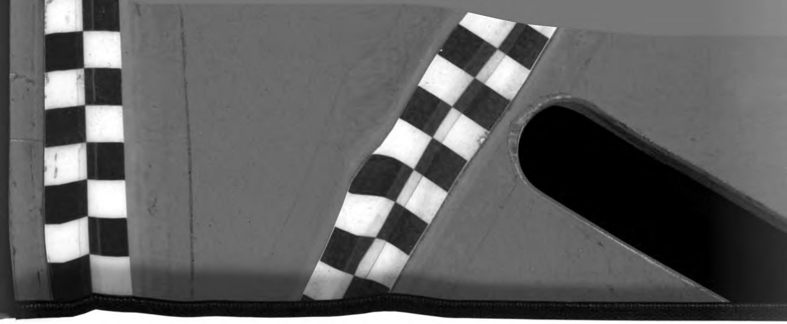


ABSTRACT

NOCTURNAL ECOLOGY OF THE SPRINGHARE, PEDETES CAPENSIS, IN BOTSWANA

By

Thomas M. Butynski

The springhare, Pedetes capensis, was studied in the Kalahari Desert, Republic of Botswana, from August, 1971 through August, 1974. Night surveys totalling 253 hours provided data on springhare habitat selection, social grouping, activity pattern and the effect of moonlight and weather on activity.

Throughout the study period springhare utilization of Kalahari dry lakebeds was greater than on the surrounding bushveld.

Springhares were strictly nocturnal. Activity pattern, group size and distance from burrow sites were closely related to the time after sunset.

Low temperatures, moderate to heavy precipitation, and the amount of moonlight altered normal springhare activity patterns.

Except for adult males, all springhares participated in group formation to the same extent. Apparently little social cohesion existed within groups.

NOCTURNAL ECOLOGY OF THE SPRINGHARE,

PEDETES CAPENSIS, IN BOTSWANA

By

Thomas M. Butynski

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Fisheries and Wildlife

1975

ACKNOWLEDGMENTS

The culmination of this thesis is due to a cooparative effort between the Botswana Department of Wildlife and National Parks, the United States Peace Corps and Michigan State University.

Deepest appreciation goes to my major advisor, Dr. George Petrides, for his guidance and encouragement.

I am grateful to my committee members, Dr. Rollin Baker, Dr. John King and Dr. Duane Ullrey, and to Ms. Maureen Slavin and Mr. Richard Kasul for their critical review of this paper.

Mr. Alec Campbell, Director, Botswana Department of Wildlife and National Parks, Dr. Wolfgang von Richter, FAO Wildlife Ecologist, and Mr. Lindsey Birch, Chief Game Warden, deserve special thanks for their support and direction through several difficult periods.

My warmest thanks are extended to Ms. Carol Fisher, Ms. Anita Longenecker, Mr. Dennis Longenecker, Mr. Jeffrey Dawson, Mr. Gregory Mann, Mr. Derek Massey, and Mr. "Kutse" Aaron for their keen interest and assistance throughout this study.

Lastly, I wish to thank Mr. Andrew Anderson, Director of Botswana Meteorological Services, and Mr. John Swanepoel, Secretary of the South African Astronomical Observatory, for providing valuable meteorological data.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure | Page

INTRODUCTION

Throughout its range in southern Africa, the springhare, Pedetes capensis, is killed in considerable numbers for meat and to alleviate crop damage. Butynski (1973) estimated that 2.5 million springhares valued at 1.5 million dollars (U.S.) are harvested annually in the Republic of Botswana, and that as much as 10 percent of the country's agricultural crops are destroyed annually by this species.

This paper is concerned with the nocturnal ecology of the springhare as determined from night surveys. The data presented here were collected from August 1971 through August 1974 as part of a larger study of the ecology of the springhare in the Kalahari Desert, Republic of Botswana.

Most studies of small, nocturnal mammals are based upon indirect data obtained from periodic trapping and laboratory experiments. Although such studies often contribute considerably towards an understanding of a species' behavior, there is no way of knowing to what extent they reflect behavior under truly natural conditions. The springhare, due to its large body size, high population densities and preference for open habitats, offered a unique opportunity to study several aspects of the ecology of a free-living nocturnal rodent. This paper is concerned with habitat selection, social groupings, activity patterns and the effect of moonlight and weather on springhare activity as determined from night surveys.

The Springhare

The springhare (Figure 1) is a nocturnal, saltorial rodent inhabiting much of the southern third of Africa (Dorst and Dandelot 1970). The fossil record indicates that the species has changed little over several million years (Meester 1965, Coe 1969). Its phylogeny remains uncertain. Wood (1962) states that the springhare is "neither related ancestrally or collaterally to other rodents."

Adult springhares weigh 3.0-3.5 kg and attain a total length of 80-88 cm, half of which comprises the tail. Males are slightly larger than females. The sex ratio is at parity in fetuses, immatures and adults.

Springhares are polygamous. Breeding occurs during all times of the year, with no breeding peaks evident. Seventy to 80 percent of adult females are pregnant at any given time. From zoo records (Rosenthal and Meritt 1973, Velte 1975), the gestation period is approximated to be 75-80 days in length. Typically springhares bear only one young at a time; twins are rare. New-born springhares weigh 300 g and are well developed, yet are completely dependent upon the mother and confined to the burrow until they attain a weight of 1.3-1.5 kg. The growth rate of the young and the age at sexual maturity have not been documented.

Sexual maturity is reached when the animals attain a weight of 2.6-2.8 kg. After their first emergence from the burrow, young springhares rapidly become independent of their mothers. With a high proportion of adult females pregnant, postpartum oestrus seems probable. It follows that the time between birth and independence of offspring is similar to the length of the 75-80 day gestation period.

Figure 1. The springhare, Pedetes capensis.

Springhare burrow systems are complex. Burrows are 8-30 m in length, with an average depth of 1 m. Burrows may occur singly, but often large numbers are found within a small area, especially where limited sites are available around favorable feeding areas. From two to ten or more surface holes may be associated with a single burrow system. Burrow chambers are absent and springhares probably sleep and rear their young where passageways join. Although groups of burrows often are termed "colonies", in most cases only one adult springhare is associated with each burrow system.

A food habits study of springhares in the Kalahari (Butynski unpublished) indicates that these animals feed almost entirely upon green grass seeds during January, February and March. At other times green grass stems and leaves, corms, roots and rhizomes are eaten. Springhares are highly selective feeders. Food parts are nipped from the plant, rapidly manipulated with the fore paws and directed into the mouth. Uningested food is not brought into the burrow.

When grazing, springhares move like rabbits, putting their weight on the toes of the front feet and then bringing the hind feet forward. At other times only the hind feet are used, and hops of 20 cm or leaps of 2 m are made. The tail, which is swung back and forth when hopping, serves as a balance organ.

Study Area

Observations were made in the Kutse Game Reserve and in the adjacent southern part of the Central Kalahari Game Reserve, Botswana, Springhare burrow systems are complex. Burrows are [illegible] in length, with [illegible] of [illegible] but often large numbers are found within small areas, especially where limited [illegible] favorable feeding areas [illegible] 1971). From two to [illegible] surface holes may be associated with a single burrow system. Burrow chambers are absent and springhares probably sleep and rear their young in [illegible] passageways. Although groups of burrows often are termed "colonies", in most cases only one adult springhare is associated with each burrow system.

[illegible] study of springhares in the Kalahari (Butynski unpublished) indicates that [illegible] feed almost entirely upon green grass [illegible] during January, February and March. At other times green [illegible] and leaves, [illegible], roots and rhizomes are eaten. Springhares [illegible] selective feeders. Food parts are nipped from the [illegible] manipulated with the fore paws and directed into the mouth. Ingested food is not brought into the burrow. [illegible]

When [illegible] springhares move like rabbits, putting their weight on the [illegible] front feet and then bringing the hind feet forward. At other times only the hind feet are used, and hops of 20 cm or less [illegible]. The tail, which is swung back and forth when hopping, [illegible] of [illegible] mm.

[illegible]

Study Area

Observations were made in the [illegible] Game Reserve and the adjacent southern part of the Central Kalahari Game Reserve, Botswana.

unless otherwise noted (Figure 2). These two game reserves are near the Tropic of Capricorn between latitudes 23°-24° South and longitudes 24°-25° East. They provide habitats that are representative of the Southern and Central Kalahari Bush Savannah (Wear 1971, Smithers 1971), which lies between latitudes 22°-25° South and longitudes 20°-26° East.

Aeolian sands cover the Kalahari Desert to a depth of 120 m. These soils tend to be structureless, mildly acid and of low fertility (Leistner & Werger 1973). The topography is predominantly flat or gently undulating.

Widely scattered throughout the region are circular, flat-bottomed, seasonally-flooded depressions. In southern Africa these are called pans (Figures 3 & 4). These lie 5 m or more below the surrounding plain and are associated with old drainage systems. On the study area these are characterized by compact, clayey calacareous soils and by bordering sand dune formations. The dense, short grass cover, and the paucity of woody vegetation on the pans (Figure 5), strongly contrast with the scattered bush and tall grass on the surrounding bushveld. Study area pans varied from 0.1 to 1.0 kilometers in diameter.

The rainy season in the Kalahari is from October to April. Rainfall can vary 70 percent from the yearly mean average of 375 mm. There is no perennial surface water in the region. Water may persist for two to three months in pans after good rains.

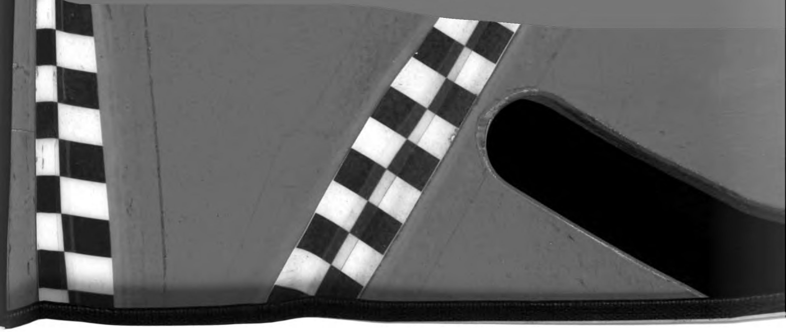
Four vegetative types were recognized within the study area. These were classified as (1) pan, (2) pan thicket, (3) bushveld or unless otherwise noted (Figure 2). These two game reserves are near the Tropic of Capricorn between latitudes 23°-24° South and longitudes 24°-25° East. They provide habitats that are representative of the Southern and Central Kalahari [illegible] (Weare 1971, Smithers 1971), which lies between latitudes [illegible]-25° South and longitudes 20°-26° East.

Aeolian sands cover the Kalahari Desert to a depth of 120 m. These soils tend to be structureless, mildly acid and of low fertility (Leistner & Werger 1973). The topography is predominantly flat or gently undulating.

Widely [illegible] throughout the region are circular, flat-bottomed [illegible] depressions. In southern Africa these are called pans (Leistner [illegible]). These lie 5 m or more below the surrounding [illegible] and are associated with old drainage systems. On the study area these are characterized by compact, clayey calcareous soils and by bordering sand dune [illegible]. The dense, short grass cover, and the [illegible] of woody vegetation on the pans (Figure 5), strongly contrast with the scattered bush and tall grass on the surrounding [illegible]. Study area pans varied from 0.1 to 1.0 kilometers in diameter.

