PREY CAPTURE BY THE LARGER FISSIPEDS: THE AFRICAN LION

by

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ABSTRACT

Predation by large fissipeds is examined using the specific example of the African lion. It is found that the lion is able to adjust its strategy and tactics at each phase of prey capture (search, stalk, attack, and subdue) so as to achieve a consistently high overall capture success with different prey and conditions.

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INTRODUCTION

The habitat of the African lion (*Panthera leo*) and its tolerance of man when not hunted makes it the ideal subject for analysis of the mechanisms of large mammal predation. Prior to the initiation of this study, the only major study of predation by a large felid was that of Schaller (1967) on the tiger (*Panthera tigris*). Subsequently, there has been publication of material on the North American mountain lion (*Felis concolor*) by Hornocker (1969, 1970), the cheetah (*Acinonyx jubatus*) by McLaughlin (1970) and Eaton (1970), the African lion (and other predators) in the Serengeti National Park of Tanzania by Schaller (1972), and the African lion in Nairobi Park by Rudnai (1973?).

The large canids have received rather more extensive examination. The wolf (*Canis lupus*), in its role as a predator, has received particular attention both in North America (Murie, 1944; Cowan, 1947; Thompson, 1952; Stenlund, 1955; Mech, 1966, 1970; Shelton, 1966; Rausch, 1967; Pimlott, 1967) and in Europe (Pulliainen, 1965). Also, Estes and Goddard (1967) have reported on predation by the hunting dog (*Lycaon pictus*) in Ngorongoro Crater, Tanzania. Recently, Kruuk (1972) has published a comprehensive study which provides major insight into predation by the canid-like hyaenid, the spotted hyaena (*Crocuta crocuta*) in Northern Tanzania. The works of Pienaar (1969) and Kruuk and Turner (1967) consider predation by several large African predators.

The characteristic which relates the larger fissipeds to one another, but largely distinguishes them from their smaller relatives is their general tendency to take prey of approximately their own size (Bourlière, 1963).

Concomitant with the increasing knowledge of specific examples of large mammal predation, there has been the development of new theroetical approaches. One of the most significant is the components analysis concept propounded by Holling (1965, 1966). This approach emphasizes the ordered nature of biological systems and involves subdividing a process into simple units which are sufficiently uncomplicated to be describable in a consistent manner by two or more variables. The value of this approach lies in the ability to use the results to examine situations different to those which were involved in the initial analysis.

The aim of this study is to examine predation by larger fissipeds using the specific example of the African lion. This will involve the precise definition (with mathematical expressions) of the strategies and tactics of prey capture by the lion. Such a study requires extensive observations of predation by lions under a variety of conditions. In this regard, the Ngorongoro Conservation Area, Tanzania was ideal.

STUDY AREA[1]

Location and Physiography

The study was conducted largely within Ngorongoro Crater in northern Tanzania. This amazing geologic feature, properly termed a caldera, was part of the Serengeti National Park from 1940 to 1959 but has since been designated as part of the 3200 square mile Ngorongoro Conservation Area.

The floor of the crater lies approximately 2000 feet below the rim and covers about 102 square miles. The lowest elevation is 5600 feet at Lake Makat. This alkaline lake varies in depth from year to year and in some years is entirely dry. Several small hills occur near the foot of the walls, especially in the eastern and northern parts of the crater. In the north some of the hills reach considerable size and the slope of the walls is reduced from an otherwise steep 45° - 70° to a more gentle 15°. The central plain is essentially flat (Pickering, 1968).

Permanent fresh water is available at several streams and springs near the base of the wall in the southern half of the crater. The only permanent water in the northern half is the Munge stream which flows across the crater into Makat Lake. The flow of this stream in the dry season is underground, however, for about one-third of its length forming the Maandusi swamp. A number of temporary ponds are formed during the rainy season.

[1] See Figure 1.

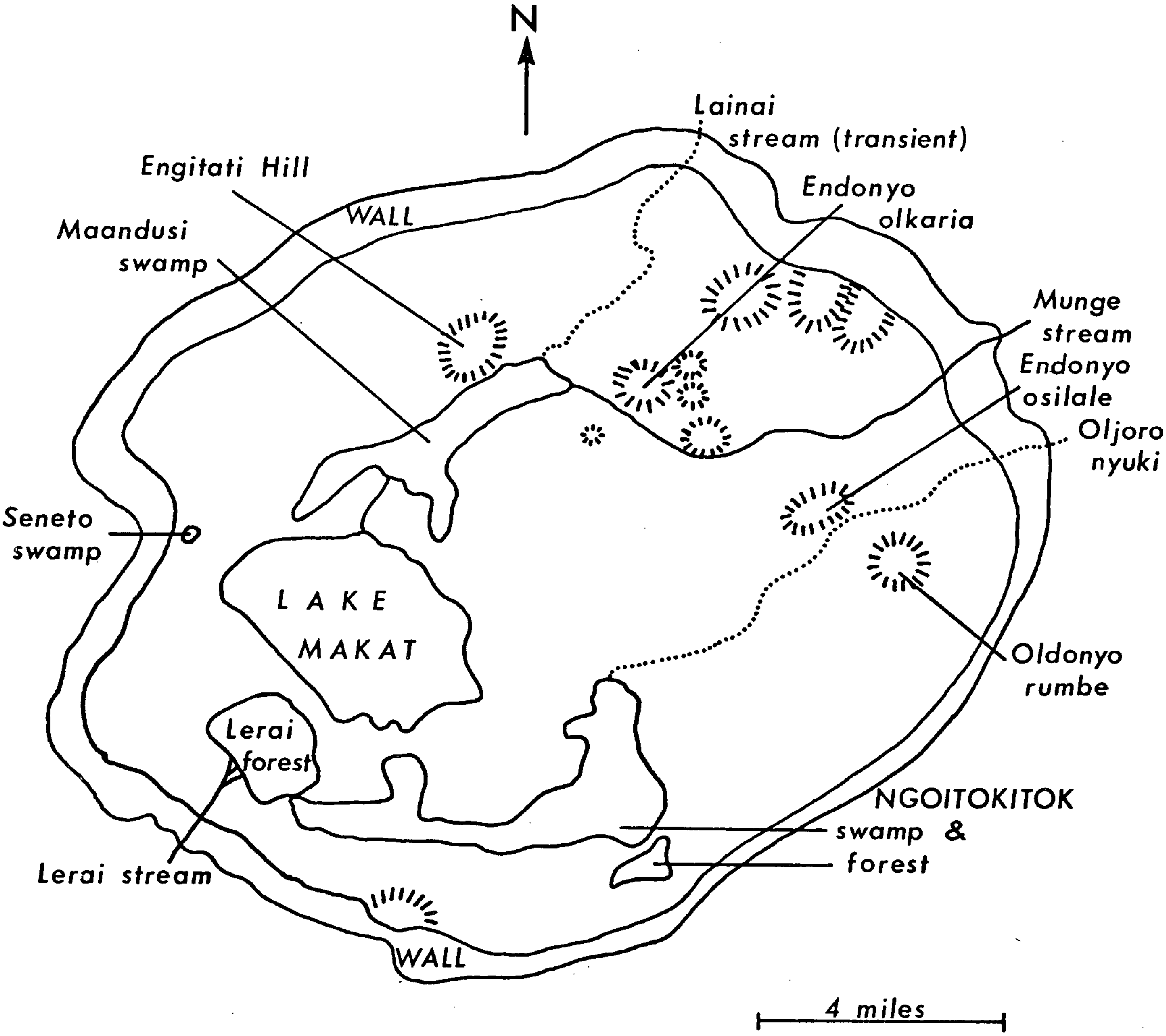

N
Lainai stream (transient)
Engitati Hill
Endonyo olkaria
Maandusi swamp
WALL
Munge stream
Endonyo osilale
Oljoro nyuki
Seneto swamp
LAKE MAKAT
Oldonyo rumbe
Lerai forest
NGOITOKITOK swamp & forest
Lerai stream
WALL
4 miles

Figure 1

NGORONGORO CRATER

Human activity takes several forms. Firstly, throughout the study, there were three Masai villages located in the crater. This would correspond to about 100 to 250 people plus 500 to 2000 cattle. Also, two semipermanent cabins were located in the crater for official use. The location of the crater between Ngorongoro townsite and the Nainokanoka-Empakaai region resulted in foot traffic through the area. Automobile traffic between these two locations was officially encouraged to use an alternate route; however, for much of the study this was not possible because the bypass road was impassable. Automobiles were also in the crater, associated with tourist activity. Limited control of the movement of these latter vehicles has resulted in a serious proliferation of roads, erosion, and some destruction of vegetation types. Maintenance activity, particularly road upgrading also takes place. One hill (Endonyo Osilale) has been considerably altered by the removal of gravel.

Climate

The alternation of wet and dry seasons, although variable, is the most significant climatic feature which affects predation. Usually, two rainy periods (November to December and February to June) alternate with two relatively dry periods (Anderson and Talbot, 1965). The short dry period in January has little immediate effect upon ungulate food supplies. However, as the dry season progresses, major changes in the feeding patterns of the ungulates occur. The western portion of the crater receives less rain (12 to 15 inches per year) than the remainder of the crater (20 to 30 inches per year) (Herlocker and Dirschl, 1972).

The mean monthly temperature is fairly constant at about 68 degrees F. (Kenworthy, 1966), but the diurnal fluctuation is large (about 20.5 degrees F.) (Kendrew, 1953).

The prevailing wind is from the southeast during the day. There is generally no wind at night.

Vegetation

Herlocker and Dirschl (1972) have described the vegetation of the Ngorongoro Conservation Area including Ngorongoro Crater.

The greatest portion of the crater floor is open grass plain, within which different grassland communities can be identified. *Odyssea jaegeri* dominates the short grassland in the vicinity of Lake Makat. Beyond this, *Digitaria scalarum*, *D. milanjiana*, *Sporobolus marginatus*, and *Cynodon dactylon* dominate an extensive area (about one-half of the total crater floor) of short to medium grassland. This area plus the *Odyssea jaegeri* grassland provides the major grazing potential in the crater. Taller, less palatable grasslands dominated by *Andropogon greenwayi* and *Pennisetum mezianum* occur in two regions in the west-central portion of the floor. Grassland of similar length, dominated by *Andropogon greenwayi* and *Digitaria scalarum* is found around most of the northern half at the base of the wall.

Two extensive areas of reed swamp (and one small area) are present in the crater. Ngoitokitok swamp, located in the southeast portion of the crater, is dominated by *Cyperus immensus*. Maandusi swamp, fed by the

Munge stream in the north half of the crater, is dominated by *Aeschynomene schimperi*. The borders of these swamps (and also a moist area northwest of Engitati hill) have grassland communities occupied by *Panicum repens*, *Sporobolus spicatus*, and *Cyperus laevigatus*. These are important dry season feeding areas for the ungulates.

Two small woodland communities, dominated by the fever tree (*Acacia xanthophloea*) are present on the crater floor: Lerai forest southwest of Lake Makat and Ngoitokitok forest southeast of Ngoitokitok swamp. Various species of bush are found peripherally on the crater walls and occupy a portion of the floor in the northeast corner.

Fauna

Ngorongoro Crater has a fascinating assemblage of fauna. Fifty-five species of mammals (ole Saibull, 1966) and 182 species of birds (Fosbrooke, 1966) have been recorded within the crater. Additional sightings made during this study suggest that further species (particularly small mammals) should be included.

There are five large carnivores: hunting dog, spotted hyaena, leopard, (*Panthera pardus*), lion, and cheetah; and seventeen large ungulates: elephant (*Loxodonta africana*), Burchell's zebra (*Equus burchelli*), black rhinoceros (*Diceros bicornis*), hippopotamus (*Hippopotamus amphibius*), bushbuck (*Tragelaphus scriptus*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*), defassa waterbuck (*Kobus defassa*), bohor reedbuck (*Redunca redunca*), mountain reedbuck (*Redunca fulvorufula*), kongoni (*Alcelaphus buselaphus*), wildebeest (*Connochaetes taurinus*), klipspringer (*Oreotragus oreotragus*), steinbok (*Raphicerus campestris*), impala (*Aepyceros melampus*), Thomson's gazelle (*Gazella thomsonii*), and Grant's gazelle (*Gazella granti*).

The spotted hyaena (estimated at 430 by Kruuk, 1972) and the lion are common in the crater, but the leopard is only occasionally seen. At one time both wild dog (Estes and Goddard, 1967) and cheetah were resident in the crater; however, during this study, groups of wild dog were in the crater only briefly, and cheetah in small numbers during the dry season.

Table I gives estimates of the population sizes of several ungulate species which are energetically important to the lion population. The differences seen in the population counts of zebra and wildebeest between seasons correspond to movements of a portion of the population out of the crater during the wet season (Estes, 1969). Many of these move only a short distance into the Malanja depression which is adjacent to the western side of the crater. Some, however, travel as far as seven miles to the Balbal depression.

The low 1971 eland count is likely the result of the majority of this small population being in an inaccessible location at the time of the census. Further counts would be necessary to confirm the possible increase in Thomson's gazelle in 1971.

Two species not indicated in Table I because they are difficult to census, but which were taken with some frequency by lions are: bohor reedbuck, numbering several hundred in Maandusi and Ngoitokitok swamps,

TABLE I. Estimates of the numbers of the major plains ungulates in Ngorongoro Crater

SPECIES	DATE OF COUNT*				ESTIMATE USED IN THIS STUDY
	Oct. 69	Jan. 70	Apr. 70	Aug. 71	
Wildebeest	18238	14011	14422	16797	17000
Zebra	5734	3104	4267	5523	5500
Thomson's Gazelle	3769	3862	2576	5166	3750 for 1970
Grant's Gazelle	1478	1620	1798	1492	1700
Eland	329	490	478	98	475
Kongoni	140	167	136	154	150
Waterbuck	37	130	114	not counted	125

* These data were supplied by the Ngorongoro Conservation Authority from total counts made by Mweka College

and buffalo, common in the surrounding highland forest. A few male buffalo may be found in the crater at all times of the year, but herds of mixed age and sex appear only in the dry season.

METHODS

General

Study was concentrated upon predation by a lion pride living along the Munge stream in the northern half of the crater. Observations were restricted to this one pride to obtain temporally continuous data on the same lions. This also eliminated much of the bias which can result from random observations (such as, differing ease of detecting kill types and confusion as to which predator species was responsible for a kill).

Only one successful kill was seen involving male lions. This study is therefore primarily an analysis of prey capture by female lions, and unless otherwise stated, references to lions will refer to the female.

Components analysis requires the subdivision of the predatory process into simpler units. The basic partitioning is shown in Figure 2 where prey capture is envisaged as a consecutive set of events. Once the threshold for initiation is reached, the predator proceeds from one event to the next until an event is unsuccessful. In this case, the predator begins again at the first event (search). Table II defines these prey capture events or phases.

Activities other than prey capture occur during the digestive pause (Holling, 1965), when the predator is sufficiently sated that it need not actively seek food. For this study digestive pause is also taken to include the time spent eating. Of course, priorities such as reproduction or danger could temporarily terminate the prey capture cycle at any point.

