitter failure, other than battery failure, have been found in the collars which were recovered:

- i. Collar joint. Nearly all of the above collars had loops made from 24 g aluminium. The joint in the loop could not be soldered. One radio collar started transmitting intermittently after 29 days. Contact with the animal was lost on the 31st day but it was killed by a lion that night and the collar recovered the next day. The cause of the intermittent signal was traced to a faulty contact in the loop. Moisture had penetrated the seal and slight corrosion had occurred. Araldite had also seeped in between the over-lapping sections of aluminium and reduced the area of contact. This fault has been

largely circumvented by using a copper loop and soldering the joint before sealing it thoroughly.

ii. Variable capacitor ( $C_3$ ). The 17 transmitters built before June, 1969 were fitted with a 10 - 40 pica-farad ceramic trimmer. Final tuning of the transmitters was greatly facilitated by this component. However the connections between the capacitance plates and the leads of the component are easily damaged. Hair line breaks may not be discovered in time. Such breaks cause a very variable pulse rate in the transmitter, intermittent signal and even complete failure. A variable pulse rate and intermittent transmission has been traced to a faulty trimmer in one of the recovered collars and is thought to have resulted in the eventual failure of two others. The fault has also been located in a few transmitters before they were encapsulated. The use of a fixed value capacitor successfully overcame this problem.

The signals from two transmitters currently on warthog have occasionally changed from their characteristic pulse to a high speed, almost burring, signal. This has lasted for a day or two before reverting to the normal pulse rate. A test transmitter running in the laboratory exhibited the same change in pulse rate. A slight push of the electrolytic capacitor  $C_2$  which controls the pulse rate was sufficient to cause the signal to return to normal. It is possible that this component in the transmitters in question had been slightly damaged while soldering it in place or when bending the leads.

There have not been any other indications of faulty components leading to transmitter failure. Reliability is considered to be primarily a function of using high-quality components and of exercising great care in assembling the transmitters. This is

particularly necessary if transmitters are to be built on remote field stations where sophisticated test equipment is not available.

With only one exception the radio collars which have been recovered have been entirely intact. No indications of fracture to the transmitter/battery housing have been observed. The single damaged collar is illustrated in Fig. 4. The aluminium loop had been broken near the battery housing and moisture had penetrated, via the collar, into the acrylic encapsulated part of the collar. The large mud pack on this collar was almost certainly a contributing factor to the damage. The animal probably made greater efforts than it might otherwise have done to rid itself of what must have been a very uncomfortable collar. Despite an obvious reduction in the size of this animal's neck as a result of the constricting collar it was in very good condition when recaptured at the end of October. It had worn the collar for  $8\frac{1}{2}$  months. Apart from this collar no indications of moisture penetrating the transmitter/battery housing have been observed.

Three collars are known to have been shed by warthog. Two of these have been picked up and both were intact and undamaged. The two collars which have been recovered from animals killed by predators were also completely intact. The collar with an aluminium loop and faulty contact (described above) resumed transmission when it was picked up.

#### Tracking system and range.

The distance at which these transmitters can be received is very largely a function of the antenna and receiver being used. A



commercially available S.S.B. communications transceiver fitted with a frequency converter has been used in this study. The transceiver has a communication channel on about 5 MHz. Various antennas are used to track the tagged warthog. The antennas and ranges obtained with them are as follows:

i. Base stations. There are two base stations each with a vertically polarized, stacked, 5 element yagi antenna atop a self supporting mast. One mast is 16.5 m (54 ft.) high and the other 11 m (36 ft.) high. Two 5 element yagis on each mast are separated by a twelve foot boom. Both base stations are situated on the edge of an escarpment which overlooks the study area and effective antenna height is probably greater than 30 metres. Transmitters on warthog can be received adequately from these stations at ranges of up to 8 km (5 miles).

ii. Portable receiving stations. These comprise a 3 or 4 element yagi attached to a tubular telescoping mast which can be extended to a height of approximately 7.3 m (24 ft.). Ranges from these antennas vary greatly. In flat, wooded terrain with a canopy height generally greater than 8 m the range is between 1 and 2 km. These antennas will however provide a range of up to 6 km when used from points along the escarpment and an effective height of greater than 25 m.

iii. Loop antennas. These are used for homing in on animals and ranges of 600 m or more are usual during the wet season. Ranges of about 1,000 m are usual in the drier months of the year when the cover and vegetation are very much less dense.

The above receiver/antenna system has proved to be entirely



adequate for locating and "homing in" on warthog tagged with radio collars. Animals can usually be found within half an hour of obtaining an initial bearing from one of the portable stations.

An animal's position can of course be determined by triangulation from these antennas. Although sometimes quite accurate, such locations can also be extremely inaccurate and I have therefore made little use of triangulation techniques despite the great increase in the quantity of information this would have provided. Home ranges of warthog have therefore been determined almost entirely by homing in on the signal and observing tagged animals. On contact an animal's position is located on 1 : 5,000 aerial photographs of the study area. Each photograph has a 100 yd. grid drawn on it and the animal's position can be described to within 10 yards by reference to the photograph number, grid square and by visual division of the particular grid square into tenths in first the horizontal axis and then the vertical axis (east-west and north-south axes). A complete locality reference would, for example, be as follows : Photo No. 0123, G8.55. Apart from the greater accuracy achieved by direct observation of tagged animals, valuable information on their activities, behaviour and group structure is also obtained.

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