The rainy season in the Kalahari is from October to April. Rainfall [illegible] mean [illegible] of 375 mm. There is no permanent [illegible] the rainy [illegible] water may persist for two to three months in pans after good rains.

[illegible] types were recognized within the study area. These were classified as (1) pans; (2) pan thickets; (3) bush [illegible]



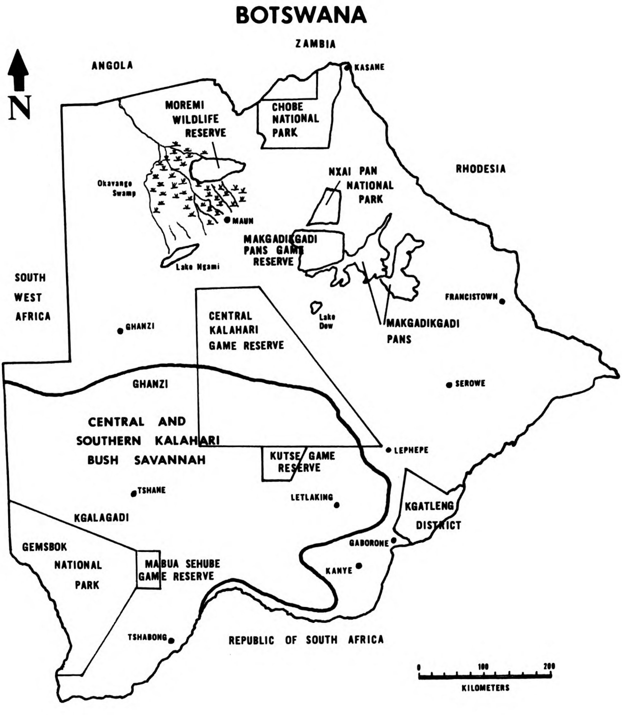


Figure 2. Map of Botswana showing the location of the Kutse and Central Kalahari Game Reserves and other places mentioned in this paper.

Figure 3. Aerial view of a Kalahari pan.

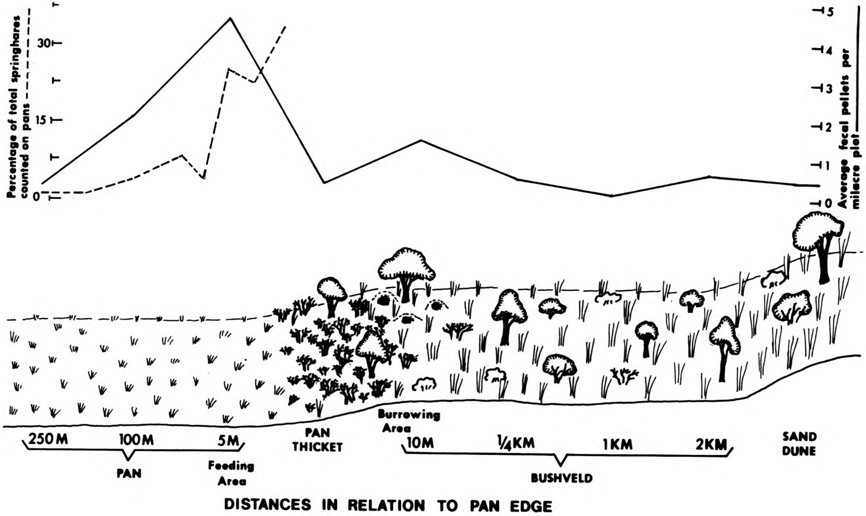


Figure 4. Vegetation zones in the Kalahari study area showing relativespringhare use as determined by fecal pellet counts and night counts.

Figure 5. A typical Kalahari pan.

Figure 5. A typical Kalahari pan.

savannah and (4) sand dune. The first and third types were subdivided into zones according to distance from the pan thicket (Figures 3 & 4).

Due to differential utilization of the pan surface by springhare, three zones were arbitrarily chosen at distances of 5 m, 100 m and 250 m from the edge of the pan thicket. All three zones were typified by their flat topography, mineral-rich clay soils, dense, short grass cover and a paucity of woody vegetation except for occasional dense clumps of the schrub, Acacia mellifera, in the lowest lying areas (Table 1) (Figure 5).

All vegetation zones not found on the pan surface were located on loose sandy soils. A well defined zone of dense woody vegetation surrounds most pans. Generally forming a band 10-100 m in width this zone was referred to as the pan thicket (Figures 3, 4, & 6). The plant species composition and growth here was distinct from both that found on the pan surface and in the bushveld (Table 1).

More than 99 percent of the vegetation on the study area was classified as bushveld (Figures 3, 4, & 7). The vegetation there was a mosaic created by differences in the relative abundance of a small number of grass and woody species (Table 1). Springhares in the bushveld were few and thus, for the purposes of the present study, it was most useful to divide this extensive habitat into zones on the basis of distance from the nearest pan thicket, i.e., up to 10 m, 1/4 km, 1 km and over 2 km.

Sand dune vegetation (Figure 4) although similar to that of the lower-lying bushveld, typically tended to exhibit the taller and coarser grass species and the taller tree species (Table 1).

savannah and (4) sand dune. The first and third types were subdivided into zones according to distance from the pan thicket (Figures 3 & 4).

Due to differential utilisation of the pan surface by springhare, three zones were arbitrarily chosen at distances of 5 m, 100 m and 250 m from the edge of the pan thicket. All three zones were typified by their flat topography, mineral-rich clay soils, dense short grass cover and a paucity of woody vegetation except for occasional dense clumps of the schrub, Acacia mellifera, in the lowest lying areas (Table 1) (Figure 5).

All vegetation zones not found on the pan surface were located on loose sandy soils. A well defined zone of dense woody vegetation surrounds most pans. Generally forming a band 10-100 m in width this zone was referred to as the pan thicket (Figures 3, 4 & 6). The plant species composition and growth here was distinct from both that found on the pan surface and in the bushveld (Table 1).

More than 99 percent of the vegetation on the study area was classified as bushveld (Figures 3, 4, & 7). The vegetation there was a mosaic created by differences in the relative abundance of a small number of grass and woody species (Table 1). Springhares in the bushveld were few and thus, for the purposes of the present study, it was most useful to divide this extensive habitat into zones on the basis of distance from the nearest pan thicket, i.e., up to 10 m, 1/4 km, 1 km and over 2 km.

Sand dune vegetation (Figure 4) although similar to that of the lower-lying bushveld, typically tended to exhibit the taller and coarser grass species and the taller tree species (Table 1).

Table 1. Dominant plant species associated with each of nine vegetation zones in the Kalahari study area.

Vegetation zone(s)	Dominant woody species	Dominant grass species
250 m, 100 m and 5 m from pan edge.	Acacia mellifera	Sporobolus ioclados Enneapogon devauxii Tragus berteronianus
pan thicket	Acacia mellifera Catophractes alexandri Rhigozum brevispinosum	Eragrostis atherstoni Schmidtia pappophoroides Digitaria spp. Tragus berteronianus Enneapogon cenchroides
10 m, 1/4 km, 1 km, and 2 km or more from the nearest pan thicket	Grewia flava Grewia retinervis Acacia giraffae Bosia albitrunca Lonchocarpus nelsii Terminalia sericea Acacia mellifera Dichrostachy cinerea Bauhinia macrantha Ziziphus mucronata Ochna pulchra	Schmidtia pappophoroides Eragrostis lehmanniana Aristida uniplumis Aristida congesta Urochloa spp. Triraphus fleckii Anthephora pubescense Eragrostis pallens
sand dune	Baekea africana Ochna pulchra Grewia flava Lonchocarpus nelsii Terminalia sericea Ziziphus mucronata	Aristida meridionalis Aristida uniplumis Schmidtia pappophoroides Eragrostis lehmanniana

Figure 6. Typical Kalahari pan thicket.

Figure 7. Bushveld vetetation typical of the Southern and Central Kalahari Bush Savannah.

Vegetation cover values were determined for the nine vegetation zones on the study area (Table 2). A detailed description of the Southern and Central Kalahari vegetation type is presented by van Rensburg (1971) and Wear (1971). The Kutse Game Reserve is described by Dawson and Butynski (1975).

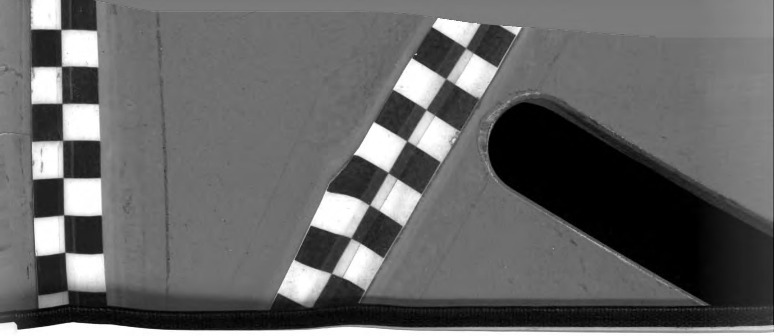


Table 2. Wet and dry season vegetation composition and springhare use of Kalahari habitats.

Vegetation zone and season	Number of transects	Woody litter	Grass litter	Basal grass	Grass canopy	Woody canopy	Average Tree height (m)	Number of springhare pellets per milacre plot
<u>250 m on pan</u>								
Dry Season	6	0.0	6.3	16.0	33.3	0.0	0.0	0.23
<u>100 m on pan</u>								
Dry Season	11	0.0	14.5	17.8	55.3	0.9	0.0	2.14
Wet Season	16	0.1	16.6	20.4	72.7	0.0	0.0	--
<u>5 m onto pan</u>								
Dry Season	12	0.5	7.7	10.8	18.2	0.2	0.0	4.72
Wet Season	14	0.0	16.4	22.7	58.8	0.1	0.0	--
<u>pan thicket</u>								
Dry Season	12	19.8	11.5	2.8	34.7	37.0	1.8	0.39
Wet Season	15	14.5	15.7	4.4	39.2	39.2	1.8	--

10 m into bushveld								
Dry Season	10	5.0	13.0	4.0	74.8	19.2	1.3	1.69
Wet Season	11	8.5	21.6	5.3	42.9	15.6	2.1	--
1/4 km in bushveld								
Dry Season	11	7.3	18.5	7.8	52.4	12.9	1.5	0.64
Wet Season	4	3.0	9.0	8.0	39.5	9.5	1.0	--
1 km into bushveld								
Dry Season	9	10.2	12.4	6.4	40.7	14.0	1.6	0.16
Wet Season	8	4.4	7.8	8.8	44.2	11.2	1.0	--
2 km into bushveld								
Dry Season	14	10.4	7.2	5.3	23.2	15.3	1.1	0.88
Wet Season	25	8.1	8.2	8.6	40.2	10.8	1.4	--
sand dune								
Dry Season	13	19.7	18.6	4.3	43.1	17.5	1.7	0.46
Wet Season	3	9.3	12.0	6.7	44.7	13.3	1.3	--

METHODS

A modification of Riney's (1963) line-point transect method provided data on vegetation composition, soil type and relative springhare use of 52 habitat types located throughout Botswana. Riney (1963), Caughley (1964) and Child (1968) all found this technique suitable in semi-arid vegetation types.