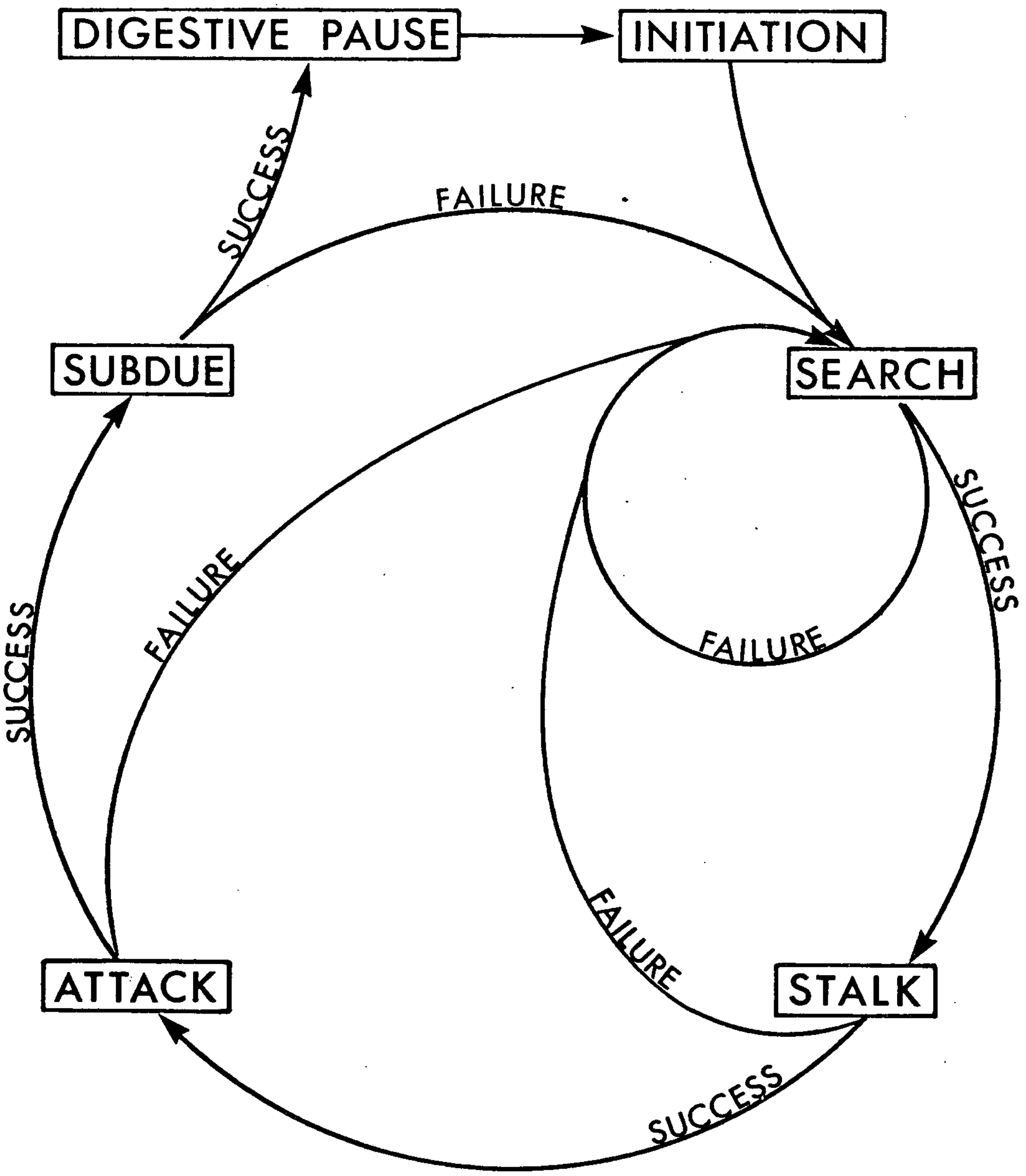

DIGESTIVE PAUSE
INITIATION
SUCCESS
FAILURE
SUBDUE
SEARCH
SUCCESS
FAILURE
SUCCESS
FAILURE
FAILURE
ATTACK
STALK
SUCCESS

Figure 2

PREY CAPTURE
(see Table II for definitions)

TABLE II. Prey capture events or phases

NAME	DEFINITION
Search	The reduction of predator-prey distance for prey which has not been specifically located.
Stalk	The reduction of predator-prey distance for prey which has been specifically located such that the prey is unaware or minimally alarmed by the predator.
Attack	An active approach by the predator which ignores disturbance to the prey and which maximizes the probability of predator-prey contact (although for very formidable prey this would be in a manner which also reduced the probability of harm to the predator.
Subduing	The killing of prey which has been brought into contact with the lion.

The basic method of analysis involved measuring the maximum number of variables affecting each event, while observing the lions during actual prey capture situations. Observations were made from a vehicle (Land Rover). This had a negligible effect upon the animals so long as the vehicle maintained a reasonable distance, because the animals were well habituated to vehicles. To keep contact with the lions at night, smaller vehicle-lion distance was necessary. This did not affect the lions but could affect the prey animals. However, reactions of the prey during moonlight driving suggested that the prey is disturbed very little. Particular care was taken during the critical stalk phase at night. When the lion showed signs of having located a prey animal, the vehicle was stopped and the lion allowed to stalk out of view. The vehicle was then advanced only after some time had elapsed (usually running could be heard). Headlights were never used, but brief sweeps of a small spotlight to relocate the lion were necessary. This had no apparent effect upon most prey animals (or the lions). However, lights could not be used around Thomson's or Grant's gazelle as these two species did show a reaction to artificial light.

Search

Prey searching is largely a function of movement patterns and dispersion of the prey and their relation to environmental stimuli. These features were not directly measurable by the basic method used for all other aspects. Furthermore, these are complex variables which would require investigation using the same kind of component analysis as used in this study for the other aspects of prey capture. This had to be considered of secondary importance as a research objective.

Predator search rate was calculated using a wristwatch (yielding seconds) and the odometer (yielding one-tenth mile units) on the research vehicle.

Stalk

It was considered desirable to obtain a more precise evaluation of the visual aspects of the stalk than could be derived from direct observation alone. An experimental situation was therefore designed including many variables involved in an actual stalk. An artificial lion-like predator constructed from wood fibre, cotton towel, and cardboard was used. Preliminary trials indicated that in the majority of cases only the head was visible when this pseudo-predator was hidden in vegetation, and thus, in the experimental technique eventually adopted, only an artificial head resembling a lion's was used. The experimental procedure involved the following steps:

1. The artificial lion head was placed in vegetation 100 to 200 yards from a group of prey animals and in the line of their general orientation. This was done while hidden behind the vehicle so that the prey could not detect the researcher's movement.
2. The vehicle was withdrawn from the area of the predator, placed in either a lateral position (if the prey were moving) or a position on the far side of the prey, and then halted.

3. In successful trials the prey would eventually move towards the pseudo-predator. At some position one or more animals would detect and react to the "predator". Only those trials in which the prey were undisturbed and in which they showed a definite reaction to the pseudo-predator were accepted.
4. The following variables were then measured:
    a. age, sex, and species of prey
    b. area of predator visible (This was done by photographing a known area grid and the hidden pseudo-predator from the position of the prey. Prey eye height was determined in advance through comparing photographs of normally moving animals of known ages and sexes with a known height surveyor-type pole photographed in the same position).
    c. light and reflectivities using a Gossen foot-candle meter (Model TRI-LUX)
    d. predator-prey distance using a semi-professional steel tape
    e. angle of orientation using sightings from a leveled tripod with degree scale on the base

Four prey species were studied in these experiments: wildebeest, zebra, Grant's gazelle, and Thomson's gazelle. Initially, more than 200 successful trials were recorded for each species. On the average, slightly less than one half hour was required for each trial.

Cover conditions associated with actual lion stalks were measured as the average of five height readings on a graduated pole. The pole was 100 feet from the observer and viewed from a height of forty inches. Wind direction was also recorded for most stalks.

Attack and Subdue

The force-velocity attack features of the predator and prey were measured by filming actual attacks. Two variations of this system were adopted. The more general technique involved two cameras a known distance apart filming the attack. A second technique used only one camera if two conditions existed -- a hill near the attack site and a flat attack site. In this case, the camera was positioned on the hill and the attack filmed; later, a grid pattern was constructed at the site of the attack and filmed from the original camera location. All films were subsequently examined on a Vanguard Motion Analyzer (Model M-16 CW). The positions of the predator, prey, and orientation marker were punched frame by frame into paper tape. This information plus knowledge of the film speed and the field parameters allowed the calculation of predator and prey velocities.

The Lion Population

The lion population was censused by the total count method. Differences in the probability of seeing various lions excluded other possibilities.

Individual lions were identified by a variety of features: spot patterns near the buccal vibrissae (Pennycuick and Rudnai, 1970), freckle patterns on the nose, and scars and other conspicuous irregularities.

Age estimates were made on the basis of qualitative comparisons with known age individuals.

The Prey Populations

Total counts were undertaken by Mweka College (see Table I). Estimates for specific areas at specific times were made using the strip census technique from the research vehicle. Strips were approximately 947 feet wide on each side of the vehicle. Prior to each census a measured distance of 947 feet was observed in order to facilitate visual estimation of the strip width. The open nature of the terrain and vegetation made detection of all desired animals virtually certain excepting Thomson's and Grant's gazelle fawns. These were censused using approximately 94.7 foot strips on either side of the vehicle.

Condition of lion-killed ungulates was, when possible, determined by the method of Cheatum (1949) based upon the texture and colour of the femur marrow. Sinclair and Duncan (1972) have since shown that this is a valid method for tropical ruminants. It was not possible to estimate the condition of live populations.

The ages of lion-killed ungulates were determined on the basis of tooth wear and replacement using the criteria of Klingel and Klingel (1966) for zebra and Talbot and Talbot (1963) for wildebeest. Other artiodactyls were placed in broad age classes using the same criteria as were used for wildebeest.

Live weights were taken from the literature (Sachs, 1967; Talbot and Talbot, 1963). In the case of age groups for which no information could be found, estimates were made based upon fractions of the adult weight. Uneaten (but weighable) portions of kills were weighed with a spring balance.

Computers.

All complex calculations were done by computer. During the synthesis stage four machines were available: IBM 1130, IBM 360/67, IBM 370/168, and PDP 11/45.

THE LION POPULATION

Discussion

A lion pride, as defined for this study, is a group of lions which interact peacefully with one another. This agrees with Schaller (1972), but differs from Rudnai (1973?) who treats a pride as a group of lions frequently found together. The former definition is preferred because it yields a more consistent pride area through time and also in this study corresponds to the pride territory.

Prey capture is affected by the number of lions and the pride area; thus, examination of the pride dynamics in the crater is relevant to the major aim of this study.

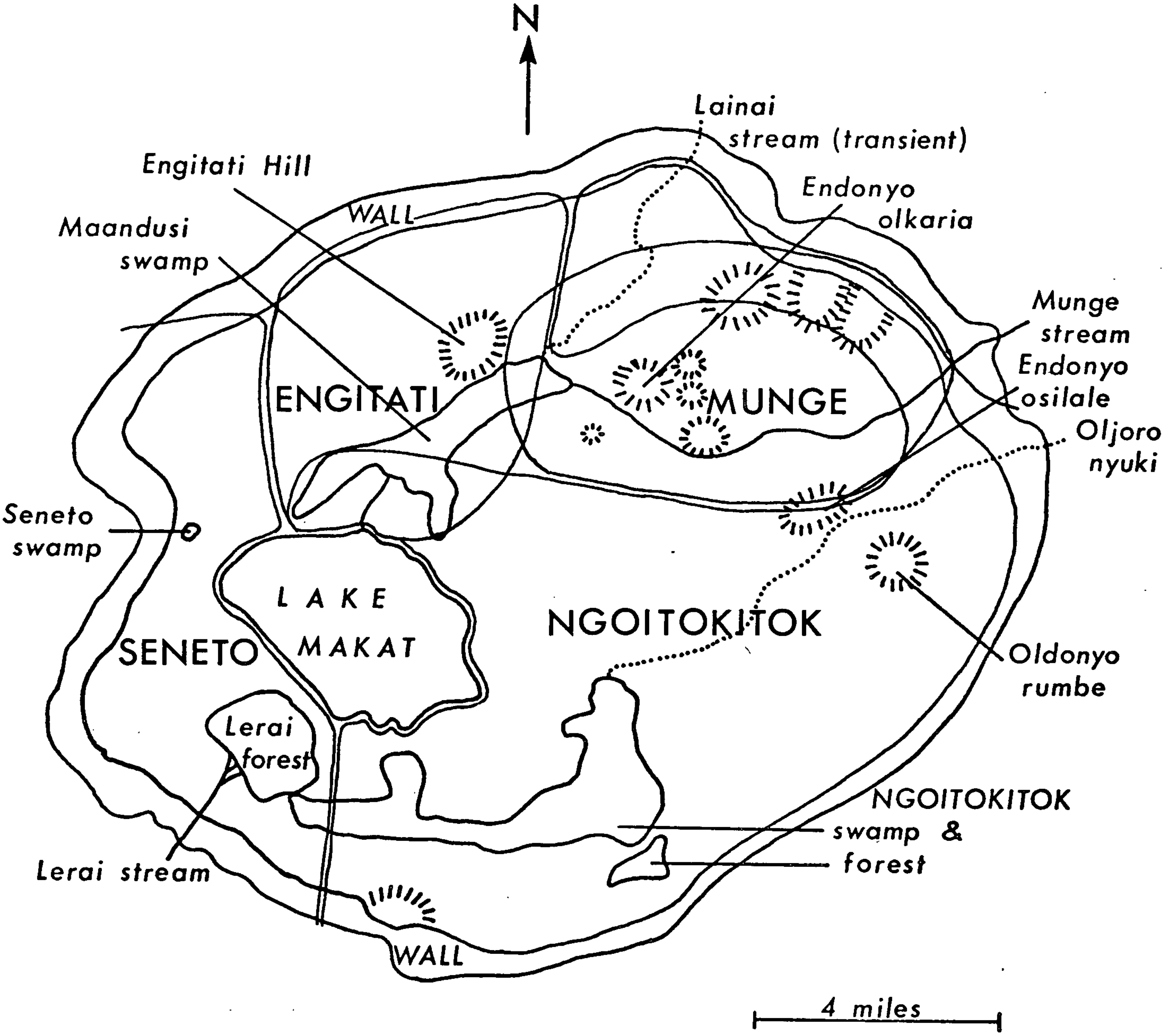
The pride compositions are given in Table III and the pride areas in Figures 3, 4, and 5. Based on limited observations and rangers' reports, the Ngoitokitok pride area outside the crater was not extensive. Several sightings of the Seneto pride however indicated that in addition to the area shown in the crater, a considerable portion of the Malanja area west of the crater was also in their pride area. This would mean a total Seneto pride area approximately fifty per cent greater than the size of that shown in Figures 3, 4, and 5. All together the prides shown in these figures would occupy approximately 135 square miles with a mean pride area of 33.75 square miles based on an occupancy by four prides. This corresponds to a mean of 1.93 square miles per lion based upon 70 lions total. In addition, occasional sightings indicated that

TABLE III. Lion Populations in Ngorongoro Crater

DATE	AGE							TOTAL	AREA
	greater than 3 to 4 years		2 to 4 years		1 to 2 years		less than 1 year		
	male	female	male	female	male	female	both sexes		
	10	6	0	0	3	6	?	25	Seneto
January	1	1	2	1	0	0	2	7	Engitati
	2	4	0	0	1	2	8	17	Munge
1970	0	3	10	3	0	0	0	16	Ngoitokitok
	13	14	12	4	4	8	10	65	All Areas
	10	6	0	0	2+?	?	?	39	Seneto
January	2	2	0	0	0	0	3[a]		Engitati
1971		4	0	0	2	6	2		Munge
	9	6	0	0	0	0	10[b]	25	Ngoitokitok
	21	18	0	0	4	6	15	64	All Areas
	9	6	2	0	0	0	9	26	Seneto
January	9	3	2[c]	3[c]	0	0	5	41	Munge
1972		6	0	0	3	4	6[d]		Ngoitokitok
	18	15	4	3	3	4	20	67	All Areas[e]

a. one born in 1970 but dead by January 1971, not included.
b. four of these were born in January, 1971.
c. these were usually in the former Engitati area.
d. three more cubs were born in February, 1972.
e. one former Engitati female still in crater at this time although with no home area. It died May 1972.