Springhares were counted during the night. A spotlamp connected to a 12-volt battery was manipulated by an observer located in the back of a truck. Surveys were made on pans and along the roads connecting the pans. While on the pans, the truck maintained a distance of 50 m from the pan's edge and a speed of 20 kph. This insured that all portions of the pan were adequately searched. Springhare eyes glow particularly brightly when caught by light. In suitable, flat, open country, such as on pans, springhares were readily located at distances of 300 m or more. The "dazzling effect" of the light usually made approach to within 20 m of the springhares possible and springhares generally remained at their feeding sites until the necessary data were collected. Information recorded consisted of estimates of distance from the edge of the pan at which each springhare was feeding, group size, and the time and location of the sighting.

A modification of Riney's (1963) line-point transect method provided data on vegetation composition, soil type and relative springhare use of 52 [illegible] throughout Botswana. Riney (1963), Caughley [illegible] all found this technique suitable in semi-arid [illegible].

Springhares were counted during the night. A spotlamp connected to a 12-volt battery was manipulated by an observer located in the back of a truck. Surveys [illegible] on pans and along the roads connecting the pans. While on the pans, the truck maintained a distance of 50 m from the pan's edge and a speed of 20 kph. This insured that all portions of the pan were adequately searched. Springhare eyes glow particularly brightly when caught by light. In suitable, flat, open country, such as on pans, springhares were readily located at distances of 300 m or more. The "dazzling effect" of the light usually made approach to within 20 m of the springhares possible and springhares generally remained at their feeding sites until the necessary data were collected. Information recorded consisted of estimates of distance from the edge of the pan at which each springhare was feeding, group size, and the time and location of the sighting.

The distance of springhares from the edge of the pans was estimated visually by three or four experienced observers. A more sophisticated measurement technique was not used because the loss of time and disturbance of springhares would have resulted in loss of other data. Errors resulting from visual estimates are thought to be consistent ones. The accuracy of the visual estimates is considered to be adequate for the present analysis.

In most cases, springhare social groups were distinct and it was easy to determine which animals were associated with one another and which were not. Only in areas of high springhare densities did it occasionally become difficult to determine if a springhare was associated with a group. An arbitrary distance of less than 30 m between springhares was chosen to indicate whether two springhares were of the same group. Caughley (1964) and Frith (1964) also found it necessary to use an arbitrary distance in their work on group sizes in kangaroos.

Cloud and wind conditions were recorded during the count. The South African Astronomical Observatory provided charts and graphs from which the time of sunset, moonrise and moonset, and moonlight intensity were calculated. Minimum temperature for the area covered was interpolated each night from data available for the two nearest Botswana Weather Bureau stations; Lephepe, 140 km to the east, and Letlhakeng, 110 km to the south, and also from readings made at the Khutse Game Reserve Camp.

The distance of springhares from the observer was, through- estimated visually by three or four experienced observers. A more sophisticated measurement technique was not used because the time and disturbance of springhares would have resulted in errors of other data. Errors resulting from visual estimates were likely to be consistent ones. The accuracy of the visual estimates was considered to be adequate for the present analysis.

In most cases, springhares were well spaced out and it was easy to determine which animals were associated with one another and which were not. Only in areas of high springhare densities did it occasionally become difficult to determine if a springhare was associated with a group. An arbitrary distance of less than 30 m between springhares was chosen to indicate whether two springhares were of the same group. Caughley (1964) and Frith (1964) also found it necessary to use an arbitrary distance in their work on group sizes in kangaroos.

Cloud and wind conditions were recorded during the count. The South African Astronomical Observatory provided charts and graphs from which the time of sunset, moonrise and moonset, and moonlight intensity were calculated. Minimum temperature for the area covered was interpolated each night from data available for the two nearest Botswana Weather Bureau stations; Lephepe, 140 km to the east, and Letlhakeng, 110 km to the south, and also from readings made at the Khutse Game Reserve Camp.

Night surveys were made each month from January 1972 through August 1973 except for May 1972. The average number of surveys per month was 2.25 (S.D. = 0.62) and the average number of hours per survey was 3.3 (S.D. = 1.40). An additional 18 surveys were carried out from September 1973 through August 1974. For comparative purposes, 25 surveys were conducted in the Kgatleng District of eastern Botswana and in the Nxai Pan and Chobe National Parks of northern Botswana (Figure 2). A total of 85 surveys, averaging 3.0 hours (S.D. = 1.3) per survey, were conducted for a total of 253 hours of observation time.

Night surveys were made each month from January 1972 through August 1973 except for May 1972. The average number of surveys per month was 2.25 (S.D. = 0.62) and the average number of hours per survey was 3.3 (S.D. = 1.40). An additional 18 surveys were carried out from September 1973 through August 1974. For comparative purposes, 25 surveys were conducted in [illegible] and in the [illegible] (Figure 2). A total of [illegible] surveys [illegible] per survey, were conducted [illegible] spring-times [illegible] the noise of the survey truck and [illegible] nearly [illegible] by the ob- [illegible] to lower itself [illegible] than remain in an upright [illegible] The numbers of springhares [illegible] and density of [illegible]

The [illegible] from those on the [illegible] could be de- [illegible] and scattered [illegible] considerably during all [illegible] once sighted, [illegible] about at distances of up to [illegible] that few of the springhares [illegible] uncounted. The width

RESULTS

Springhare Utilization of Pans

Visibility along transects was influenced by vegetation type and seasonal variations in vegetation. Grass cover on the pans varied from 1 cm to 50 cm in average height depending upon the season, amount of rainfall and grazing intensity. During all seasons, springhares were disturbed or alerted by the noise of the survey truck and moved to an upright position. In this position their eyes were nearly 40 cm above the surface of the pan and readily noticed by the observers. On only one occasion was a springhare seen to lower itself to the ground and attempt to hide rather than remain in an upright posture or to run towards its burrow. The numbers of springhares counted were not affected by changes in the height and density of pan vegetation (Table 2).

Night surveys in the bushveld differed from those on the pan in that the maximum distance at which springhares could be detected was reduced. In the bushveld, the grasses and scattered woody vegetation restricted the visibility considerably during all seasons. Nonetheless, springhares in the bushveld, once sighted, were easily followed and resighted as they moved about at distances of up to 100 m. This makes the author confident that few of the springhares within 100 m of the observers went uncounted. The width of the pan transects [illegible] the diameter of the pan while the width of bushveld transects was determined by the effects of the taller vegetation [illegible]. In both cases the average width of the transect [illegible] 100 m. [illegible] surveys made on the

Springhare Utilization of Pans [illegible]

Visibility [illegible] springhare type and seasonal [illegible] varied from 1 cm to 50 cm [illegible] amount of rainfall and grazing [illegible] hares were disturbed or alerted [illegible] moved to an upright position [illegible] their eyes were nearly 40 cm above the surface of the pan [illegible] the observers. On only one occasion was a springhare seen to lower itself to the ground and attempt to hide rather than remain in an upright posture or to run towards its burrow. The numbers of springhares counted were not affected by changes in the height and density of pan vegetation (Table [illegible]; Figure [illegible]) both indicate that [illegible]

Night surveys in the bushveld differed from those on the pan in that the maximum distance at which springhares could be detected was reduced. In the bushveld, the grasses and scattered woody vegetation restricted the visibility considerably during all seasons. Nonetheless, springhares in the bushveld, once sighted, were easily followed and recounted as they moved about at distances of up to 100 m. [illegible] springhares within 100 m of the observers were encountered. [illegible] of the pan transects was limited by the average diameter of the pan while the width of bushveld transects was determined by the effects of the taller vegetation on visibility. In both cases the average width of the transect approximated 200 m. Thus surveys made on the pan and on the bushveld were probably comparable.

From night surveys, the time interval between springhare sightings on the pan was 2.87 minutes compared to 6.54 minutes for on the bushveld ($Z = 2.38$, $p < 0.01$). Based on vegetation transects, an average of 2.36 springhare pellets were found per pan milacre plot as opposed to 0.70 pellets per bushveld milacre plot ($Z = 7.90$, $p < 0.001$).

Neither the numbers of springhares counted on the pans r = 0.08, Z = 0.42, p > 0.20) nor the distance out onto the pans to which springhares moved to feed changed with the time of year (r = 0.09, t = 0.03, p > 0.20).

Night surveys ($r = -0.89$, $t = 4.36$, $p < 0.01$) and pellet counts ($f = -0.44$, $t = 2.57$, $p < 0.02$) (Figure 4) both indicate that springhare utilization of the pan surface was heaviest along the edges and decreased towards the center. Pellet counts showed that springhares spent more than twice as much time along the pan edge than at 100 m from the edge.

Daily Activity and Feeding Pattern

Activity is defined here as the time spent above ground. The time interval between springhare sightings during night surveys provided an index to the daily activity pattern of springhare of the pan transects was [illegible] while the width of [illegible] of the taller vegetation [illegible] width of the transect [illegible] pan and on the bushveld [illegible] From night surveys [illegible] sightings on the pan [illegible] on the bushveld [illegible] an average of 2.36 [illegible] as opposed to 0.70 [illegible] 0.001). [illegible] Neither [illegible] r = 0.08, Z = 0.42, [illegible] which springhares [illegible] 0.09, t = 0.03, [illegible]

Night surveys [illegible] counts (r = 0.44, [illegible] springhare utilization [illegible] and decreased towards the center. [illegible] hares spent more than twice as much time along the pan edge [illegible] 100 m from the edge. [illegible]

Daily Activity and Feeding Pattern

Activity is defined [illegible] time spent above ground. The time interval between springhare sightings during night surveys provided an index to the daily activity pattern of springhare populations associated with Kalahari pans. Similarly, trapping has been used as an indirect index in determining the activity of small mammals (Sedorowicz 1960, Getz 1968, O'Farrell 1974).

Springhares are strictly nocturnal and were not seen above ground during the daylight or crepuscular hours. Emergence did not occur prior to 30 minutes after sunset and burrows were reentered no later than the first half hour before sunrise. The time interval between springhare sightings on the pans (Figure 8) decreased over the period from one to five hours after sunset ($r = -0.68$, $t = 3.33$ $p < 0.01$), remained more or less constant for the period between four and nine hours following sunset ($r = -0.04$, $t = 0.15$, $p > 0.20$) and increased from eight hours after sunset until approximately one hour before sunrise ($r = 0.74$, $t = 2.74$, $p < 0.05$). This activity pattern, with its prolonged peak, persisted throughout the year ($r = 0.08$, $Z = 0.42$, $p > 0.20$).

Springhares left their burrows at the start of the feeding period with empty or near-empty stomachs. The dry weights of 550 springhare stomach contents, when plotted against the time after sunset at which the springhares were killed, showed a steadily increasing weight ($r = 0.96$, $t = 5.70$, $p < 0.0005$) (Figure 9). The average distance of springhares out from the pan edge increased as the night progressed ($r = 0.62$, $Z = 3.14$, $p < 0.001$) (Figure 10). The average distance from the pan edge at one hour after sunset was 32 m. This increased to 96 m at 10 hours after sunset.

populations associated with [illegible]. Similarly, trapping has been used as an indirect index in determining the activity of small mammals (Sedorowicz 1960, West 1968, O'Farrell 1974).

Springhares are strictly nocturnal and were not seen above ground during the daylight or twilight hours. Emergence did not occur prior to 30 minutes after sunset and burrows were reentered no later than the first half hour before sunrise. The time interval between springhare sightings on the pans (Figure 8) decreased over the period from one to four hours after sunset ($r = -0.58$, $t = 3.33$ $p < 0.01$), remained more or less constant for the period between four and nine hours following sunset ($r = -0.04$, $t = 0.15$, $p > 0.20$) and increased from eight hours after sunset until approximately one hour before sunrise ($r = 0.74$, $t = 2.74$, $p < 0.05$). This activity pattern, with its prolonged peak, persisted throughout the year ($r = 0.08$, $Z = 0.42$, $p > 0.20$).

Springhares left their burrows at the start of the feeding period with empty or near-empty stomachs. The dry weights of 550 springhare stomach contents, when plotted against the time after sunset at which the springhares were killed, showed a steadily increasing weight ([illegible], $p < 0.0005$) (Figure 9). The average distance of springhares out from the pan edge increased as the night progressed ($r = 0.82$, $Z = 3.14$, $p < 0.001$) (Figure 10). The average distance from the pan edge at one hour after sunset was 32 m. This increased to 95 m at 10 hours after sunset.

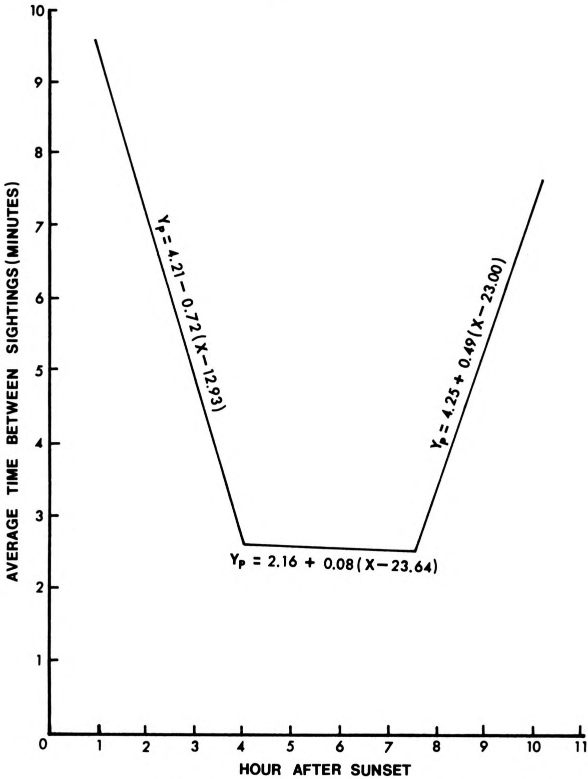


Figure 8. Average time between springhare sightings on Kalahari pans and time after sunset.

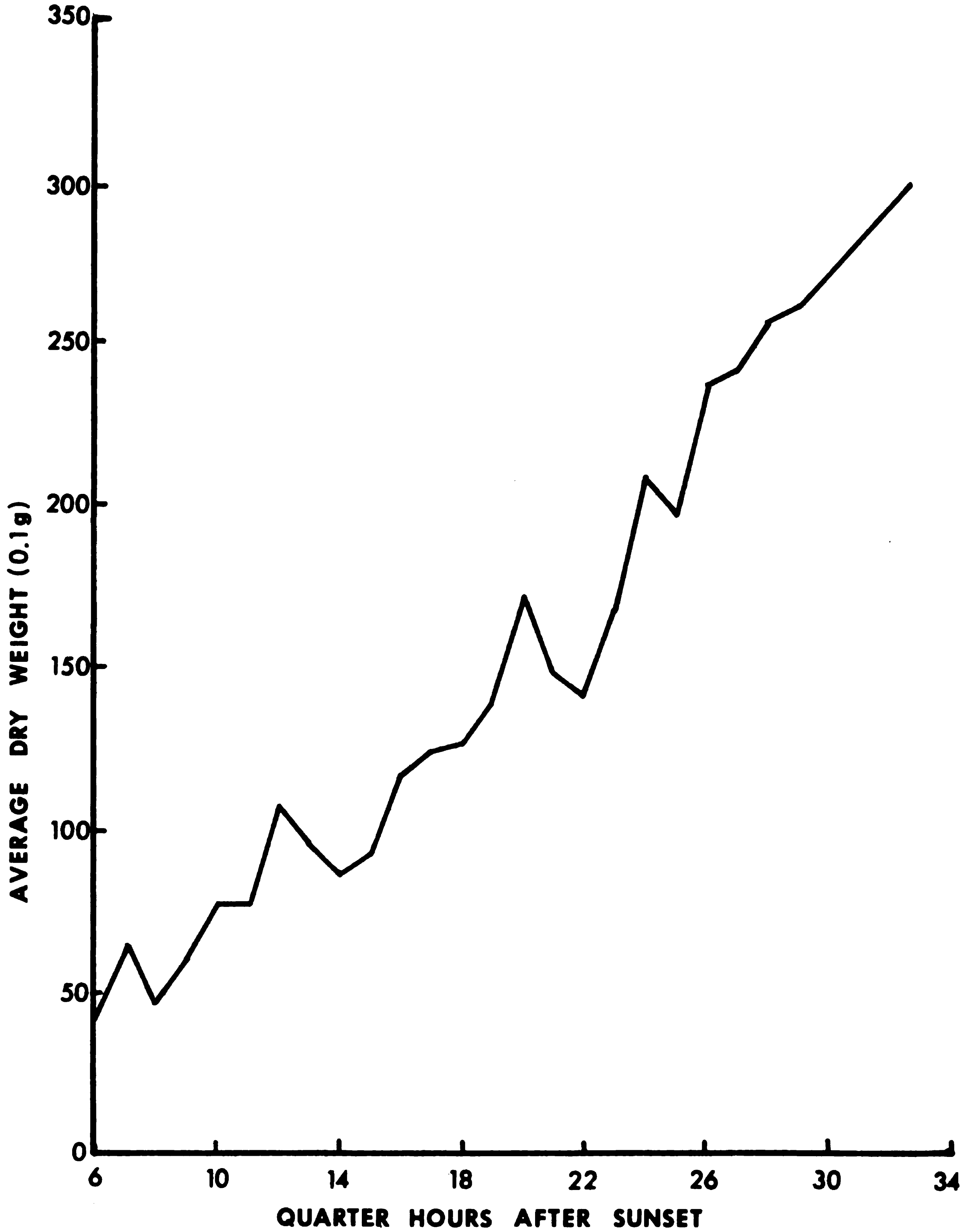


Figure 9. Relationship between the average dry weight of springhare stomach contents and time after sunset.

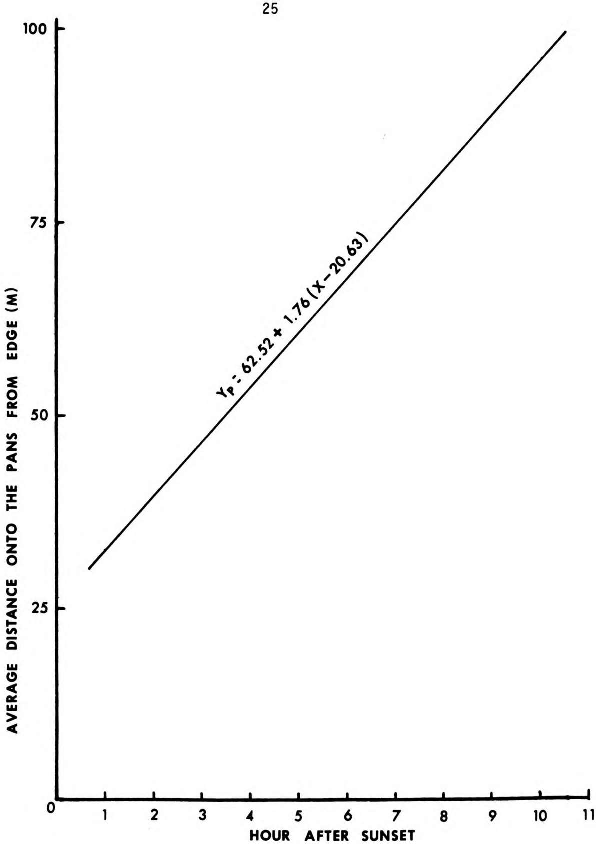


Figure 10. Relationship between the average distance of springhares onto Kalahari pans and time after sunset.

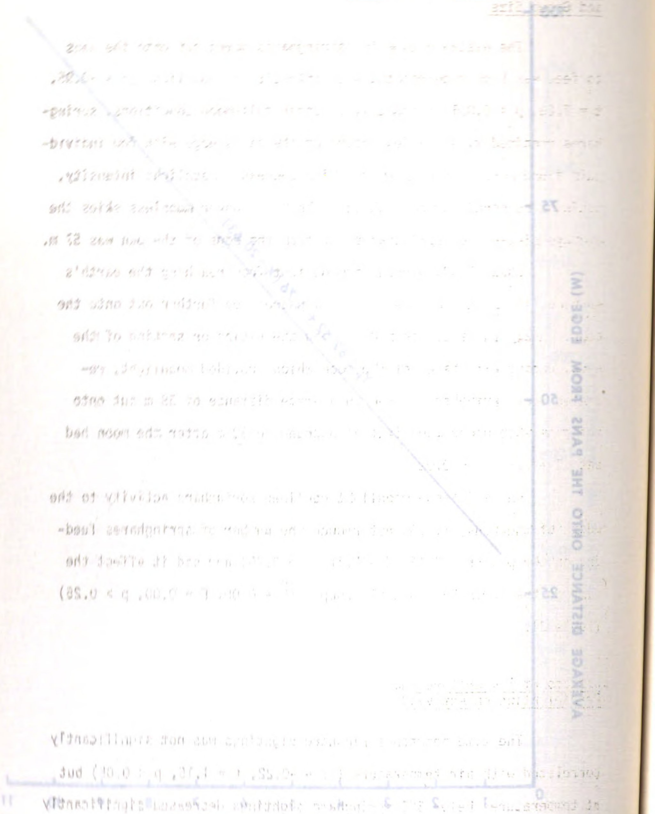


Figure 10. Relationship between the average distance of springhares onto the pans and time after sunset.

Effects of Moonlight on Activity and Group Size

The distance to which springhares moved out onto the pans to feed was highly correlated with intensity of moonlight ($r = -0.95$, $t = 7.23$, $p < 0.001$) (Figure 11). Under full-moon conditions, springhares remained within a few meters of the pan's edge with few individuals found more than 20 m away. With decreased moonlight intensity, springhares moved further out onto the pan. Under moonless skies the average distance of springhares out from the edge of the pan was 57 m.