Figure 3: January 1970 Lion Pride Areas


N
Lainai
stream (transient)
Engitati Hill
Endonyo
olkaria
Maandusi
swamp
WALL
Munge
stream
Endonyo
osilale
Oljoro
nyuki
ENGITATI
MUNGE
Seneto
swamp
LAKE
MAKAT
NGOITOKITOK
SENETO
Oldonyo
rumbe
Lerai
forest
NGOITOKITOK
swamp &
forest
Lerai stream
WALL
4 miles

NGORONGORO CRATER

Figure 4: January 1971 Lion Pride Areas

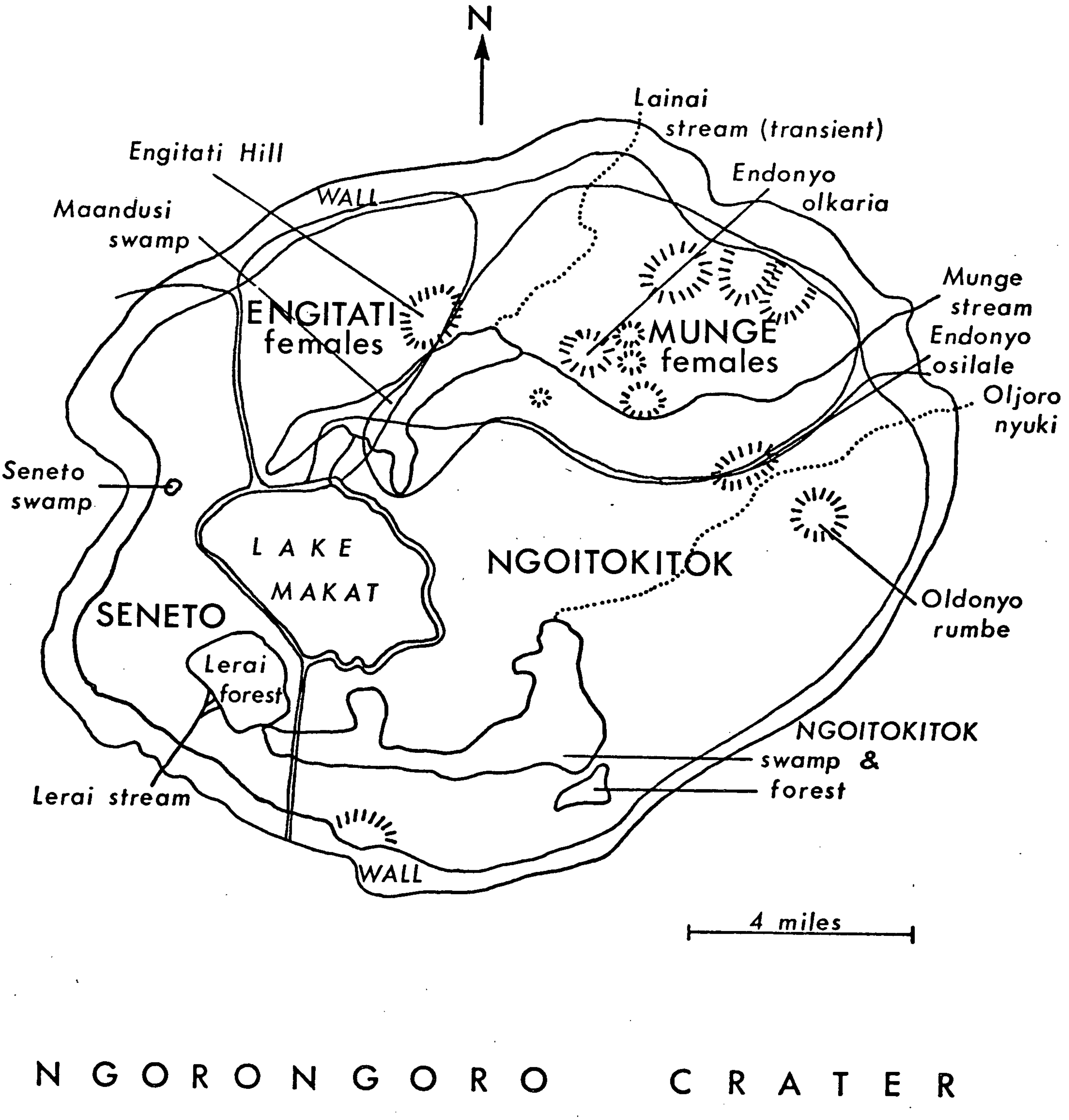
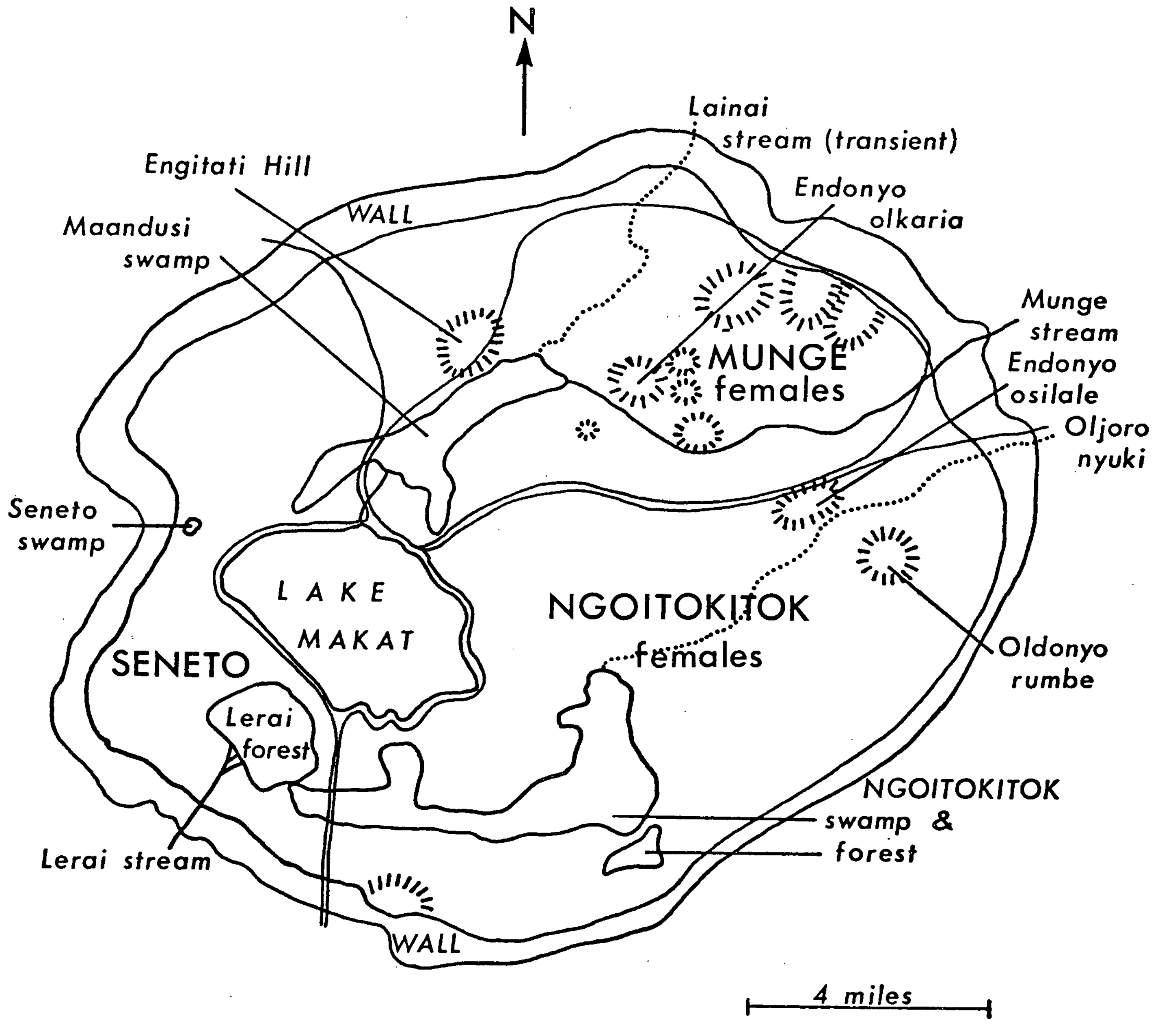

N
Lainai
stream (transient)
Engitati Hill
Endonyo
olkaria
WALL
Maandusi
swamp
Munge
stream
ENGITATI
females
MUNGE
females
Endonyo
osilale
Oljoro
nyuki
Seneto
swamp
LAKE
MAKAT
NGOITOKITOK
Oldonyo
rumbe
SENETO
Lerai
forest
NGOITOKITOK
swamp &
forest
Lerai stream
WALL
4 miles
NGORONGORO CRATER

Figure 5: January 1972 Lion Pride Areas


N
Lainai stream (transient)
Engitati Hill
Endonyo olkaria
WALL
Maandusi swamp
Munge stream
MUNGE females
Endonyo osilale
Oljoro nyuki
Seneto swamp
LAKE MAKAT
NGOITOKITOK females
SENETO
Oldonyo rumbe
Lerai forest
NGOITOKITOK swamp & forest
Lerai stream
WALL
4 miles

NGORONGORO CRATER

another pride was located north of the crater.

The original delineation of the prides and most of the information for Figure 3 was determined by Des Meules (personal communication). The pride areas shown for the three years represent areas where the lions might spend the day resting and do not include occasional transgressions into new areas. A large number of sightings are involved including observations of moving lions. These pride areas were territories (Burt, 1943) since non-pride members were attacked within the area and pride members fled from other pride areas if they met strange lions. The result is little boundary overlap. However, near the boundaries or at times of strife, defense was variable though generally as activity shifted deeper into one territory or the other the "home lions" would become the aggressors. Schenkel (1966) and Makacha and Schaller (1969) report a similar situation for Nairobi and Lake Manyara Parks, respectively. The lower density situation in the Serengeti however apparently leads to territories within home ranges (Schaller, 1972). Likewise, Eloff (1973) studying the low density Kalahari lion suggests a system somewhat similar to that in the Serengeti.

The situation in January of 1970 was less complex than in later years in that the adult males and females of the prides utilized the same areas. (Variation in the male and female areas has been noted for other locations also -- Schenkel, 1966; Makacha and Schaller, 1969; Rudnai, 1973?; and Schaller, 1972). Soon after this however (February and March, 1970), the three Engitati males disappeared. This was likely the result of strife since male EM_2 of that pride was found considerably lacerated at one stage. The two Munge males then extended their range over much of the former Engitati area. Also the Munge females encroached somewhat upon the Engitati female area in August and September. This may have been a result of the new activity of the males or a desire to utilize the hunting potential of the Maandusi swamp. A two to four year old male which was part of a group of four Ngoitokitok lions (three females and one male, probably siblings) sometimes found along the Lainai stream, also disappeared and his three female companions no longer used that location. The result of these changes is seen in the January 1971 map (Figure 4).

Late in January of 1971 the Ngoitokitok males began to make excursions into the Munge female area. This was facilitated by the Munge males often being in the Engitati female area. The Munge males were aggressive to these intruders when they encountered them, but, if outnumbered, they retreated. The Munge males were no longer seen by April 1971. Encounters between the Seneto and Ngoitokitok males were also observed. One observed encounter led to a serious fight in which one Seneto male was killed and one Ngoitokitok male injured. No area changes resulted from these latter encounters, however.

These interactions between males also affected the females. The Ngoitokitok males, for example, were seen several times to chase the

Munge females in the early stages of the expansion. One Munge female (MF $_3$) disappeared at this stage. Also, after the disappearance of the Munge males, the Engitati females lost their former area and female EF$_2$ was not seen again. The other Engitati female (EF $_1$) was seen in several locations in the crater until she died in May of 1972. Figure 5 shows the results of the Ngoitokitok male expansion.

Table III reflects these changes in pride area. Two other features can be noted from this table. Firstly, the relative constancy of the total number of lions in the crater (1970 and 1971 would have somewhat more lions then indicated as the number of Seneto cubs was uncertain). This number has apparently been fairly constant for some years excepting a period beginning in 1962 when extensive numbers of Stomyx flies resulted in death and emigation of some lions (Wright, 1960; Fosbrooke, 1963; and Kruuk, 1972). Secondly, as would be expected from the constant total combined with limited adult losses, very few cubs reached adulthood. Schaller (1972) notes the same situation for the Serengeti. Loss of subadults was largely the direct result of hostility by the older members of the pride. This phenomenon seems to be density dependent. This is evident directly from this study where the Ngoitokitok and to a lesser extent the Engitati prides which had low adult densities at the commencement of the study received a considerable input of subadults, while the more crowded Munge and Seneto prides did not. Furthermore, lion density in the Serengeti was found by Schaller (1972) to be 0.41 lions per square mile and in that area subadults were generally repulsed from the pride at two and a half to three and a half years. The Ngorongoro lion density was about 0.52 lions per square mile and there the subadults were repulsed from the Munge and Seneto prides at one and a half to two and a half years. Subadult lions in Nairobi park (which has a lion density of 0.62 lions per square mile (Rudnai, 1973?)) were found by Schenkel (1966) to be attacked by the adults at one and a half to two years. It will be shown for this study that this aggression against subadults is occurring in the absence of food shortage for the adults and Schaller (1972) has come to the same conclusion for the Serengeti. It would seem therefore that this is an internal density-dependent mechanism regulating the population sizes of lions as has been suggested for some other animals by Wynne-Edwards (1962). It must be noted however, as does Schaller (1972), that there is a general correlation between the equilibrium sizes of lion populations in different areas and the available food supply. Perhaps an internal mechanism is set so that the lion density is regulated below the level of food limitation for the area.

It is difficult to envisage how the lion could relate to its food supply in such a manner. However, a simpler hypothesis can describe the data just as well. Firstly, as outlined above, the age and extent to which subadults are ousted from the pride can be directly related to lion density. These individuals are, however, less able to obtain food for themselves as evidenced by their physical appearance which is often quite emaciated. Schaller (1972) also reports this for the Serengeti. This inability to obtain sufficient food is probably a combination both of inexperience at prey capture and their often being chased from food they have obtained by any adults in the area. (This has been witnessed). Thus the proportion of surviving subadults will be directly related to the ease of obtaining food (which will generally be related to the prey densities).

The hostility of the adults in the pride seems to lessen as the subadults reach adulthood. This was indicated by the Ngoitokitok pride. The three subadult females originally spent much of their time in peripheral areas such as Lainai and towards Lerai, away from the main areas occupied by the adult females. Later in the study they were often seen in the same subarea, and sometimes with the older females. Similarly, in the Serengeti, Schaller (1972) observed a case of decreased aggression to a subadult as it increased in age.

Thus the recruitment of new adults and hence the population size will depend upon the number of surviving subadults. Subadults which depart from the original pride area for an extensive period of time, such as the Serengeti nomad lions (Schaller, 1972) are usually not accepted back into the pride, except in the case of males deposing pride males. Because the subadults generally require a higher density of prey to survive, the adult population will rarely reach the level of food limitation.

Synopsis

There are typically several adults of each sex per pride. This presents the possibility of the tactic of group hunting. The area associated with each pride is a territory thus tactical manouvers must be restricted to this area.