When clouds prevented moonlight from reaching the earth's surface, it was noticeable that springhares fed further out onto the pans. Analysis of counts made during the rising or setting of the moon, during all phases of the moon which provided moonlight, revealed that springhares moved an average distance of 38 m out onto the pans when under moonlight as opposed to 58 m after the moon had set ($Z = 2.30$, $p < 0.02$).

While intense moonlight confined springhare activity to the edges of the pans, it did not reduce the number of springhares feeding on the pan ($r = 0.14$, $Z = 0.77$, $p > 0.20$) nor did it affect the size of the springhare social groups ($X^2 = 0.00$, $F = 0.00$, $p > 0.25$) (Table 3).

Effects of Temperature and Precipitation on Activity

The time between springhare sightings was not significantly correlated with air temperature ($r = -0.22$, $t = 1.15$, $p < 0.05$) but at temperatures below 5°C springhare sightings decreased significantly ($X^2 = 11.79$, $p < 0.005$) (Figure 12). At temperatures below 1°C few springhares were seen.

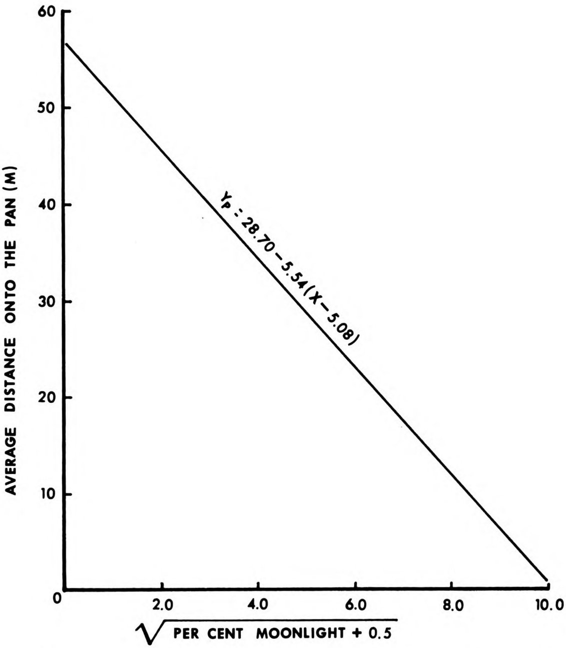


Figure 11. Relationship between the average distance of springhares onto Kalahari pans and moonlight intensity.

Table 3. Occurrence of springhare groups by size on Kalahari pans on moonlit and moonless nights.

Number of individuals per group	1	2	3	4	5	6	Totals
Moonless nights							
Numbers of groups	749	156	30	4	6	2	947
Percentages	79.1	16.5	3.2	0.4	0.6	0.2	100.0
Moonlit nights							
Numbers of groups	345	66	13	2	-	-	426
Percentages	81.0	15.5	3.1	0.5	-	-	100.0

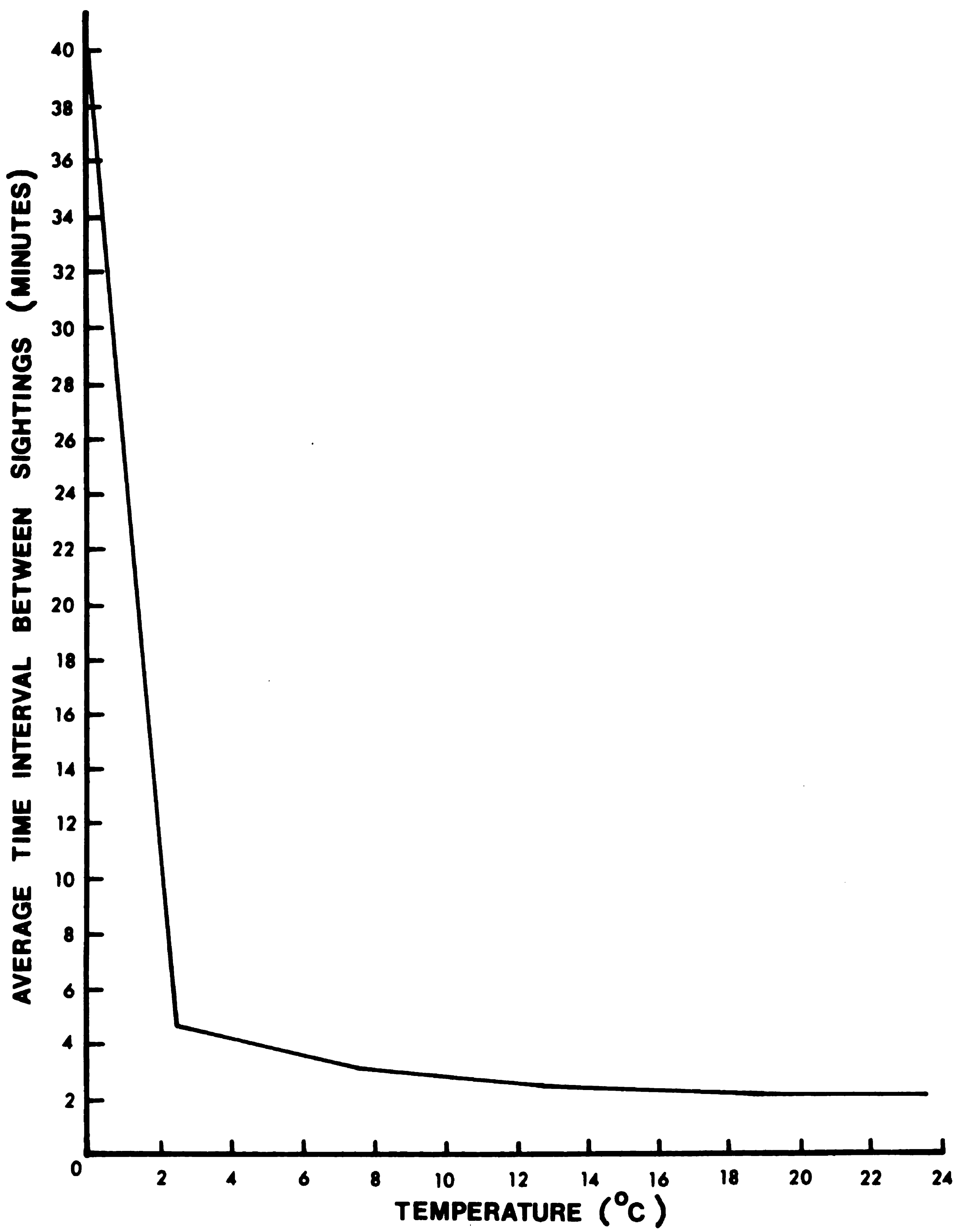


Figure 12. Relationship between temperature and the average time between springhare sightings on Kalahari pans.

Springhares remained active under conditions of light rainfall but ceased to be above ground when precipitation became moderate to heavy.

Home Range

Springhares associated with pans usually ranged 25-250 m, and occasionally as far as 400 m from their burrows to feed. The shape and size of the home range was determined by the position of the burrow relative to the feeding area and the size and quality of the latter. Thus, the home range of those springhares which fed on Kalahari pans was larger and more T-shaped than the circular home ranges of individuals which had burrows located immediately on the feeding area, as was often the case in eastern Botswana (Figure 13). The frequent occurrence of springhare feeding groups indicates considerable home range overlap, especially in dense populations.

Sizes of Social Groups

Springhare groups usually formed on the pans. This was indicated by the fact that when these groups split up, each individual moved in a different direction and to different burrow systems. Thirty-six percent of springhares on pans occurred in groups (Table 4). Thirty-five percent of the springhares on the bushveld were observed to feed in groups. A significant difference existed in the percentage of springhares that foraged in groups in the Kalahari (36%) and the Kgatleng District of eastern Botswana (47%) ($X^2 = 17.78$, $p < 0.005$).

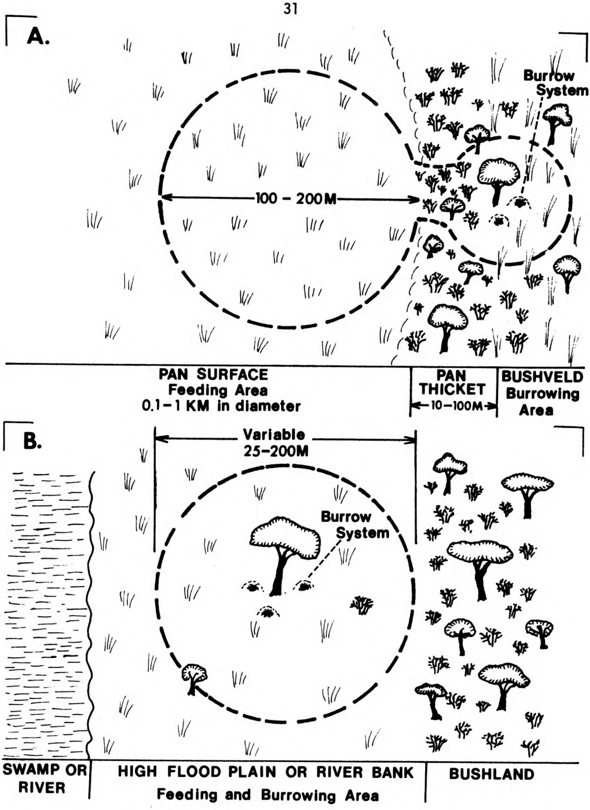


Figure 13. Approximate shapes and sizes of springhare home ranges on Kalahari pans and on the floodplains and river banks of northern and eastern Botswana.

Table 4. Occurrence of springhare groups by size in four areas of Botswana.

Group size	1	2	3	4	5	6	Total
Kalahari pans							
No. of groups	1134	222	43	6	6	2	1413
% of all groups	80.2	15.7	3.0	0.4	0.4	0.1	100.0
No. of springhare	1134	444	129	24	30	12	1773
% of all springhare	64.0	25.0	7.3	1.4	1.7	0.7	100.0
Kalahari bushveld							
No. of groups	127	19	6	3	-	-	155
% of all groups	81.9	12.3	3.9	1.9	-	-	100.0
No. of springhare	127	38	18	12	-	-	195
% of all springhare	65.1	19.5	9.2	6.1	-	-	100.0
Kgatleng District							
No. of groups	245	60	25	1	2	1	334
% of all groups	73.4	18.0	7.5	0.3	0.6	0.3	100.0
No. of springhare	245	120	75	4	10	6	460
% of all springhare	53.3	26.0	16.3	0.9	2.2	1.3	100.0

Northern Botswana							
No. of groups	68	18	3	1	-	-	90
% of all groups	75.6	20.0	3.3	1.1	-	-	100.0
No. of springhare	68	36	9	4	-	-	117
% of all springhare	58.1	30.8	7.7	3.4	-	-	100.0
Total							
No. of groups	1574	319	77	11	8	3	1992
% of all groups	79.0	16.0	3.9	0.6	0.4	0.2	100.0
No. of springhare	1574	638	231	44	40	18	2545
% of all springhare	61.8	25.1	9.1	1.7	1.6	0.7	100.0

Frequency of occurrence of different sized groups was inversely related to the size of the group ($r = -0.98$, $t = 9.33$, $p < 0.0005$) (Figure 14) (Table 4). No difference ($X^2 = 1.98$, $p > 0.25$) was found between group size frequency on the pans and in the bushveld.

Springhare group size increased with the length of time after sunset ($r = 0.34$, $Z = 1.89$, $p < 0.05$) (Figure 15). There were 1.07 individuals per group on the average at one hour after sunset, but 1.34 per group at nine hours after sunset. Group size did not vary with the distance of the group onto the pan ($r = 0.26$, $t = 0.43$, $p > 0.20$).

The cumulative frequency of occurrence of different sized springhare groups graphed a straight line when plotted on a normal probability scale against numbers per group (Caughley 1964, Cassie 1954) (Figure 16). The only exception was a deflection in group sizes between one and two.

<u>Composition of social groups</u>

Springhares were shot to determine the age and sex composition of the populations and of groups (Table 5). Combined data for the Kalahari and Kgatleng District showed that neither males nor females were found in groups significantly more often ($Z = 1.19$, $p > 0.10$). All springhares were divided into five categories: adult males, immature males, pregnant females, adult females not pregnant and immature females. Only adult males were found in groups more often than indicated by their relative occurrence in the population ($X^2 = 4.07$, $p < 0.05$).

Frequency of occurrence of different sized groups was inversely related to the size of the group ($r = -0.96$, $t = 9.33$, $p < 0.0005$) (Figure 14) (Table 4). No difference ($\chi^2 = 1.98$, $p > 0.25$) was found between group size frequency on the pans and in the bushveld.

Springhare group size increased with the length of time after sunset ($r = 0.34$, $Z = 1.89$, $p < 0.05$) (Figure 15). There were 1.07 individuals per group on the average at one hour after sunset, but 1.34 per group at nine hours after sunset. Group size did not vary with the distance of the group onto the pan ($r = 0.26$, $t = 0.43$, $p > 0.20$).

The cumulative frequency of occurrence of different sized springhare groups graphed a straight line when plotted on a normal probability scale against numbers per group (Caughley 1964, Cassie 1954) (Figure 16). The only exception was a deflection in group sizes between one and two.

Composition of social groups

Springhares were shot to determine the age and sex composition of the populations and of groups (Table 5). Combined data for the Kalahari and Kgatleng District showed that neither males nor females were found in groups significantly more often ($Z = 1.19$, $p > 0.10$). All springhares were divided into five categories: adult males, immature males, pregnant females, adult females not pregnant and immature females. Only adult males were found in groups more often than indicated by their relative occurrence in the population ($\chi^2 = 4.07$, $p < 0.05$).

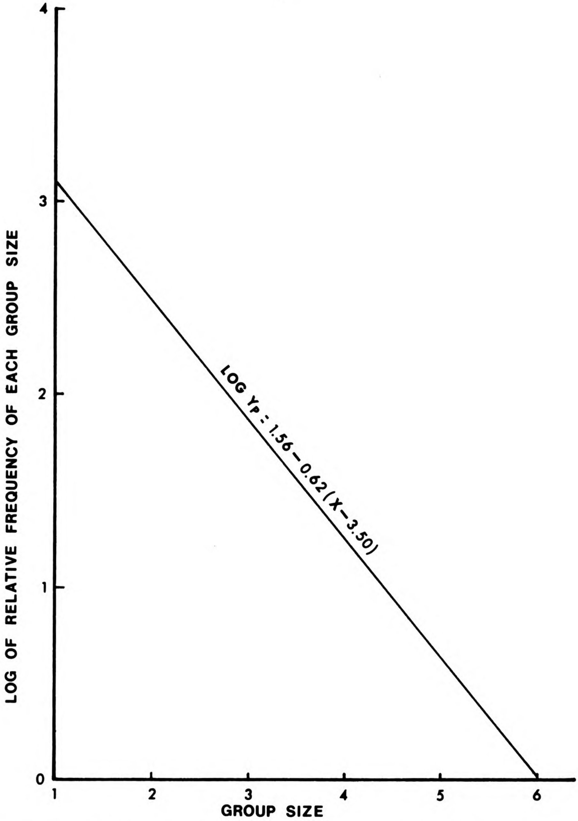


Figure 14. Relationship between springhare group size and frequency of occurrence in Botswana.

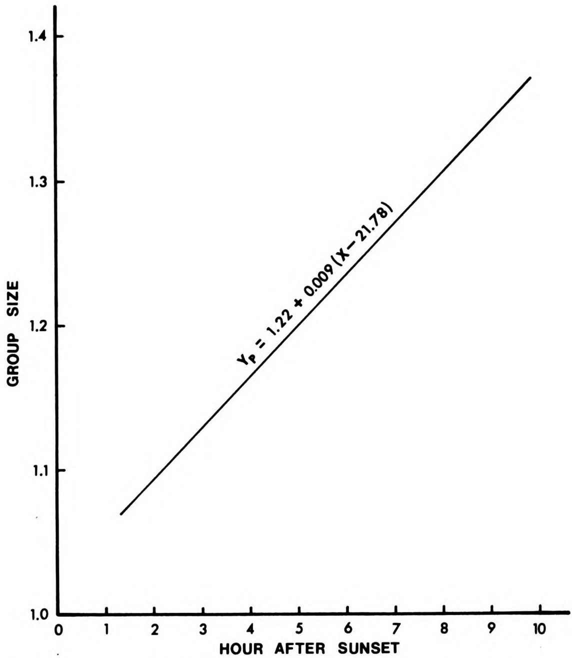


Figure 15. Relationship between average springhare group size and time after sunset.

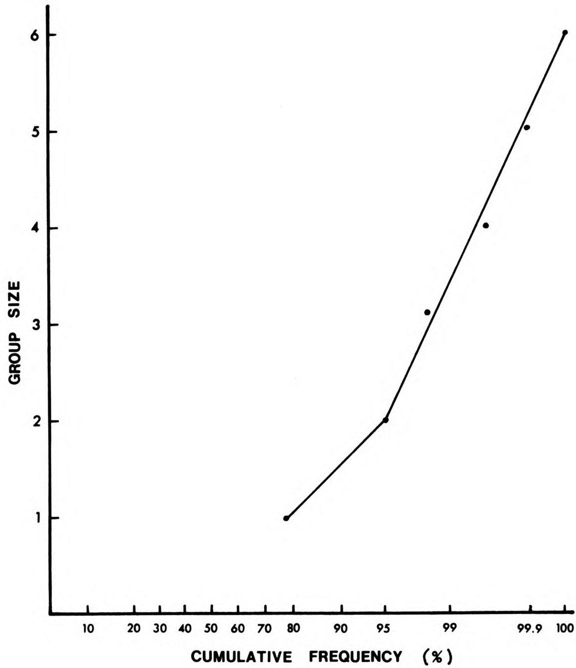


Figure 16. Springhare group size plotted against cumulative frequencies on a normal probability scale.

Table 5. Reproductive status of individuals in springhare social groups.

Reproductive status	Individuals sampled from groups	Percentage in population	Percentage in groups	Preference* ratio
Adult males	30	40	1.33	31
Immature males	20	15	0.75	12
Adult females not pregnant	8	8	1.00	6
Adult females pregnant	27	26	0.96	29
Immature females	14	12	0.86	9

* Percentage in groups/percentage in population.

The number of sexually homogeneous groups did not differ from the number of sexually heterogeneous groups ($X^2 = 0.75$, $p > 0.20$). The number of all male groups was not significantly different from the number of all female groups ($Z = 0.89$, $p > 0.15$).

DISCUSSION

Springhare Utilization of Pans

Estimates of springhare densities were not attempted. This is because transects were not consistently surveyed over the same route during comparable time periods. Furthermore, weather factors had a considerable effect on springhare activity and springhares were removed from the area.

Springhares are found throughout the Kalahari (Smithers 1971) but their numbers vary according to soil and vegetation factors. Pellet counts and night surveys indicated that springhare densities are significantly higher on and around pans than in the surrounding bushveld. Numerous pellet counts made in other parts of the Kalahari indicate that this is a general phenomenon.

Pellet counts probably provided the more accurate indicator of springhare activity between the pan and bushveld. The pan to bushveld pellet count ratio was 3.4 : 1 as opposed to the 2.3 : 1 ratio calculated from direct observations. The difference between the two ratios was attributed largely to the fact that much of the data for bushveld night surveys were collected within the immediate vicinity of pans where springhare densities were affected by the proximity of the pans. On the other hand, 64 percent of the pellet

counts for the bushveld were made at distances of 1 km or more from the nearest pan. Thus the pellet counts were more representative of springhare densities under conditions independent of pan influences.

Considerable differences have been found (Butynski unpublished) in the nutritional qualities between foods available to springhares on the pans and on the bushveld. During all seasons, springhare food plants on the pans have higher protein, mineral and water contents than do those on the bushveld. The flat, open surface of the pan and its associated short grass cover are optimum for predator detection and avoidance. The openness of the pan may facilitate certain kinds of social behavior.

Time of year and associated vegetation changes result in differential utilization of habitats in the case of many mobile mammals. This, however, does not occur in the Kalahari springhares. Some feeding takes place in the vicinity of the burrows during all seasons, but most feeding occurs on pans. Despite the fact that an exploitable food resource probably occurs in the vicinity of the burrows during the wet season, springhares continue to move from the bushveld, through the pan thicket and onto the pans to feed during all times of the year.

Springhare burrows were not located on the hard-packed, occasionally-flooded surface of the pan but rather in the sandy soils of the bushveld immediately beyond the pan thicket and, less frequently, within the pan thicket. The fact that the pan edge is the closest part of the pan to the burrows probably explains why springhare activity was heaviest here.

counts for the bushveld [illegible] the

[illegible] pans. Thus the [illegible] counts were more representative of

springhare densities under conditions independent of pan influence.

Considerable differences [illegible]

lished) in the nutritional quality [illegible]

bares on the pans and on the bushveld, particularly [illegible] when pan

food plants on the pans have higher [illegible]

than do those on the bushveld. The flat, open surface of the pan and

its associated short grass cover [illegible] predator detection

and avoidance. [illegible]

of social behavior. [illegible] short grass cover

Time of year and associated vegetation changes result in

differential utilization of habitats in the case of many mobile mam-

mals. This, however, does not occur in the Kalahari springhare.

Some feeding takes place in the vicinity of the burrows during all

seasons, but most feeding occurs on pans. Despite the fact that an

exploitable food resource probably occurs in the vicinity of the

burrows during the wet season, springhares continue to move from the

bushveld, through the pan thicket and onto the pans to feed during

all times of the year.

Springhare burrows were not located on the hard-packed, occasionally-flooded surface of the pan but rather in the sandy soils of the bushveld immediately beyond the pan thicket and, less frequently, within the pan thicket. The fact that the pan edge is the closest part of the pan to the burrows probably explains why springhare activity was heaviest here.

No relationship was found between the time of year and the distances out onto the pan that springhares were observed. Food was apparently equally abundant on the edges and center of the pan. The occurrence of feeding in the center of the pan may result in more equitable utilization of food resources. Such behavior may make the animals more susceptable to predation, particularly at times when pan grasses are tall and thick and the springhares' ability to see and move about is reduced.