Predator strategy and its effectiveness is a critical component in survival. Furthermore there should be detectible differences between the values of the components of prey capture strategy and success between pride members and the subadults evicted from the pride.

PREY CAPTURE INITIATION

General

The factors which affected the initiation of prey capture activity by the lion are prey stimulation, hunt rhythm, and hunger. They are defined as follows:

Prey stimulation -- is the inverse of the amount of energy which must be utilized by the lion in order to place it in an attack situation (see Table IV).

Hunt rhythm -- is the activity cycle (diurnal or nocturnal) which the lion has been using for type III prey capture (see Table IV).

Hunger -- is a function of the period of time since last feeding and the amount consumed at that feeding.

These factors were consistent within the normal size range of prey, but for very large prey (such as rhinoceros) or very small prey they did not apply. Likewise there had to be a reasonable probability of success for prey capture to be attempted. Thus for example, a lion would not stalk a prey animal which was watching it.

Prey Stimulation

Prey stimulation was considered to consist of three levels based upon the number of active prey capture events involved. Prey capture was therefore divided into three types as shown in Table IV.

TABLE IV. Events involved in each of the three basic prey capture types

	Events or Phases			
Type	Active Search	Active Stalk	Attack	Subdue
I			*	*
II		*	*	*
III	*	*	*	*

"Active" refers to the lion having to move during that event. Furthermore, the active search of type III prey capture must be associated with the goal of prey capture. Experience by the observer generally permitted the determination of the lion's goal in moving; however, the criterion which was used was the subsequent behaviour of the lion. If the result of the movement by the lion was not to shift to a good resting site, obtain water, join other lions, or any other obvious goal, but instead involved only travel through an area which in the past had proved suitable for prey capture, then the goal was assumed to be prey capture. Special circumstances such as a wounded animal or stormy weather might provide extra stimulus to initiate prey capture activity by the lion. These occurrences were however of minor importance during this study.

Hunt Rhythm

Kühme (1966) and Kruuk and Turner (1967) consider nocturnal prey capture activity to be the norm for the Serengeti lion, as does Rudnai (1973?) for the Nairobi lion. Schaller (1972) found that the lion was nocturnal but that availability of diurnal prey seemed to result in considerable daytime activity. The situation at Ngorongoro showed variation in prey capture timing. The effect of light upon capture success will be considered in detail in later sections. However, the gross difference between day and night was that in the day, vegetation or topography was essential for cover while during the night, darkness itself was adequate. Generally the prey animals showed a distinct avoidance of areas which had suitable lion cover. The lions therefore often had no option but to hunt at night when the cover constraint no longer applied. Such was the situation for February, March, and May of 1970. The range of nocturnally available densities of the two major prey is shown in Table V and for all observations in that period, type III hunting was invariably nocturnal. Types I and II hunts occurred at all times of the day, as was found by Rudnai (1973?) for Nairobi Park lions. The situation changed however during the dry season of 1970. It can be seen from the data of August and September, 1970 (Table V) that prey densities were extremely low in the night hunting area. At the same time, during the day prey were moving into the Maandusi swamp to graze and along the Munge stream to graze and obtain water -- both areas of good lion cover.

TABLE V. Mean prey densities in nocturnal type III areas of the Munge lions (Number/10^6 sq. ft.)

DATE	PREY DENSITIES	
	WILDEBEEST	ZEBRA
February, March and May, 1970	24.68	4.77
August and September, 1970	0.40	0.02
October 7 to October 21, 1970	22.87	1.08
October 22 to November 26, 1970	1.73	0.55
November 26 and onwards, 1970	27.59	0.69

As noted in the section on methods, no measure of the precise pattern of prey movement into these areas of good cover was obtained. A qualitative measure of the increased frequency can however be obtained by examining the number of kills per day made by the lions as a result of diurnal type I and type II hunts (Table VI). These hunts depend upon prey being near cover in the same way as do diurnal type III hunts and so the increase in the number of kills implies an increase in the type III potential. All type III hunts during the August to November 1970 period were diurnal. The lions were therefore able to adjust their prey capture activity patterns in order to obtain food at the time of day when it was available. Furthermore, the indication is that the lion tended to continue to be active only during one time of the day and not to expand its activity over the entire twenty-four hour period. During the period October 7 to 21, 1970 a large number of wildebeest moved into the Munge area presenting the possibility of favourable night hunting (Table V). The lions however did not change their activity pattern, but continued to use only diurnal type III prey capture. Because the period of favourable nocturnal potential was comparatively short this would seem not to indicate any preference for one activity period over the other, but rather to suggest a tendency to remain on the same activity cycle.

TABLE VI. Number of diurnal kills per day from type I and II hunts

DATE	NUMBER PER DAY	SAMPLE SIZE
February, March, & May 1970	0.041	49
August to November, 1970	0.347	101

Hunger

Holling (1965) has conducted an extensive analysis of the effect of hunger on all aspects of predation using a mantid as the experimental animal. He concluded that hunger could potentially affect all aspects of predation and also the inclination to eat killed prey. Various species of small cats (Leyhausen, 1956) however, seem to be virtually independent of hunger (that is, have very low hunger thresholds) for all phases of prey capture except search. This seems also to apply to the lion, in that types I and II hunts were undertaken by reasonably gorged individuals. Kruuk (1972) concluded similarly for the hyaena as did McLaughlin (1970) for the cheetah. The situation is less clear for the wolf, but the work of Mech (1970) seems to support a similar conclusion. The primary effect of hunger upon prey capture by larger fissipeds therefore seems to be upon search, although Rudnai (1973?) suggests that the intensity of the stalk varies with hunger. This aspect is examined below and necessitates determining the hunger level.

A difficulty arose when measuring food intake for lions under natural conditions however in that a number of lions were often eating from the same kill simultaneously. This was further complicated by having different ages and sexes of lions represented since average consumption for all the lions eating was then of little use. An approximate measure of the portioning of the available food can, for such a case, be derived by estimating the daily energy expenditure of the various age and sex types of lions and then assuming that for an extended period of time, if energy is expended it must be balanced by incoming energy if no loss of body weight occurs. Although lions were not weighed, their short fur facilitated visual estimation and for the lions involved in this aspect there was no indication of weight loss. This evaluation is undertaken in the Appendix.

The evaluation of energy intake and loss in the Appendix can be used for two facets of prey capture. Firstly, it allows the calculation of the consumption rate for the individual lions (this is examined in the Appendix) and secondly it permits the determination of the hunger level of the lions. Hunger is a function both of the period of time since feeding and the amount consumed at that feeding. This assumes that the effect of the hunger level prior to feeding is negligible in contrast to the amount of satiation produced by the new food intake. Since the threshold for type III hunts appeared to approximately correspond to completion of digestion (as evidenced by the amount of abdominal distension), this assumption is probably valid. Figures 6 and 7 illustrate the relation shown by the lion data for the threshold of active search initiation for in-phase diurnal and nocturnal type III hunts. Digestion and hence the commencement of satiation would begin as soon as feeding starts, and thus the time interval is calculated from the onset of feeding. The requirement that the initiation of active search will not occur out of phase necessitates modification of the actual time interval if initiation occurs soon after the start of the phase period of any day. A mean value was used in such cases, between the end of that phase period the previous day and the actual time of initiation. The

Figure 6. Effect of hunger on active search initiation - diurnal

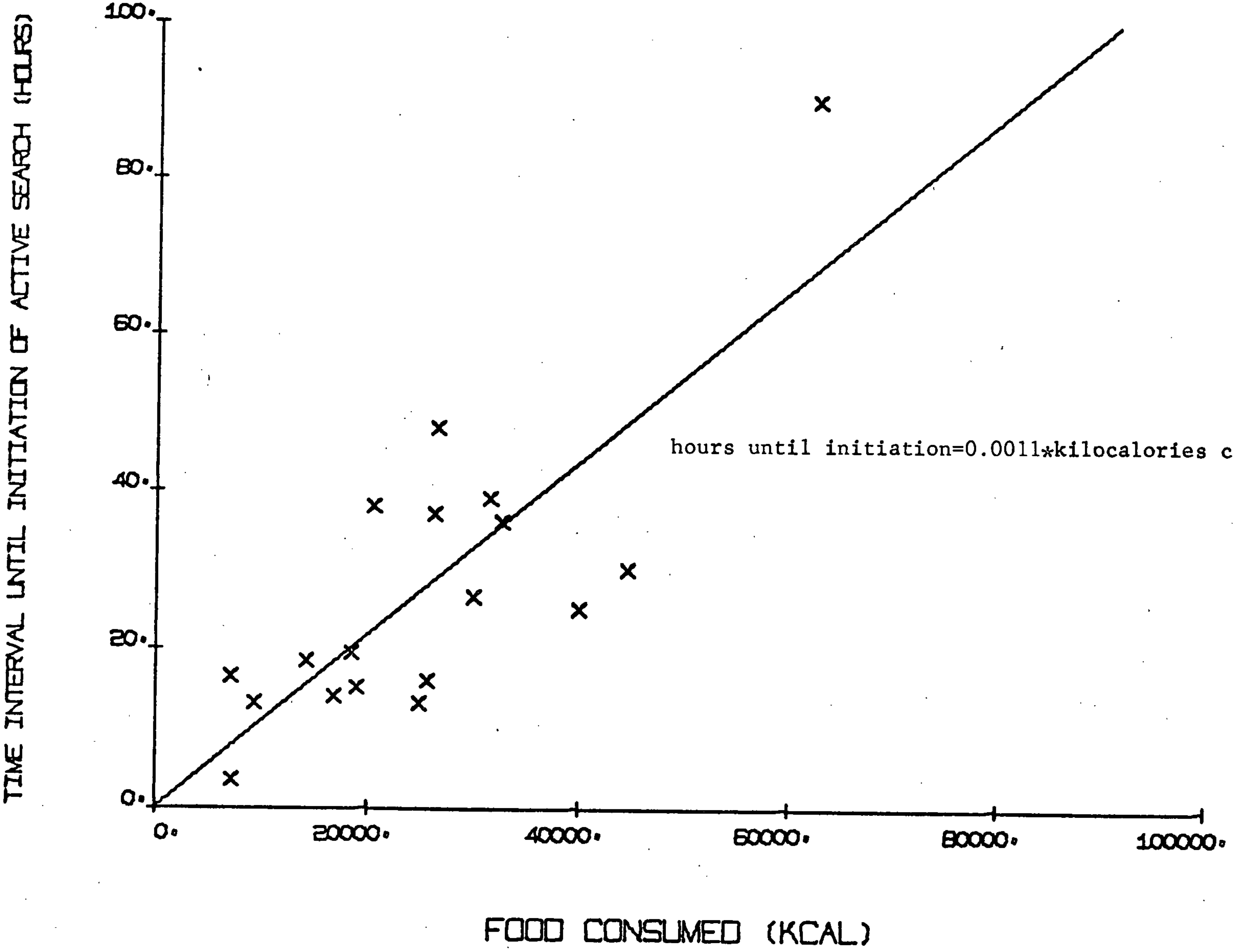


Figure 7. Effect of hunger on active search initiation - nocturnal

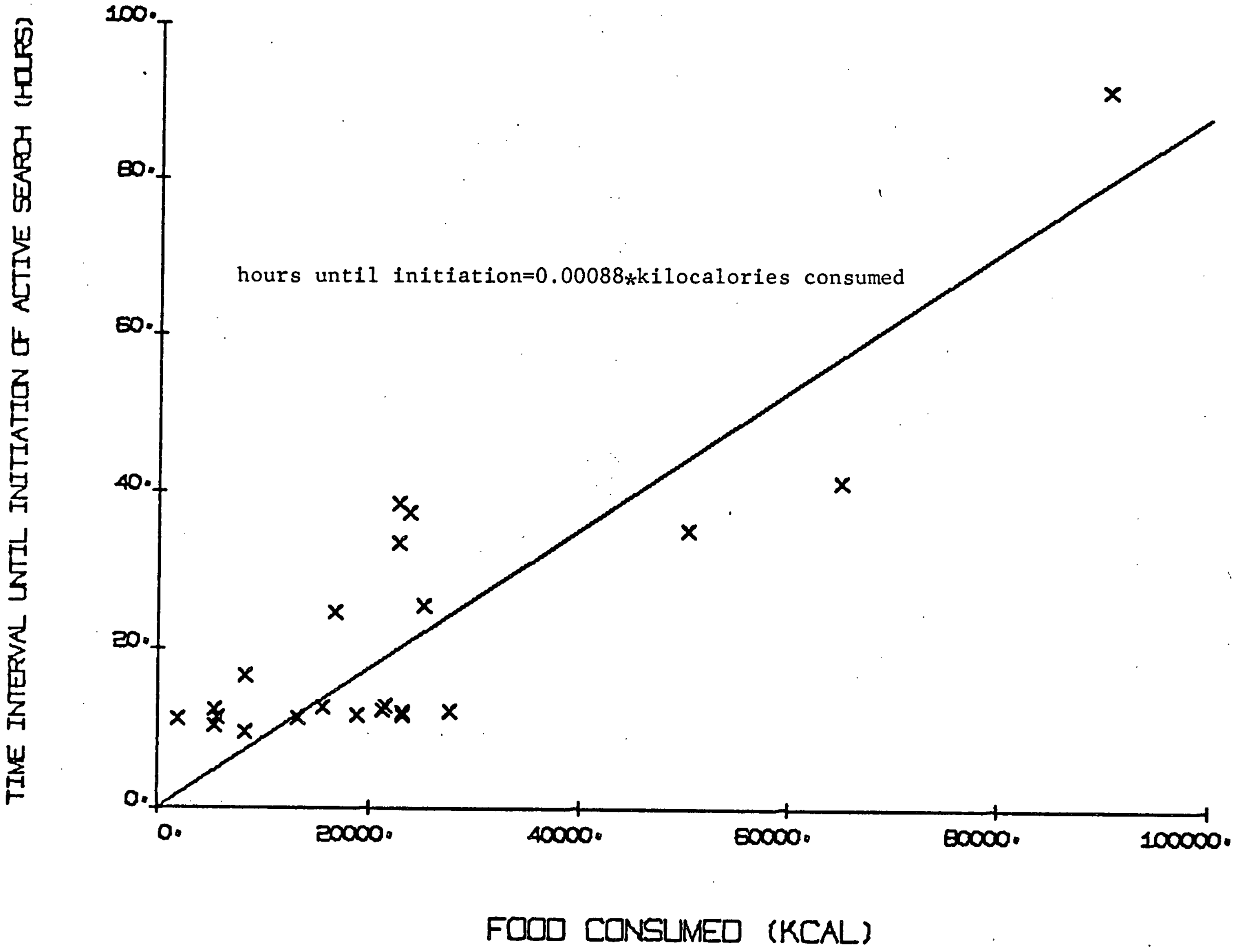
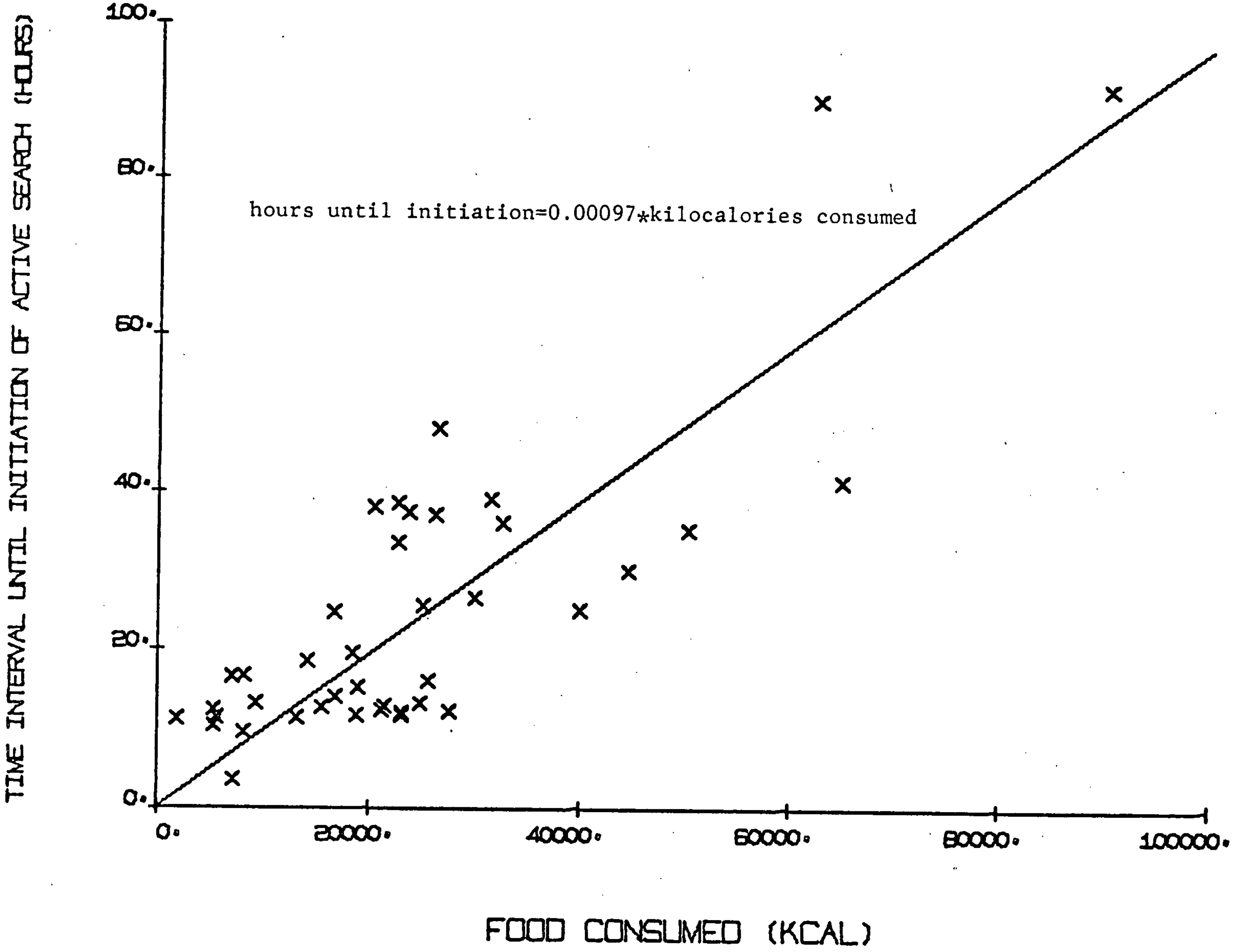