Habitats with the highest springhare utilization (Table 5) should represent near-optimum conditions (Dice 1931, Jewell 1935). The most suitable springhare habitats support a short grass cover with little or no woody vegetation, and have suitable sandy soils for burrowing. In Botswana, the vegetation in such areas consists largely of <u>Sporobolus</u> spp., <u>Cynodon dactylon</u> or <u>Odyessea paucinervis</u>, grass species which normally occur on soils which are relatively moist and fertile. In northern and eastern Botswana portions of floodplains of rivers and swamps best meet these criteria, while in the Kalahari pans provide the best habitat. Night surveys indicate that springhares have a strong preference for flat, open, short grass habitats.

<u>Daily Activity and Feeding Pattern</u>

Comparison of data from night surveys of springhares throughout Botswana indicates that the nocturnal activity patterns are similar. A simple nocturnal activity pattern can be inferred from direct observations of free-living springhares, the steadily increasing weight of stomach contents throughout the night and the

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

increasing distance at which springhares were found out onto the pans as the night progresses. Springhares emerge between one-half and five hours after sunset and feed more or less steadily while above ground. There is only one activity peak every 24 hours which is a pattern similar to that described for several other rodents. These include Peromyscus maniculatus and Apodemus sylvaticus whose stomachs also have been shown (Ashby 1972) to become progressively fuller as the night proceeds. There is no evidence to suggest discontinuous feeding or the presence of more than one activity peak in the springhare as is the case in most species of rodents (Miller 1955, Brown 1956, Reynolds 1960, Kikkawa 1964, Bergstedi 1965, Cross 1970).

Effect of Moonlight on Activity and Group Size

Although activity of most mammals is more or less fixed from day to day, it is not inflexible. Certain weather conditions and moonlight are known to be particularly disruptive to activity of small mammals and must be taken into consideration when interpreting activity and population data.

The intensity of moonlight is of considerable importance as a factor in reducing the activity of many nocturnal mammals (Blair 1951, Pearson 1960, O'Farrell 1974, Lockard and Owings 1974a). On the other hand, moonlight has been shown to have a stimulating effect on the behavior of some species including Peromyscus eremicus (Owings and Lockard 1971). In contrast, moonlight has no apparent effect on

No relationship was found between the [illegible] the distances out onto the pan that springhares were observed. Food was apparently equally abundant on the edges and the center of the pan. The occurrence of feeding in the center of the pan may be [illegible] which results in a equitable utilization of food resources. Such behavior [illegible] these animals more susceptible to predation, particularly [illegible] grasses are tall and thick and the springhares' ability to see and move about is reduced. [illegible] to suggest discontinuous [illegible]

Habitats with the highest springhare [illegible] spring- should represent near-optimum conditions (Dice 1952, Jewell 1966, Brown [illegible]). The most suitable springhare habitats support a short grass cover with little or no woody vegetation, and have suitable sandy soils for burrowing. In Botswana, the vegetation in such areas consists largely of *Sporobolus* spp., *Cynodon dactylon* or *Odyessea paucinervis*, grass species which normally occur on soils which are relatively moist and fertile. In northern and eastern Botswana portions of floodplains of rivers and swamps best meet these criteria, while in the Kalahari pans provide the best habitat. Night surveys indicate that springhares have a strong preference for flat, open, short grass habitats.

Daily Activity and Feeding Pattern

Comparison of data from night surveys of springhares throughout Botswana indicates that the nocturnal activity patterns are similar. A simple nocturnal activity pattern can be inferred from direct observations of free-moving springhares, the effect on increasing weight of stomach contents throughout the night and the increasing distance at which springhares were found out onto the pans as the night progresses. Springhares emerge between one-half and five hours after sunset and feed more or less steadily while above ground. There is only one activity peak every 24 hours which is a pattern similar to that described for several other rodents. These include *Peromyscus maniculatus* and *Apodemus sylvaticus* whose stomachs also have been shown (Ashby 1972) to become progressively fuller as the night proceeds. There is no evidence to suggest discontinuous feeding or the presence of more than one activity peak in the springhare as is the case in most species of rodents (Miller 1955, Brown 1956, Reynolds 1960, Kikkawa 1964, Bergstedi 1965, Cross 1970).

Effect of Moonlight on Activity and Group Size

Although activity of most mammals is more or less fixed from day to day, it is not inflexible. Certain weather conditions and moonlight are known to be particularly disruptive to activity of small mammals and must be taken into consideration when interpreting activity and population data.

The intensity of moonlight is of considerable importance as a factor in reducing the activity of many nocturnal mammals (Blair 1951, Pearson 1960, O'Farrell 1974, Lockard and Owings 1974a). On the other hand, moonlight has been shown to have a stimulating effect on the behavior of some species including *Peromyscus eremicus* (Owings and Lockard 1971). In contrast, moonlight has no apparent effect on

Dipodomys nitratoides (Lockard and Owings 1974b), *Peromyscus leucopus* (Orr 1959) and the several desert rodents observed by Jorgensen and Hayward (1965) and Chew and Butterworth (1964).

This study indicates that, although moonlight inhibits springhare movements on pans, it does not reduce the amount of time which springhares spend above ground. In fact, it seems possible that a reduction in the range over which the springhares forage could increase the time spent above ground, especially if fewer or poorer foods were encountered in the reduced area of activity.

Blair (1943) found that *Peromyscus maniculatus* moved about less and seldom moved into the open on bright moonlit nights. He proposed that the decrease in movement rendered them no more, and possibly less, vulnerable to predation during the full than during the dark of the moon. Direct observations of wild springhares showed that as the moon rose in the sky, and as the shadows produced by trees and shrubs became reduced in size, the springhares moved closer to those trees and shrubs in order to remain within the shadows. Fall (1968) recorded similar behavior for *Peromyscus leucopus* and Justice (1960) observed this phenomenon for *Dipodomys merriami*. It may be that the principle effect of bright moonlight on springhares is to restrict their movements so as to reduce the dangers of predation.

Doucet and Bider (1969) suggested that a combination of moonlight intensity and lunar periodicity is responsible for decreased *Microtus pennsylvanicus* activity under full-moon conditions. In response, O'Farrell (1974) has proposed that, since the ten desert

rodents studied by him showed a sudden increase in activity when clouds obscured the moon, moonlight intensity alone could explain the variance in rodent activity and lunar periodicity probably does not affect rodents. Springhares too move into open areas more freely whenever the moon becomes hidden by clouds. The present study and a study by Justice (1960) support O'Farrell's hypothesis.

Effects of Temperature and Precipitation on Activity

Springhare activity is suppressed under temperatures approaching freezing and almost totally curtailed at temperatures below freezing. Over much of Botswana, temperatures below 0°C can be expected to occur during only four or five nights out of the year. Thus, such low temperatures occur so seldom as to be relatively insignificant in affecting the total activity and welfare of the springhare.

Moderate to heavy rains inhibit above ground activity in the springhare. In the Kalahari, heavy rains generally last for only a few hours. When rains persist for several days, however, it is likely that springhare activity patterns are adversely affected as Pearson (1948) found for viscachas (*Logidium peruanum*) in Peru.

Size and Composition of Social Groups

It is not known why more springhares in the Kgatleng District are found in groups than in the Kalahari. If springhare densities in the Kgatleng District are higher than in the Kalahari, this might rodents studied by him showed a sudden increase in activity when clouds obscured the moon, moonlight intensity alone could explain the variance in rodent activity and lunar periodicity probably does not affect rodents. Springhares too move into open areas more freely whenever the moon becomes hidden by clouds. The present study and a study by Justice (1960) support O'Farrell's hypothesis.

Effects of Temperature and Precipitation on Activity

Springhare activity is suppressed under temperatures approaching freezing and almost totally curtailed at temperatures below freezing. Over much of Botswana, temperatures below 0°C can be expected to occur during only four or five nights out of the year. Thus, such low temperatures occur so seldom as to be relatively insignificant in affecting the total activity and welfare of the springhare.

Moderate to heavy rains inhibit above ground activity in the springhare. In the Kalahari, heavy rains generally last for only a few hours. When rains persist for several days, however, it is likely that springhare activity patterns are adversely affected as Pearson (1948) found for viscachas (Lagidium peruanum) in Peru.

Size and Composition of Social Groups

It is not known why more springhares in the Kgatleng District are found in groups than in the Kalahari. If springhare densities in the Kgatleng District are higher than in the Kalahari, this might explain the greater incidence of grouping in that area. This does not appear, however, to be the case. It is felt that other factors also affect the size of springhare foraging groups.

Burrows in eastern Botswana are generally located on feeding grounds, making it unnecessary for springhares to move more than a few meters to feed. Thus animals emerging from their burrows do not disperse to feed as do those on the Kalahari pans. In consequence, the most suitable feeding areas on the Kgatleng District are smaller than those on the Kalahari. The small size, and the proximity of the eastern Botswana springhare feeding grounds to the burrowing sites, seem to be responsible for the larger group size in that area.

Group size in free-living small mammals has been poorly documented. Although it seems that the groups would offer members an advantage in predator detection and avoidance (Etkin 1964), there is no concrete evidence for this in small mammals. For example, in the springhare, it can be questioned that if group formation does indeed provide an advantage why are not groups larger, why does not a higher proportion of the population participate in group formation more often, why is not maximum group size reached earlier in the activity period, and why does not group size increase with distance out onto the pan or under conditions of increasing moonlight where susceptibility to predation presumably is greatest? It appears that springhare groups may not be as important an anti-predator mechanism as was originally thought. Grouping may be more significant as a means by which reproductive, learning and territorial activities are facilitated.

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

Cloudsley-Thompson's (1961) general observation that "truely social animals are seldom nocturnal, but nocturnal species may form aggregations for feeding . . ." applies well to springhares. It may be that, although springhares could benefit from a more complex social organization, it is not possible, under nocturnal conditions, to maintain the degree of contact between individuals that this would require.

There appears to be little social cohesion within springhare groups. Limited observations of free-living springhares reveal that, in most cases, individuals join and leave groups without any apparent reaction from other members. Occasionally individuals come together for a few hours, feed in the vicinity of each other and then separate without any additional interaction. At other times, individuals follow one another around, feed within two meters of each other and then separate after several hours. Indications are that springhares prefer to feed in groups but that, except for single animals, groups are formed only when it is "convenient" to do so as, for example, around those food supplies and burrowing sites where animals are concentrated.

The absence of deviation from a normal curve (Figure 13), between groups of two and six springhares, indicates that the size of the group does not affect the "urge" of a springhare to join it. Thus the average group size is directly related to and dependent upon springhare densities. The deflection in Figure 13 between groups of one and two springhares indicates that single springhares tend to avoid being alone and, therefore, form or join groups when it is

"convenient" to do so. A similar social grouping was reported by Caugley (1964) for red kangaroos (Macropus rufus) and gray kangaroos (Macropus canguru) in Australia and by Rood (1972) for three species of Caviinae in Argentina.

Springhare groups include a proportionate number of immature animals. It appears that when young springhares initiate above ground feeding activities, they do so without any special attention from the adults. The low incidence of milk in the stomachs of immature individuals indicates that springhares rapidly become independent of the adults upon leaving the burrow.

Springhares do not appear to group according to sex, age or reproductive status other than the slightly higher than expected incidence for adult males as calculated from their presence in the overall population. This fact, coupled with the high proportion of single individuals and direct observations on behavior, all indicate that springhares are semi-social animals, that the individual does not need to participate in group activities in order to survive, that distinct individual home ranges are not present except in low density situations and that actively defended territories do not exist or, at least, are not associated with an area outside of the immediate vicinity of the burrow.

SUMMARY

Several aspects of the ecology of the springhare, _Pedetes capensis_, were studied in the Kalahari Desert, Republic of Botswana, from August 1971 through August 1974.

Eighty-five night surveys totalling 253 hours of observation were analysed, along with associated environmental conditions and data from social group composition.

Fecal pellet counts and night surveys showed springhare utilization of Kalahari pans to be 2.3 to 3.4 times greater than in the surrounding bushveld. This difference was attributed to the more suitable food resource on the pans and to the flat, open nature of the pan surface which may have facilitated social interactions, namely reproduction, and enhanced predator detection and avoidance.

Springhare utilization of pans and the distances out onto the pans to which they moved to feed was not affected by time of year. Burrows were located on the bushveld and this probably accounted for the considerably higher springhare activity on the pan perimeter than further out onto the pan.

Springhares are strictly nocturnal; they emerge from their burrows beginning at least 30 minutes after sunset and return not later than one-half hour before sunrise. The number of springhares on the pans increased until approximately five hours after sunset,

levelled off for 3-4 hours and then decreased rapidly towards sunrise. The steadily-increasing weight of springhare stomach contents throughout the night and direct observations on activity indicated that springhares fed almost continuously while above ground. The distances out onto the pans at which springhares fed, and the size of their social groups increased throughout the night.

Weather altered springhare activity patterns somewhat but only extreme conditions, particularly temperatures approaching freezing and moderate to heavy precipitation, significantly reduced springhare activity.

Moonlight did not affect the amount of time springhares spent above ground but it severely limited their movements. There was an inverse relationship between the distance springhares moved out onto the pan and the amount of moonlight present. Clouds, apparently by reducing the amount of moonlight, promoted springhare movement out onto the pans. Moonlight, however, did not reduce the number of springhares present on the pan nor did it have any evident effect on the size of social groups. The withdrawal of springhares from moonlit areas was probably related to predator avoidance.

The frequency of occurrence of springhare social groups was inversely related to size of the group. Most springhares fed singly. In the Kalahari 39 percent were found feeding in groups. This differed significantly from the 47 percent found feeding in groups in eastern Botswana. Average group size did not differ between animals on the pans and on the bushveld. Group size increased directly with the length of time after sunset. The distance out onto the pan had no bearing on the size of the group.

Males and females participated in groups in equal numbers, although adult males occurred in groups more often than expected from their relative abundance in the population. The number of sexually homogeneous groups did not differ from the number of sexually heterogeneous groups. The number of all-male groups was not significantly different from the number of all-female groups. Springhare groupings may be more important in facilitating reproductive, territorial and social activities than as aids in predator avoidance.

There was a tendency for springhares to avoid being alone. Apparently little social cohesion existed within springhare groups, with individuals joining and leaving groups without any noticeable reaction from the other members. The size of the group did not seem to affect the springhares' "urge" to join it.

Springhares had overlapping home ranges. No territoriality was observed but possibly may occur in the area immediately around the burrow system.

Males and females participated in groups in equal numbers, although adult males occurred in groups more often than expected from their relative abundance in the population. The number of sexually homogeneous groups did not differ from the number of sexually heterogeneous groups. The number of all-male groups was not significantly different from the number of all-female groups. Springhare groupings may be more important in facilitating reproductive, territorial and social activities than [illegible] in predator avoidance.

There was a tendency for springhares to avoid being alone. Apparently little social cohesion existed within springhare groups, with individuals joining and leaving groups without any noticeable reaction from the other members. The size of the group did not seem to affect the springhare's 'tendency' to join it.

Springhares had overlapping home ranges. No territoriality was observed but possibly may occur in the area immediately around the burrow system.

LITERATURE CITED

LITERATURE CITED

Ashby, K. R. 1972. Patterns of daily activity in mammals. Mammal Review, 1:52-62.

Bergstedi, B. 1965. Distribution, reproduction, growth and dynamics of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollic* (Melchoir) and *Apodemus sylvaticus* (Linné) in southern Sweden. Oikos, 16:132-150.

Blair, W. F. 1943. Activities of *Peromyscus* with relation to light intensity. J. Wildlife Mgmt., 7:92-97.

________. 1951. Population structure, social behavior and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus leucocephalus*). Contrib. Lab. Vert. Biol., Univ. Michigan, 48:1-47.

Brown, L. E. 1956. Field experiments on the activity of the small mammals, *Apodemus*, *Clethrionomys* and *Microtus*. J. Mamm., 126:549-564.

Butynski, T. M. 1973. Life history and economic value of the spring-hare (*Pedetes capensis* Forster) in Botswana. Botswana Notes and Records, 5:209-213.

Caughley, G. 1964. Social organization and daily activity of the red kangaroo and the grey kangaroo. J. Mamm., 45:429-436.

Cassie, R. M. 1954. The uses of probability paper in the analysis of size frequency distributions. Aust. J. Marine Freshwater Res., 5:531-522.

Chew, R. M., and B. B. Butterworth. 1964. Ecology of rodents in Indian Cave (Mojave Desert), Joshua Tree National Monument, California. J. Mamm., 45:203-225.

Child, G. 1968. An ecological survey of northeastern Botswana. A report to the Government of Botswana. U.N.D.P., F.A.O., No. TA2563, Rome. 155 pp.

Cloudsley-Thompson, J. L. 1961. Animal Behaviour. The Macmillan Co., New York, 162 pp.

Coe, M. J. 1969. The anatomy of the reproductive tract and breeding in the springhare, Pedetes surdaster larvalis Hollister. J. Reprod. Fert. Suppl., 6:159-174.

Cross, R. M. 1970. Activity rhythms of the harvest mouse Micromys minutus (Pallas). Mammalia, 34:433-450.

Dawson, J., and T. M. Butynski. 1975. The Kutse Game Reserve. Biol. Conser., in press.

Dice, L. R. 1931. Methods of indicating the abundance of mammals. J. Mamm., 12:376-381.

Dorst, J. and P. D. Dandelot. 1970. A field guide to the larger mammals of Africa. Collins, London, 287 pp.

Doucet, G. J., and J. R. Bider. 1969. Activity of Microtus pennsylvanicus related to moon phase and moonlight revealed by the sand transect technique. Canadian J. Zool., 47:1183-1186.

Etkin, W. 1964. Types of social organization in birds and mammals. Pp. 1-307, in Social behavior and organization among vertebrates (W. Etkin ed.), Univ. of Chicago Press, Chicago, 307 pp.

Falls, J. B. 1968. Activity. Pp. 543-570, in Biology of Peromyscus (J. A. King ed.). Spec. Publ. Amer. Soc. Mamm., 2:Xiii+1-593.

Frith, H. J. 1964. Mobility of the red kangaroo, Megaleia rufa. C.S.I.R.O. Wildl. Res., 9:1-19.

Getz, L. L. 1968. Influence of weather on the activity of the red-backed vole. J. Mamm., 49:565-570.

Jewell, M. E. 1935. An ecological study of the freshwater sponges of northeastern Wisconsin. Ecol. Mongr. 5:461-504.

Jorgensen, C. D., and C. L. Hayward. 1965. Mammals of the Nevada test site. Brigham Young Univ. Sci. Bull., Biol. Ser., 6:1-81.

Justice, K. E. 1960. Nocturnalism in three species of desert rodents. Unpublished Ph.D. Dissertation, Univ. of Arizona, Tempe, 220 pp.

Kikkawa, J. 1964. Movement, activity and distribution of the small rodents Clethrionomy glareolus and Apodumus sylvaticus in woodland. J. Anim. Ecol., 33:259-299.

53

Leistner, O. A., and M. J. Werger. 1973. Southern Kalahari physio-sociology. Vegetatio, 28:353-399.

Lockard, R. B., and D. H. Owings. 1974a. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. J. Mamm., 55:189-193.

________. 1974. Moon related surface activity of bannertail (Dipodomys spectabilis) and Fresno (D. nitratiodes) kangaroo rats. Anim. Behav., (in press).

Meester, J. 1965. The origin of the southern African mammal fauna. Zoologica Africana, 1:87-93.

Miller, R. S. 1955. Activity rhythms in the woodmouse, Apodemus sylvaticus and the bank vole, Clethrionomys glareolus. Proc. Zool. Soc. Lond., 25:509-519.

O'Farrell, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. J. Mamm., 55:809-823.

Orr, H. D. 1959. Activity of white footed mice in relation to environment. J. Mamm., 40:213-221.

Owings, D. H., and R. B. Lockard. 1971. Different nocturnal activity patterns of Peromyscus californicus and Peromyscus eremicus in lunar lighting. Psyconomic Sci., 22:63-64.

Pearson, O. P. 1948. Life history of mountain viscachas in Peru. J. Mamm., 29:345-374.

________. 1960. Habits of harvest mice revealed by automatic photographic recorders. J. Mamm., 41:58-74.

Reynolds, H. G. 1960. Life history notes on Merriam's kangaroo rat in southern Arizona. J. Mamm., 41:48-58.

Riney, T. 1963. A rapid field technique and its application in describing conservation status and trends in semi-arid pastoral areas. African Soil, 8:159-258.

Rood, J. P. 1972. Ecological and behavioural comparisons of three genera of Argentine Cavies. An. Behav. Monogr., 5:1-83.

Rosenthal, M. and D. Meritt. 1973. Hand-rearing sringhass at Lincoln Park Zoo. International Zoo Yearbook, 13:135-137.

Sedorowicz, J. 1960. Influence of weather on capture of Micromammalia. I Rodents (Rodentia). Acta Therio., 4:139-158.

Smithers, R. H. N. 1971. The mammals of Botswana. Museum Memoir No. 4. Mardon Printers, Salisbury, Rhodesia, 340 pp.

van Rensburg, H. J. 1971. Range ecology in Botswana. U.N.D.P. Tech. Document No. 2. Gaborone, Botswana, 139 pp.

Velte, F. F. 1975. Hand-rearing springhare Pedetes capensis. International Zoo Yearbook, (in press).

Wear, P. R. 1971. Vegetation in the Kalahari in Botswana. Botswana Notes and Records (Special Ed. No. 1). 88-95.

Wood, A. E. 1962. The juvenile tooth patterns of certain African rodents. J. Mamm., 43:310-322.

Smithers, R. H. N. [illegible] of Botswana. Museum Memoir No. 4 [illegible] Salisbury, Rhodesia. 340 pp.

van Rensburg, [illegible] in Botswana. U.N.D.P. Tech. Document [illegible] Botswana. 138 pp.

Velte, F. F. 1975 [illegible] Pogonias cappensis. International [illegible]

Wear, P. R. 1977 [illegible] in Botswana. Botswana Notes [illegible] 88-95.

Wood, A. E. 1962 [illegible] patterns of certain African rodents [illegible]