Figure 8. Effect of hunger on active search initiation - nocturnal and diurnal



amount of food consumed has been converted to kilocalories based upon 909 kilocalories per pound of food (see Appendix).

Holling's (1965) work with mantids showed an exponential relation between the two variables of hunger at the threshold of consumption. Figures 6 and 7 suggest however a linear relation for initiation of active searching within the range of the data. The line shown on the figures is the least squares regression line through the origin. There is no significant difference in these two data sets (probability of similarity is greater than 0.05) thus the threshold seems to be the same for both diurnal and nocturnal active search initiation. Figure 8 shows the combined data. The relationship at the threshold is:

$$\text{Hours until initiation} = 0.00097 * \text{kilocalories consumed}$$

with the variance in the estimate of the slope being $0.35 * 10^{-8}$ and the standard deviation about the regression line being 11.20 hours.

It is possible to consider in a general manner, how this relationship would differ for initiation of other forms of prey capture as discussed under the heading "hunt rhythm". The thresholds for initiation of attack and active stalk, either in-phase or out of phase, would have a much shallower slope than that of Figure 8. The threshold for the initiation of an out of phase active search would, in contrast, have a steeper slope.

The multiple threshold nature of initiation would have considerable significance to the lion's role as a population regulating factor for ungulate prey species. Very high prey densities would result in the lion obtaining all its food by means of types I and II prey capture since hunger would never drop below the type III (active search) threshold. The frequency of types I and II hunts (and thus kills) would, for a given set of conditions, be directly related to prey density and thus mortality caused by the lions would be a constant fraction. Once the prey density drops below the level at which the lion obtains sufficient food from types I and II hunts to remain above the type III threshold, the lion will kill a nearly constant amount of prey as density drops further. This results from the lion increasing the number of type III hunts to offset the reduced intake from type I and II hunts. The drop in density would also make type III hunts more difficult (as will be discussed in the section on searching); however, the lion need simply increase its effort (that is, increase search time). This range of prey densities would therefore show inverse density dependent mortality from lions. Only when the prey density drops below the level at which the lion can no longer successfully search and capture prey during the time which it has available for searching, would the number of prey killed decline as density decreased. This discussion refers only to short term prey density changes in which the lion's response to prey density was strictly functional and not numeric (Soloman, 1949).

Synopsis

A hunger threshold must be reached before active search (type III hunting) will commence. However the lion is an opportunist for more easily obtained prey (type I and II hunts), as there is a negligible hunger threshold for stalking and attacking prey.

If available prey densities dictate, then the lion is capable of changing its tactics to hunt either diurnally or nocturnally. It does not readily switch between the two.

SEARCHING FOR PREY

General

Search success depends upon the rate of movement of the predator and its area of detection (or reaction, whichever is less) for a given prey and the dispersion and rate of movement of the prey. These factors depend in turn upon historical and environmental circumstances.

As was noted in the section on methods, the effect of prey activities upon prey searching was not analyzed by means of components analysis. Thus, only specific features of prey activity observed during this study can be identified.

Diurnal

The necessity of cover for the lion by vegetation or topography is the major feature of diurnal searching. The important aspect of prey movement is not velocity but rather the frequency with which the prey enters or approaches these areas of good cover. The significant measure of prey density is the density of prey frequenting the cover areas.

It is of interest to examine the patterns of prey search selection which occur diurnally. Positive selection occurs if a prey type is successfully searched (that is, a stalk ensues) more frequently than would be expected on the basis of the relative densities of prey. A selectivity rating which is based upon the density and number of successful searches by the predator with a particular prey compared to all others is of little use. What is desired is the selection occurring between any two species.

This value should be constant regardless of the relative abundance of the entire prey complex, whereas the first rating would change.

Table VII summarizes the basic data required for determination of diurnal search selectivity. Expected percentages of occurrence are based upon the densities of the various prey. These densities were measured as the density of the prey within 947 feet of the good cover regions. The densities varied for different areas and times. In order to give increased sample sizes (of the number of successful searches) the data were grouped so that the range of expected percentages for each prey species within each group was less than five percent. Not surprisingly, these groups corresponded to different time periods. (These diurnal observations were made during the dry season. As the season progressed, the use of these regions by wildebeest (the most abundant species in all cases) increased relative to the use of them by other species). The observed percentage for each species is the percentage of successful searches involving that prey species out of the total number of successful searches. Approximately one-third of the total wildebeest and zebra stalks involved closely mixed herds; therefore, it was necessary to assume for each group that the proportion of these stalks directed towards each species was the same as the proportion shown by the data for unmixed herds. This results in fractional totals.

Because wildebeest were the most abundant species, they were chosen as the basic species for comparison. Thus search selectivity is defined as,

TABLE VII. The effect of species upon search success

DIURNAL

PERCENTAGES

IEAN DATE	THOMPSON'S GAZELLE		GRANT'S GAZELLE		WILDEBEEST		ZEBRA		TOTAL STALKS OBSERVED
	EXPECTED	OBSERVED	EXPECTED	OBSERVED	EXPECTED	OBSERVED	EXPECTED	OBSERVED	
5 SEPT	28.9	32.4	2.2	0.0	36.8	7.1	32.1	60.9	34.0
5 SEPT	16.0	5.6	1.8	11.1	45.7	34.7	36.4	48.6	18.0
5 SEPT	32.0	33.3	3.6	0.0	63.1	22.2	1.3	44.4	12.0
5 OCT	17.8	18.9	2.4	4.1	64.4	31.2	15.4	45.8	74.0
7 NOV	19.6	0.0	1.6	8.0	69.8	56.6	9.0	35.4	25.0
0 NOV	15.7	23.5	3.2	11.8	85.7	27.7	2.4	37.0	17.0
3 NOV	5.3	0.0	1.6	23.1	92.5	76.9	0.6	0.0	13.0

$$\text{search selectivity} = \frac{\dfrac{\text{number of stalks for a given species}}{\text{number of stalks for wildebeest}}}{\dfrac{\text{abundance of that species}}{\text{abundance of wildebeest}}}$$

Tables VIIIa, VIIIb, and VIIIc give the value of this index for each of the groups. A weighted mean and standard deviation is also shown, with the weights being the number of stalks involved in the calculation for each group. Each of the species can be seen from the tables to be searched out (on the average) more frequently than would be expected on the basis of its density compared to that of wildebeest. This could arise in several ways. Firstly, differences in the group sizes formed by the four species would result in those which form small groups being encountered more frequently, relative to their density, then those forming large groups. The observed group sizes are listed in Table IX.

TABLE VIIIa. Diurnal search selectivity for Thomson's gazelle

DATE	SELECTIVITY	SAMPLE SIZE
05 Sept.	5.7855	13.42
15 Sept.	0.4570	7.25
15 Sept.	2.9578	6.67
15 Oct.	2.1919	37.11
07 Nov.	0.0000	14.15
10 Nov.	4.6315	8.71
23 Nov.	0.0000	10.00

mean = 2.2852 standard deviation = 0.7919

TABLE VIIIb. Diurnal search selectivity for Grant's gazelle

DATE	SELECTIVITY	SAMPLE SIZE
05 Sept.	0.0000	2.42
15 Sept.	8.1244	8.25
15 Sept.	0.0000	2.67
15 Oct.	3.4836	26.11
07 Nov.	6.1644	16.15
10 Nov.	11.3617	6.71
23 Nov.	17.3438	13.00

mean = 7.4264 standard deviation = 2.1551

TABLE VIIIc. Diurnal search selectivity for zebra

DATE	SELECTIVITY	SAMPLE SIZE
05 Sept.	9.7445	23.00
15 Sept.	1.7577	15.00
15 Sept.	97.0769	8.00
15 Oct.	6.1333	57.00
07 Nov.	4.8472	23.00
10 Nov.	47.6111	11.00
23 Nov.	0.0000	10.00

mean = 13.6865 standard deviation = 9.3862

TABLE IX. Diurnal group sizes of the four major prey species during the 1970 dry season

SPECIES	MEAN GROUP SIZE
Wildebeest	65.56
Zebra	29.58
Thomson's gazelle	21.14
Grant's gazelle	15.17

It can be seen that wildebeest formed the largest groups. Table X gives the selectivity ratings expressed in terms of group abundances.

TABLE X. Search selectivity rating relative to wildebeest, based upon group abundance

SPECIES	SELECTIVITY RATING
Zebra	6.175
Thomson's gazelle	0.737
Grant's gazelle	1.718

This transformation largely eliminates the selectivity difference between the gazelle species and the wildebeest. The rating for zebra is still far from one, however. This high rating reflects a greater readiness of zebra to approach and enter areas of good lion cover. This feature was also apparent during the field observations. No direct estimate is available of the effect of other features such as size of prey or groups upon the reactive area of the lion.

Tables VIIIa, VIIIb, and VIIIc show that in most cases there are no trends in selectivity with changing conditions (as indicated by date). This suggests that these ratings may have some general applicability to other areas with a similar diurnal prey capture situation (that is, dry season use by prey of limited resources in restricted regions of good lion cover). But different circumstances would likely not be similar.

This is seen in the latter part of November when Grant's gazelle is being more readily searched. (This was the start of the rainy season, and the difference is likely the result of changes in prey feeding patterns. Lamprey (1963) and Stewart and Stewart (1971) have both noted the difference in feeding habit of the Grant's gazelle as contrasted to the three other species, particularly at this time of the year). Rudnai (1973?) provides data which allows the calculation of the zebra search selectivity rating for Nairobi Park (0.47, sample size of 10). These data probably include both nocturnal and diurnal observations, but it serves to indicate that the factors operating under different conditions can affect these ratings considerably.

Nocturnal

The nocturnal search is not restricted by the need for solid cover, as the darkness itself is sufficient. The lion is thus freed to seek prey anywhere within its hunting area. Similarly, types I and II hunts can occur at any location. This simplifies the relationship between search success and prey density; however, as was indicated for the diurnal situation, the important feature is prey group density. This latter variable was more difficult to measure than prey density for three reasons. Firstly, the census technique tended to disturb dispersion; secondly, dispersion was difficult to distinguish at higher densities in cases where the observer was located on the same level as the prey; and thirdly, censusing had to be undertaken in daylight, and although density did not appear to change, dispersion may have. This difficulty was circumvented in May for type III hunts. May in Ngorongoro is a period of intensive territoriality by mature male wildebeest (Estes, 1969) and active searching by lion at that time took place in a breeding area. Under these circumstances, the number of wildebeest groups corresponds to the number of male wildebeest. The average number of wildebeest per group will therefore be equal to the total density of wildebeest divided by the number of males. Figure 9a shows that within this searching area the territories of the males compressed in direct proportion to the increase in density of non-calf individuals. Thus, the average number of wildebeest per group remained fairly constant (at about 2.2).

March is part of the pre-rut period of wildebeest activity (Estes, 1969). Territorial behaviour at this time is less intense then in May but still considerable. It is therefore probable that the number of groups present during this period was also equal to the number of males. Figure 9b shows that two different group sizes were present (in different areas or days). Both average group sizes (3.1, excluding the two very low densities from a peripheral area, and 9.0) are larger than the mean May group size. Increased breeding activity would therefore seem to reduce territory size. This could affect prey capture as a larger group may be easier to detect than a smaller group.

Searching is basically a matching of the area examined by the predator for prey with the area occupied by each prey group. A difficulty arises,

Figure 9a. Wildebeest: Relationship between territory size and non-calf density (May data)

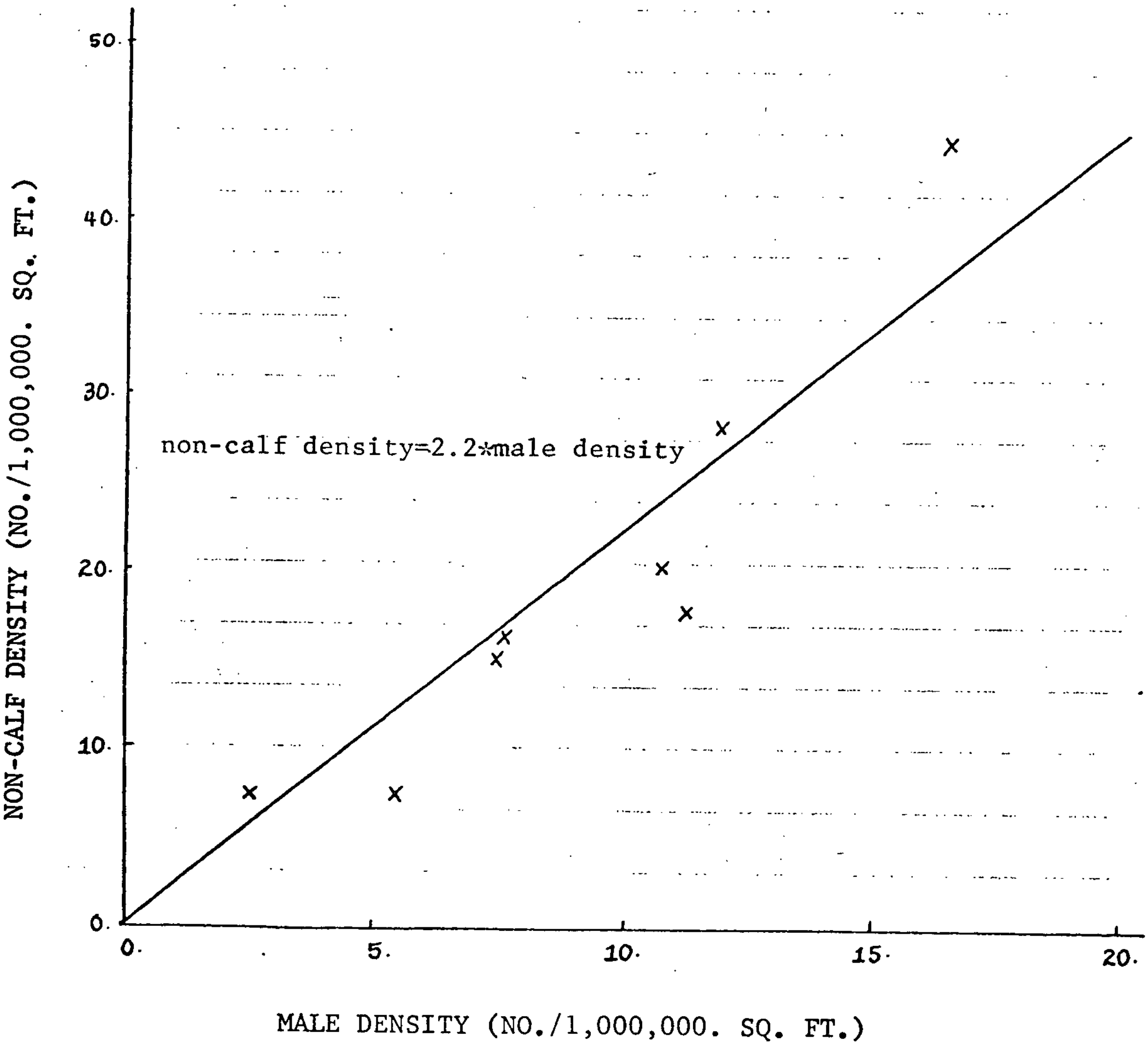
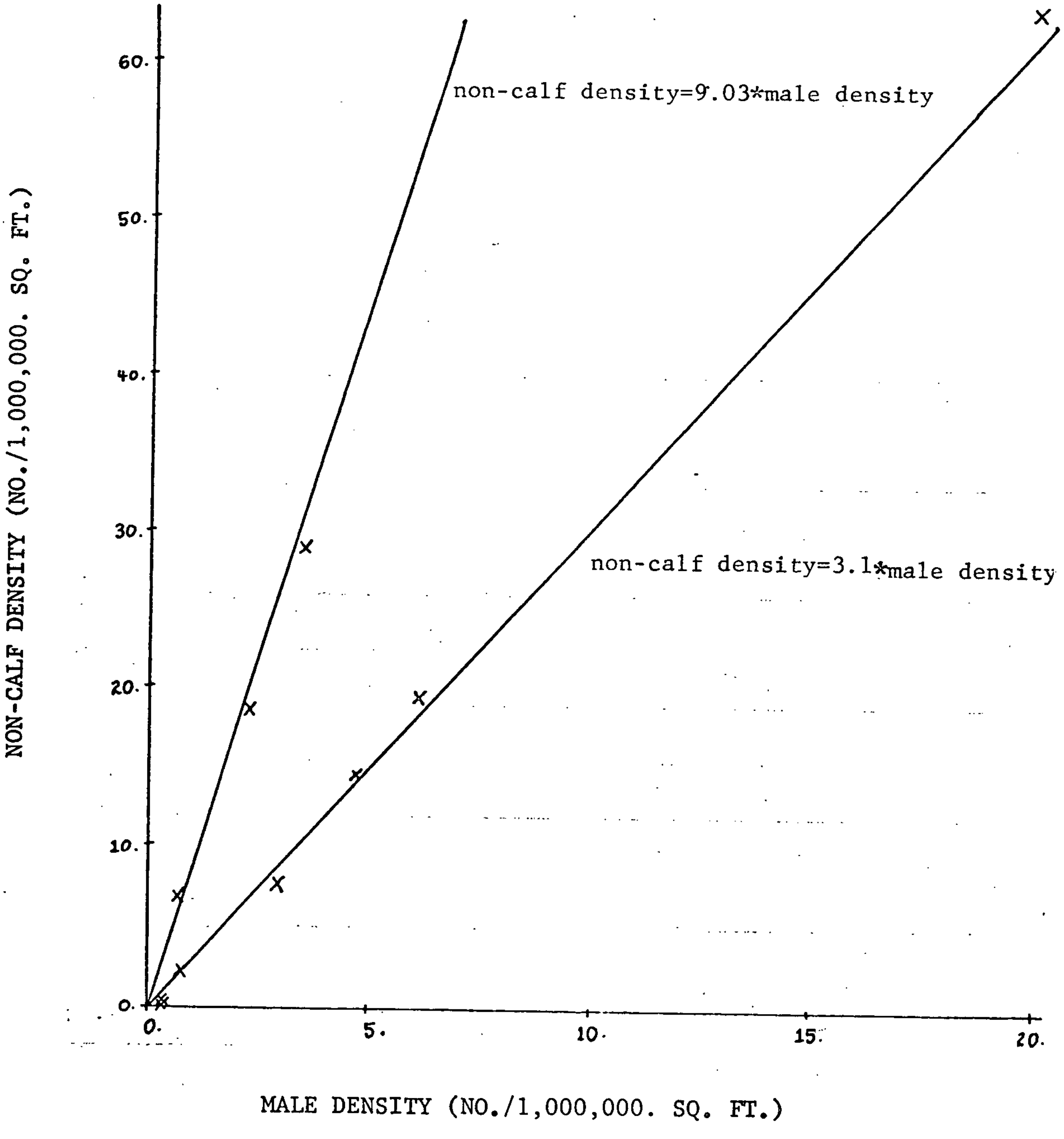


Figure 9b. Wildebeest: Relationship between territory size and non-calf density (March data)



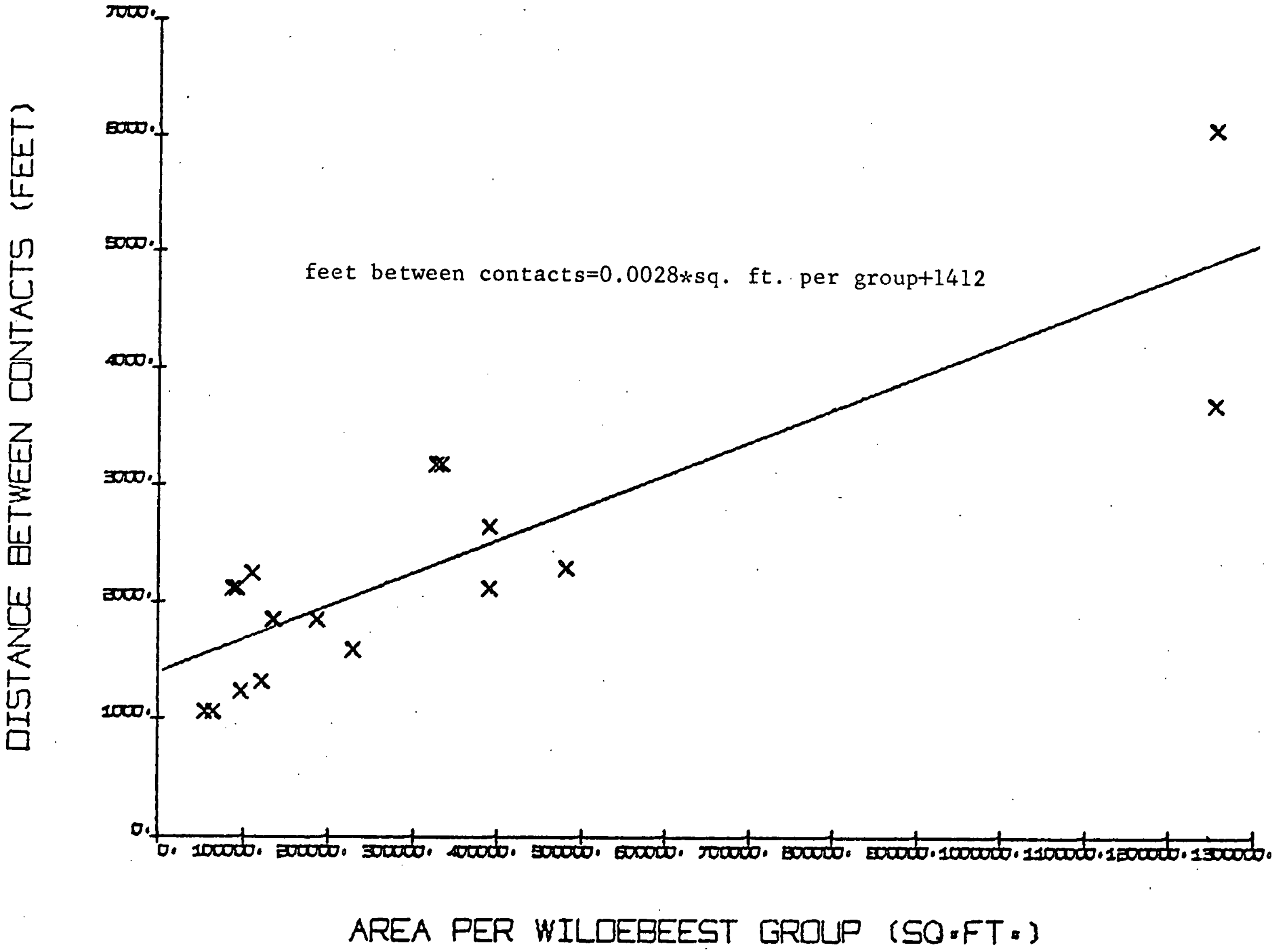
however, due to the presence of more than one prey species which may potentially be successfully searched. As shown below, it is probable that an unsuccessful stalk (following a successful search) affects considerably the subsequent search. This necessitates converting the area per wildebeest group to match the total number of successful searches. For example, consider a search sequence involving four prey contacts of which one was non-wildebeest. If the area per wildebeest group was "a", then the area searched is 3a (since three wildebeest groups were found). In order that four wildebeest groups be located in the search area, the area per group would have to be 3/4 a. This would however introduce an error if secondary attributes of the search are affected by prey density.

Figure 10 illustrates the March and May data relating the distance between contacts (successful searches) and the area per wildebeest group (modified if other prey also contacted). A linear relationship is suggested and the line shown on the figure is the least squares regression line:

$$\text{distance between contacts (feet)} = 0.0028 * \underset{\text{(sq.ft.)}}{\text{area per group}} + 1412$$

The variance of the slope and intercept are $0.18 * 10^{-6}$ and $0.4 * 10^{5}$ respectively and the standard deviation about the line is 614.2 feet. There is no significant difference between the March and May values (F ratio for common variance is 4.5, probability 0.34 and F for the test of similarity of slopes is 0.0065, probability 0.94) which suggests group size is not a major factor. The data are rather unsatisfactory because the slope is

Figure 10. Effect of area per wildebeest group upon nocturnal searching



largely determined by the two low density values on the right of the figure. Furthermore, only one of these two represents a modified area. Since the slopes of the modified data and the unmodified data would be determined almost entirely by a single point (the variance of which is not known), it would be of no value to try to compare the two statistically. The relationship expressed by the regression line must therefore be considered uncertain.

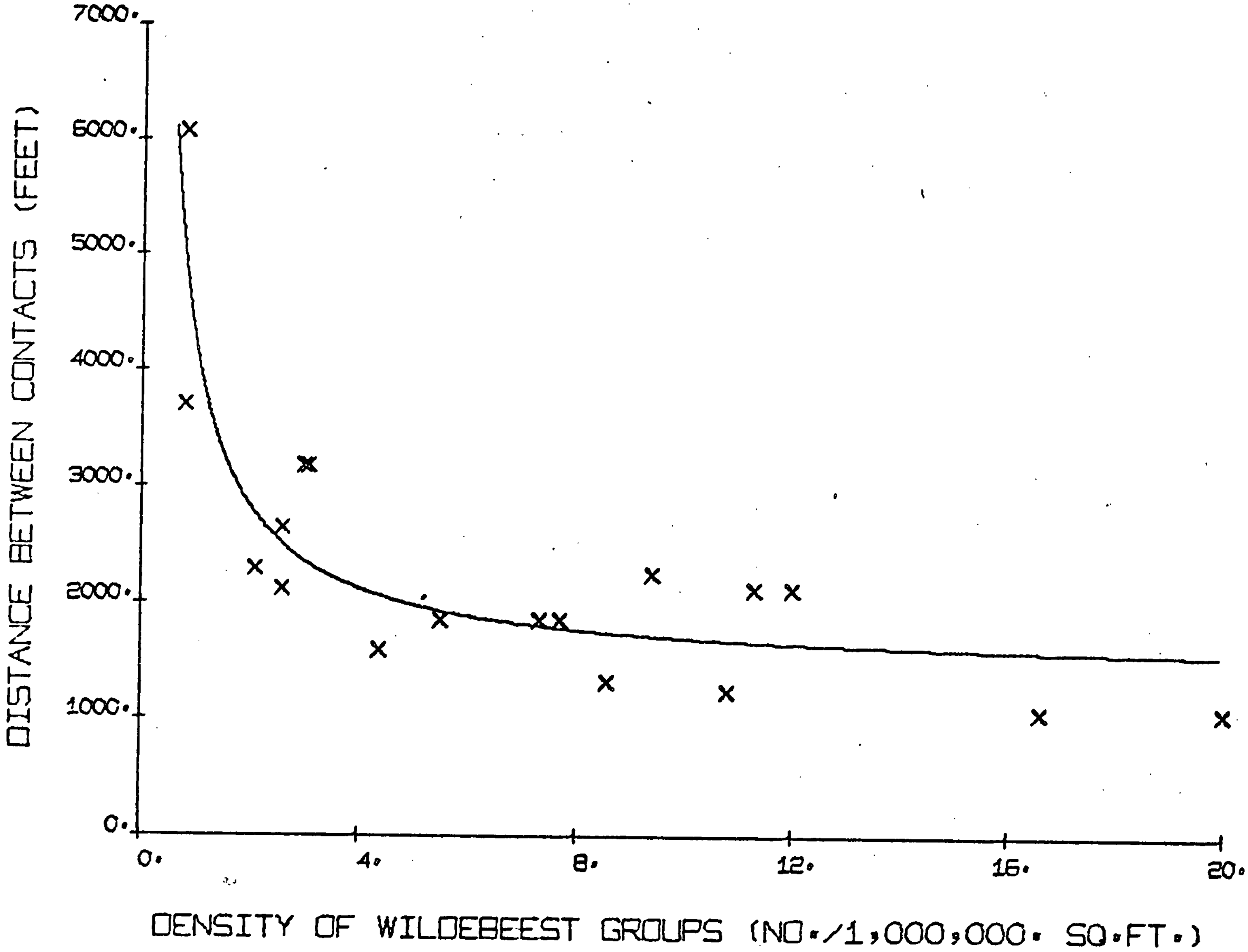
The high value of the Y-intercept could most easily be explained by assuming that each successful search resulted in disturbance to the surrounding prey such that they moved away from the predator. The predator must search beyond this zone before any successful searching becomes possible. (Most models which could be derived to include this feature would show an increase in the regression slope at low X-values and the data does include this possibility). The slope of the regression is however rather steep indicating a prey detection distance by lion of only 179 feet. Field observation, in contrast, suggested that detection was probably 500 to 1500 feet. A variety of assumptions could be derived to explain this. For example, the disturbance distance associated with each successful search may be inversely related to density. However, the necessary information to confirm various theories is not available. It would be unwise in such a case to extrapolate beyond the range of the data shown in Figure 10. Thus the linear relationship shown is equally satisfactory as more complex theories.

Figure 11 shows the relationship of the distance between contacts and prey group density. The line is the same as that in Figure 10. The lowest density recorded -- of 0.8 groups per million square feet -- would require 35.4 minutes of search per contact at the mean rate of search (8278.2 feet per hour with a standard deviation of 2440.71 feet per hour). The overall search rate is actually less than the mean rate because the lions make frequent halts. It is possible that these halts could be reduced if hunger increased, but they may have some function in prey location. Even at the mean search rate, the potential of low densities to limit prey capture success (which is less than search success) is evident. For example, since active searching (type III hunt) occurred only during starlight, the potential time available for searching was limited near the full moon stage of the lunar cycle.

It was not possible to identify group sizes for the February (calving season) wildebeest data nor for other species.

The initial detection distance at night suggests aural cues may be important although vision could be very useful particularly conditions providing a silhouette. There was rarely any breeze at night in this study area so olfactory detection seems unlikely. Regardless of the senses used, different species and even different conditions would be expected to result in different detection distances. This was illustrated by the two gazelle species. These animals were lying down during the period when the lions were hunting, and so would be more difficult to detect than an active

Figure 11. Effect of wildebeest group density upon nocturnal searching



wildebeest group. The result was that for a range of gazelle densities up to 16.0 per million square feet, no successful gazelle searches occurred. This phenomenon may not be strictly one of a reduced detection distance because the lions were slow to react even to a gazelle dazzled by a spotlight, in contrast to their reaction to a similar test with wildebeest. It may be that these lions did not have a "specific search image" (Tinbergen, 1960) or learned capture response (Holling, 1966) for gazelle. It may also be that the nocturnal attack situation (potential straight away flight by the gazelle) would yield too low a probability of success (see attack section).

Types I and II prey capture can also occur at night. During this study 27.6 percent (or 20.8 percent if wildebeest calves less than one month are excluded) of the night-time kills resulted from these two capture types. Lacking information on prey activity it is difficult to characterize this form of searching which depends solely upon the movement of the prey. If the lion were to remain motionless then success would probably be greater away from areas of good cover because prey largely avoided these areas at night (although less stringently during full moon periods). Prey movement rates cannot be calculated indirectly from the search success data because it was not possible to define the proportion of time when the lions were inconspicuous to the prey.

Search selectivity ratings can be calculated for the nocturnal situation as was done for the diurnal situation. Table XI presents the basic data. As was noted above, no successful gazelle searches occurred.

TABLE XI. The effect of species upon search success

NOCTURNAL

PERCENTAGES

EAN	THOMPSON'S GAZELLE		GRANT'S GAZELLE		WILDEBEEST		ZEBRA		
ATE	EXPECTED	OBSERVED	EXPECTED	OBSERVED	EXPECTED	OBSERVED	EXPECTED	OBSERVED	TOTAL STALKS OBSERVED
EB	----	----	----	----	95.4	76.0	4.6	24.0	25.0
EB	----	----	----	----	69.4	66.7	30.6	33.3	6.0
AR	----	----	----	----	81.9	83.3	18.1	16.7	18.0
AR	----	----	----	----	26.8	33.3	73.2	66.7	6.0
AR	----	----	----	----	53.8	69.2	46.2	80.8	13.0
AY	----	----	----	----	69.7	100.0	30.3	0.0	3.0
AY	----	----	----	----	87.7	100.0	12.3	0.0	30.0

Table XII lists the ratings found for the zebra.

TABLE XII. Nocturnal search selectivity for zebra

DATE	SELECTIVITY	SAMPLE SIZE
FEB.	6.5492	25.00
FEB.	1.1340	6.00
MAR.	0.9050	18.00
MAR.	0.7322	6.00
MAR.	0.5176	13.00
MAY	0.0000	3.00
MAY	0.0000	30.00

The February data showed an apparent selection for zebra over wildebeest although the March and May data showed the reverse. This can be related to the changing size of wildebeest groups. It was noted above that February is a calving period for wildebeest and at this time the herds were very large in the prey searching area. The onset of increased territoriality in March resulted in group sizes becoming much smaller, and (as seen in Figures 8 and 9) the May sizes were even smaller.

Synopsis

Searching for prey is to a considerable extent dependent upon the activities of the prey (largely unmeasured). These activities are consistent for a given species and set of conditions but differ between species and conditions.

The lion can alter its search tactics to account for a diversity of situations from diurnal type I or II (passive search) hunts to the ordered search shown by type III nocturnal wildebeest hunts.

STALKING PREY

Introduction

The prey capture strategies of the lion generally have a highly significant stalk phase (Table II). In practice, minimum quantitative criteria were necessary to distinguish weak stalks from stalk-like searches. For this study, a stalk must have lasted a minimum of one minute, yielded a predator-prey distance of less than 250 feet, or involved positive movement by the lion of at least twenty feet.

Three stalk types were recognized and these are presented below:

1.	Crouch:	the predator adopts concealing posture and zero velocity; prey unknowingly moves towards the predator.
2.	Sneak-Crouch:	the predator adopts concealing posture and at various intervals advances in a direction ultimately bringing it closer to the prey with minimal probability of the prey detecting the predator. Thus approach speed is generally reduced as the predator-prey distance is reduced.
3.	Run:	the predator adopts slight concealing posture and advances fairly regularly towards the prey with speed tending to increase as the predator-prey distance is reduced. Thus an initial positive velocity is achieved before the prey detects the predator and adopts flight behaviour. The initial portion of the stalk may or may not show considerable concealment behaviour.

It is necessary to consider what constitutes a successful stalk. The purpose of the stalk is to reduce predator-prey distance. This is accomplished simply by minimizing the probability of detection by or disturbance of the prey. The measure of success of the stalk is therefore whether or not the predator-prey distance is sufficiently reduced to allow a successful attack. This distance is not a static value, but varies for each class of prey (and set of physical conditions) and even for each individual. The definition of stalk success for predators having a less critical stalk phase would take a different form, but the above measure is satisfactory for the lion.

The Diurnal Crouch and Sneak-Crouch Stalks

The movements of the lion during the sneak-crouch stalk present the possibility of reduced stalk success compared to the crouch stalk due to increased conspicuousness. However, the movements of the lion corresponded to times when the prey was looking elsewhere. The lion constantly watched the prey during the stalk and apparently was able to evaluate whether or not the prey was alert in its direction. Rudnai (1973?) found a similar situation for lions in Nairobi National Park as did McLaughlin (1970) for cheetah in the same park. Moreover, Schaller (1972) found this to be generally the case for lions in the Serengeti National Park. If this is so then the crouch and sneak-crouch stalks should yield a similar probability of success. Furthermore, the relative effect of each class of failure should be the same. This can be evaluated from the field data for each prey species. Wildebeest and zebra often graze and travel to water together and the same is true for the two gazelle species. It was therefore not always possible to distinguish which species of each pair caused a stalk to fail. The data for the two species of each pair must then be combined.

The similarity of the detection and flight abilities (examined below) in each case reduces the error of this technique. Tables XIII and XIV compare the two stalk types for each of these two pairs of species. It can be seen that in both cases the two stalk types were not significantly different. As the mechanics of the two stalk types appear to be basically similar, they can be considered the same.

It is of interest to compare the stalk success of these stalks for the two species groups. Table XV summarizes this comparison and it can be seen that a significant difference existed. However, if only success or failure is compared and human interference is excluded, then the two species pairs were homogenous (Table XVI). The lion seems to have adjusted its prey capture to yield the same success for each species pair but with different causes of failure. McLaughlin (1970) also noted for cheetah that percent success tends to be similar for different prey and Kruuk (1972) has made the same observations for hyaena. If human interference is included in the lion data (Table XVI) then this no longer applies. However, this source of failure varies considerably with time of day and season, and thus would be difficult for the lion to predict.

Inspection of Table XV shows that the difference between the two prey pairs was largely a difference in the importance of predator related failure and random failure. This would result if the stalk times were different for these two groups. Table XVII summarizes the statistics found for this study. It can be seen that there is a significant difference between

TABLE XIII. Comparison of diurnal crouch and sneak-crouch stalks for zebra and wildebeest

Stalk Type	Unsuccessful				Successful	Totals
	Failed attack or lion seen	Other lion or cub seen	Lack of time, or cover, or not near	Human interference (tourist vehicles)		
Crouch	12	5	7	1	11(30%)	36
Sneak-crouch	29	15	31	15	21(19%)	111
Totals	41	20	38	16	32(22%)	147

excluding human interference: $x^2 = 2.46$; $0.5 > P > 0.3$
including human interference: $x^2 = 5.83$; $0.3 > P > 0.2$

TABLE XIV. Comparison of diurnal crouch and sneak-crouch stalks for Thomson's and Grant's gazelles

Stalk Type	Unsuccessful				Successful	Totals
	Failed attack or lion seen	Other lion or cub seen	Lack of time, or cover, or not near	Human interference (tourist vehicles)		
Crouch	2	1	0	1	2(33%)	6
Sneak-crouch	20	1	3	0	8(25%)	32
Totals	22	2	3	1	10(26%)	38

excluding human interference: $x^2 = 2.69$; $0.5 > P > 0.3$
including human interference: $x^2 = 1.39$; $0.8 > P > 0.7$
(and grouping it with lack
of time or cover, or not near)

TABLE XV. Effect of species upon diurnal crouch and sneak-crouch stalk success: multi-class comparison

Species	Unsuccessful				Successful	Totals
	Failed attack or lion seen	Other lion or cub seen	Lack of time, or cover, or not near	Human interference (tourist vehicles)		
Wildebeest and zebra	41	20	38	16	32(22%)	147
Thomson's and Grant's gazelles	22	2	3	1	10(26%)	38
Totals	63	22	41	17	42(23%)	185

excluding human interference: $x^2 = 13.46$; $0.01 > P > 0.001$
including human interference: $x^2 = 16.63$; $P < 0.001$
(and grouping it with lack
of time or cover or not near)

TABLE XVI. Effect of species upon diurnal crouch and sneak-crouch stalk success: two-class comparison

Species	Unsuccessful		Successful	Totals
	Including human interference	Excluding human interference		
Wildebeest and zebra	119(81%)	99(76%)	32	147(131)
Thomson's and Grant's gazelles	28(74%)	27(73%)	10	38(37)
Totals	143(77%)	126(75%)	42	185(168)

excluding human interference: $x^2 = 0.12$; $0.9 > P > 0.8$
including human interference: $x^2 = 40.43$; $P < 0.001$

TABLE XVII. Effect of species upon diurnal crouch and sneak-crouch stalk time

SPECIES	MEAN STALK TIME (minutes)	STANDARD DEVIATION	SAMPLE SIZE
Wildebeest and zebra	31.6	26.4	88
Thomson's and Grant's gazelles	6.9	9.0	25

F ratio = 21.172
$P < 0.0001$

the two groups, with wildebeest and zebra stalks having lasted on the average four and one half times longer than gazelle stalks. This is in close agreement with the difference in failure categories seen in Table XV. The reason for this difference in time will be clarified when more of the theory has been presented.

The identification of stalk time as a significant feature of the stalk necessitates the comparison of the time required for crouch as compared to sneak-crouch stalks. Tables XVIII and XIX summarize the relevant statistics and it can be seen that for both species groups there is no significant difference.

The random effects are mainly factors which depend upon the activity patterns of the prey. It is useful to know whether the effect of these is constant (for a prey species) under different conditions and circumstances. This can be evaluated by examining the proportion of failed stalks due to random factors for different activities and locations. This analysis is summarized in Tables XX and XXI. Wildebeest and zebra stalks were divided into two activities in two locations. The two feeding locations were rather similar in topography, but more alternate open grazing sites were available on the northwest side of Maandusi. The topography of the two drinking locations was quite different. It can be seen (Table XX) that there was no significant difference in stalking for the different conditions and circumstances. This was also true for the two gazelle species, but sample size permitted the examination of only two situations.

TABLE XVIII. Comparison of diurnal crouch and sneak-crouch stalk times for wildebeest and zebra

STALK TYPE	MEAN TIME (minutes)	STANDARD DEVIATION	SAMPLE SIZE
Crouch	37.7	31.3	16
Sneak-crouch	30.3	25.2	72

F ratio = 1.041
P = 0.31

TABLE XIX. Comparison of diurnal crouch and sneak-crouch stalk times for Thomson's and Grant's gazelles

STALK TYPE	MEAN TIME (minutes)	STANDARD DEVIATION	SAMPLE SIZE
Crouch	7.5	11.8	4
Sneak-crouch	6.8	8.8	21

F ratio = 0.02
P = 0.89

TABLE XX. Effect of different conditions upon diurnal crouch and sneak-crouch stalks for wildebeest and zebra

AREA/ACTIVITY	UNSUCCESSFUL Lion Related	 Random	SUCCESSFUL	TOTALS
riverine bush/drinking	12(44.4%)	9(33.3%)	6(22.2%)	27
open stream crossing or pond/drinking	28(40.6%)	26(37.7%)	15(21.7%)	69
southeast side Maandusi/ grazing	13(44.8%)	6(20.7%)	10(34.5%)	29
northwest side Maandusi/ grazing	14(48.3%)	10(34.5%)	5(17.2%)	29
Totals	67(43.5%)	51(33.1%)	36(23.4%)	154

$x^2 = 4.17$
$0.7 > P > 0.5$

TABLE XXI. Effect of different conditions upon diurnal crouch and sneak-crouch stalks for Thomson's and Grant's gazelles

AREA/ACTIVITY	UNSUCCESSFUL Lion Related	 Random	SUCCESSFUL	TOTALS
open stream crossing or pond/drinking	9(64.3%)	1(7.1%)	4(28.6%)	14
Maandusi/grazing	14(63.6%)	2(9.1%)	6(27.3%)	22
Totals	23(63.9%)	3(8.3%)	10(27.8%)	36

$x^2 = 0.06$
$0.98 > P > 0.95$

It is necessary to distinguish which variables control stalk success for each species. One possibility is the number of lions involved in the stalk. Stevenson-Hamilton (1954) felt that group hunting by lions was highly organized, as did Wright (1960). On the other hand, Kruuk and Turner (1967) considered that only accidental cooperation occurs. Schaller (1972) concluded that neither view was fully accurate, but that sometimes there was no cooperation while at other times there was. A "reasoned" cooperation seems to be implied by Schaller. All workers would agree that accidental cooperation can occur. The observations during this study all seemed to be interpretable in terms of accidental cooperation. On many occasions, only one lioness of a group would creep forward when there seemed to be ample opportunity for others to advance as well to more suitable locations. When more than one lion stalked forward they would take different routes seemingly because these routes offered the best approaches from the initial starting locations of the lions. Since movements along lateral approach channels provide better cover than ones which lead directly to the prey, the lions would tend to finish somewhat on opposite sides of the prey. If the lions were able to assess the advantage of a coördinated approach it is difficult to explain why so often only one lion would improve its position while the others did not. However, the possibility of truly cooperative hunting cannot be discounted and might be more important under some stalking conditions than others. Diurnal stalking observed in this study was generally rather restricted in that prey was usually only on the fringe of a good area of stalk cover.

Whatever the precise nature of cooperation, it would be expected that the more lions stalking, the greater the probability of attack success since more flight paths would be blocked by lions. This is offset by the increased probability of the prey detecting a predator.

Tables XXII, XXIII, XXIV, and XXV compare the stalk success where two or more lions were potentially involved. Neither species group nor stalk type showed a significant difference. (Small sample size did not permit analysis of crouch stalks for Thomson's and Grant's gazelles). Schaller's (1972) data for "stalking and running" diurnal and nocturnal hunts in the Serengeti National Park are presented in Tables XXVI and XXVII. There is no significant effect of lion number for wildebeest and zebra but for Thomson's gazelle there is a significant improvement when more lions are involved. This difference with the gazelle data for this study (Table XXV) may be due to the difference in grouping of stalk types and time of day or to differences in the dispersion and amount of cover in the two areas.

Three sensory stimuli are produced by the lion: auditory, olfactory, and visual. There seemed to be very little noise associated with the diurnal crouch and sneak-crouch stalk for this study. Lacking any quantitative measure it must be assumed insignificant; however, some stalk areas may be more prone to producing stalk noise.

TABLE XXII. Effect of the number of lions involved in diurnal crouch stalks for wildebeest and zebra

NUMBER OF LIONS	NUMBER SUCCESSFUL	NUMBER UNSUCCESSFUL	TOTALS
1	5(28%)	13(72%)	18
$\geqslant 2$	7(37%)	12(63%)	19
Totals	12(32%)	25(68%)	37

$x^2 = 0.346$
$0.7 > P > 0.5$

TABLE XXIII. Effect of the number of lions involved in diurnal sneak-crouch stalks for wildebeest and zebra

NUMBER OF LIONS	NUMBER SUCCESSFUL	NUMBER UNSUCCESSFUL	TOTALS
1	11(17%)	53(83%)	64
$\geqslant 2$	10(21%)	38(79%)	48
Totals	21(19%)	91(81%)	112

$x^2 = 0.239$
$0.7 > P > 0.5$

TABLE XXIV. Effect of the number of lions involved in diurnal crouch and sneak-crouch stalks for wildebeest and zebra

NUMBER OF LIONS	NUMBER SUCCESSFUL	NUMBER UNSUCCESSFUL	TOTALS
1	16(20%)	66(80%)	82
⩾2	17(25%)	50(75%)	67
Totals	33(22%)	116(78%)	149

$x^2 = 0.735$
$0.5 > P > 0.3$

TABLE XXV. Effect of the number of lions involved in diurnal sneak-crouch stalks for Thomson's and Grant's gazelle

NUMBER OF LIONS	NUMBER SUCCESSFUL	NUMBER UNSUCCESSFUL	TOTALS
1	4(29%)	10(71%)	14
⩾2	4(24%)	13(76%)	17
Totals	8(26%)	23(74%)	31

$x^2 = 0.102$
$0.8 > P > 0.7$

TABLE XXVI. Effect of the number of lions "stalking and running" diurnally and nocturnally for wildebeest and zebra in the Serengeti National Park (Schaller, 1972)

NUMBER OF LIONS	NUMBER SUCCESSFUL	NUMBER UNSUCCESSFUL	TOTALS
1	5(15%)	28(85%)	33
≥2	16(23%)	54(77%)	70
Totals	21(20%)	82(80%)	103

$x^2 = 0.821$
$0.5 > P > 0.3$

TABLE XXVII. Effect of the number of lions "stalking and running" diurnally and nocturnally for Thomson's gazelle in the Serengeti National Park (Schaller, 1972)

NUMBER OF LIONS	NUMBER SUCCESSFUL	NUMBER UNSUCCESSFUL	TOTALS
1	27(15%)	158(85%)	185
≥ 2	57(32%)	120(78%)	177
Totals	84(23%)	278(77%)	362

$x^2 = 15.734$
$P < 0.001$

Although Stevenson-Hamilton (1954) stated that a lion "creeps upon its prey up-wind", Schaller (1972) did not indentify any preference for wind direction. Similarly, no selection for wind direction was evident for wildebeest and zebra hunts observed during this study (Table XXVIII). (There was not a sufficient sample size for gazelle). Table XXVIII also shows that there was no evident effect of wind direction upon success for wildebeest and zebra. In contrast, Schaller (1972) found that success was 23 percent greater for a downwind as opposed to an upwind lion location Table XXIX) for Thomson's gazelle "stalking and running" in the Serengeti National Park. This may be the result of a difference in the ability of prey species to detect or respond to olfactory stimuli or it may be due to a difference in the two areas such as relative humidity or general level of lion scent in the stalking areas. If in fact gazelle do make more use of olfactory stimuli, this would partially account for the higher probability of gazelle detecting the stalking lion in contrast to wildebeest and zebra as noted in Table XV (column 1).

Auditory stimuli have been assumed unimportant and olfactory stimuli were unimportant for wildebeest and zebra stalks. Visual stimuli then must provide the major input of sensory information to the prey. Since the crouch and sneak-crouch stalks do not differ (Tables XIII and XIV) the prey is dealing primarily with the problem of detecting a motionless, concealed lion. This aspect is considered in the section entitled "visual detection".

TABLE XXVIII. Effect of wind direction upon wildebeest and zebra diurnal crouch and sneak-crouch stalks

	WIND SOURCE	PREY LION	ANGLE (degrees)
	0 to 60 (predator upwind)	60 to 120 (crosswind)	120 to 180 (predator downwind)
Number observed	36	44	39
Per Cent Success	19	18	18

TABLE XXIX. Effect of wind direction upon diurnal "stalking and running" success for Thomson's gazelle in the Serengeti National Park (Schaller, 1972)

LION POSITION	SUCCESSFUL	UNSUCCESSFUL	TOTALS
Upwind	6 (11%)	48 (89%)	54
Downwind	19 (34%)	37 (66%)	56
Totals	25 (23%)	85 (77%)	110

$x^2 = 8.15$
$0.01 > P > 0.001$

The Diurnal Run Stalk

The diurnal run stalk was generally associated with conditions of good cover (tall vegetation or other obscuring topographical features) and often with a situation involving a limited escape route for the prey. A major usefulness of the run stalk was that it provided the possibility of prey capture in areas of poor stalk conditions. Also it required less time (mean for all species was 2.6 minutes, standard deviation of 4.1) than the crouch or sneak-crouch stalks (Table XVII).

It was noted in the last section that the gazelles spent less time at a stalk site. It would therefore be expected that the faster run stalk would be more frequent for that prey group than wildebeest and zebra. The data (Table XXX) corroborate this with run stalks having been 6.9 times more common for gazelle. However, the relative frequency with which the run stalk would occur would tend to vary with different cover and resource utilization conditions. Sample size is too small to examine this with the data from this study, but a comparison can be made with the Serengeti data of Schaller (1972). The gazelle data show (Table XXXI) a tendency towards a difference although this is not significant at the one percent level. The difference is more definite for wildebeest and zebra (Table XXXII). A thorough knowledge of prey movement patterns under different conditions will be necessary to determine the expected proportions of the different stalk types.

TABLE XXX. Effect of species upon the proportion of diurnal run stalks

SPECIES	NUMBER OF RUN STALKS	NUMBER OF CROUCH AND SNEAK-CROUCH STALKS	TOTALS
Wildebeest and zebra	6(4%)	153(96%)	159
Thomson's and Grant's gazelle	14(27%)	37(73%)	51
Totals	20(10%)	190(90%)	210

$x^2 = 25.1$
$P < 0.001$

TABLE XXXI. Proportion of diurnal Thomson's and Grant's gazelle run stalks in this study compared to the Serengeti National Park (Schaller, 1972)*

	NUMBER		
LOCATION	RUN STALK	CROUCH AND SNEAK-CROUCH STALKS	TOTALS
Ngorongoro	14(27%)	37(73%)	51
Serengeti	71(45%)	86(55%)	157
Totals	85(41%)	123(59%)	208

$x^2 = 5.033$ $0.05 > P > 0.02$

* the numbers from the Serengeti refer to Schaller's "running by one lion" and "stalking by one lion" categories

TABLE XXXII. Proportion of Diurnal Wildebeest and Zebra Run Stalks in this study compared to the Serengeti National Park (Schaller, 1972)*

	NUMBER		
LOCATION	RUN STALK	CROUCH AND SNEAK-CROUCH STALKS	TOTALS
Ngorongoro	6 (4%)	153 (96%)	159
Serengeti	7 (23%)	24 (77%)	31
Totals	13 (7%)	177 (93%)	190

$x^2 = 14.39$
$P < 0.001$

The limited number of run stalks observed during this study does not allow a detailed analysis of the effect of various features upon success. The rapidity of the run stalk would tend to make olfactory detection less probable than in the case of the crouch and sneak-crouch stalks. Visual detection would be more probable (this is examined in the section "visual detection") and noise may also be more important.

The Nocturnal Run Stalk

It is less easy to characterize the nocturnal stalks since the details of the movements of predator and prey were often not observable. The run stalk, however, did seem to be the major stalk type used. This would be expected as it would presumably be difficult for the lion to "determine" whether the prey were alert in its direction which is an important requirement for the sneak-crouch stalk. If the run stalk is being used, then the stalk time should be quite short. This would be particularly true for starlight stalks where the need for cautious approach (and also the distance at which the prey can be precisely located) will be low. Table XXXIII presents the data on stalk times during moonlight and also compares zebra and wildebeest. (No gazelle stalks were observed at night). Table XXXIV presents the same information for starlight conditions. It can be seen that the stalk time is short for both species and also that there is no significant difference between the species. However, Table XXXV shows that moonlight stalks lasted significantly longer (2.64 times) than starlight stalks for the two species combined.

TABLE XXXIII. Effect of species upon moonlight stalk times

SPECIES	MEAN STALK TIME (MINUTES)	STANDARD DEVIATION	SAMPLE SIZE
Zebra	3.43	3.41	7
Wildebeest	6.33	8.91	15

$t = 0.88$
$0.5 > P > 0.1$

TABLE XXXIV. Effect of species upon starlight stalk times

SPECIES	MEAN STALK TIME (minutes)	STANDARD DEVIATION	SAMPLE SIZE
Zebra	3.29	4.19	14
Wildebeest	1.81	3.09	72

$t = 1.54$
$0.5 > P > 0.1$

TABLE XXXV. Effect of light upon nocturnal stalk times

LIGHT CONDITION	MEAN STALK TIME (minutes)	STANDARD DEVIATION	SAMPLE SIZE
Moonlight	5.41	7.62	22
Starlight	2.05	3.32	86

$t = 3.12$
$P < 0.01$

It has been shown that diurnally wildebeest and zebra receive no benefit from olfactory detection. Wind velocity in Ngorongoro Crater was generally negligible at night thus this combined with the rapid stalks would seem to indicate a low probability of olfactory stimuli being important at night. Because of the increased relative humidity at night, olfactory detection could be important in other cases having night-time breezes.

The number of lions stalking might be expected to influence the success. The diurnal movements of the lions are restricted by the need for tall cover. At night, the low illumination itself provides cover and the lions can move freely when stalking thus improving the opportunities for accidental or planned cooperation. Table XXXVI considers the effect of the number of lions active in the stalk upon stalk success.

TABLE XXXVI. Effect of the number of lions involved in nocturnal stalks upon success

NUMBER OF LIONS	NUMBER UNSUCCESSFUL	NUMBER SUCCESSFUL	TOTALS
1	31 (89%)	4 (11%)	35
≥ 2	16 (70%)	7 (30%)	23
Totals	47 (81%)	11 (19%)	58

$x^2 = 3.26$
$0.1 > P > 0.05$

Since these data were difficult to observe at night, the sample sizes are rather small and it was necessary to combine the two species and light categories. No significant effect can be shown.

Noise could have been significant because the negligible wind velocity produced less background noise than present during the day. There was no direct method of evaluating this; however, it was noted that the lions rarely searched (type III prey capture) in a long grass (one to one and a half feet) area within the pride range, but chose instead a short grass (less than 10 inches) area. This was true for a wide range of prey density differences for the two areas and was irrespective of the lion's starting location. The difference in grass height was the only obvious physiographic factor although proximity to the center of the pride area may have been a factor. It is of interest to consider that this area (providing better cover for a sneak-crouch stalk, but not much improvement for a run stalk) would be rather noisier for run stalking. The observer could detect this difference.

Visual detection will be considered in the next section, but it is of interest to examine the effect of cover upon success. Due to the leg extension necessary in the run stalk the effect of cover is not likely to be great except for quite tall cover. This is examined in Tables XXXVII and XXXVIII. It can be seen that for neither light category was there any improvement of success for longer vegetation.

TABLE XXXVII. Effect of cover height upon moonlight stalk success for wildebeest and zebra

VEGETATION HEIGHT (inches)	PER CENT SUCCESS	SAMPLE SIZE
3	14.3	7
4	25.0	8
5	16.7	6
7	0.0	10
17	25.0	4

TABLE XXXVIII. Effect of cover height upon starlight stalk success for wildebeest and zebra

VEGETATION HEIGHT (inches)	PER CENT SUCCESS	SAMPLE SIZE
3	19.5	41
4	20.0	25
7	25.9	27
17	0.0	4

Visual Detection

It has been indicated above that visual detection of the predator is probably the major factor affecting stalk success.

The simplest (involving the fewest variables) problem of visual detection is that which occurs during the crouch stalk. In this case the prey must detect a motionless predator concealed against and within a specific background. It has been shown above both intuitively and by inference from the actual field data, that this is also the detection problem involved in the sneak-crouch stalk. The literature on vision does not deal directly with a problem of this kind, but analogous situations have been examined. These studies, termed psychophysical experiments, use human observers trying to detect light stimuli of various durations and intensities against backgrounds of zero or greater illumination. These studies can be related to real life situations.

The initial task is to define the numeric value of the visual stimulus provided by the predator. Since the predator and background are not self-luminous, the difference (ΔL) between the two, results from their difference in reflectivity and the luminance of incident light from the sun (SILLM):

$$\Delta L = \left| \mathrm{RFPRD} - \mathrm{RFCOV} \right| * \mathrm{SILLM} \qquad (1)$$

where RFPRD and RFCOV are the reflectivities of the predator and background respectively. Equation (1) deals only with the luminance of the stimulus and does not include its area. A generalization termed Ricco's Law is appropriate in this regard: [1]

[1] multiplication is represented by an asterisk

stimulus area * luminance = a constant at the visual threshold

This law does not hold for very large area stimuli but is valid for small area stimuli (Graham, Brown, and Mote, 1939; Baumgardt, 1948) such as the situation being investigated here. There can be some complications due to the shape of the stimulus, (Lamar, Hecht, Schlaer, and Hendley (1948) found that the area effect was generally not independent of the shape of the area); however, for targets less than a few minutes of arc, the area is directly related to the useful flux as suggested by Ricco's Law. This would include the predator areas involved in the stalk situation.

Conversion of the predator's exposed area to an angular area (in radians) is readily accomplished:

$$\text{angular area} = \frac{\text{AREA}}{D^2} \qquad (2)$$

where AREA is the area exposed and D is the predator-prey distance. Both AREA and D must be expressed in terms of the same unit such as square feet and feet respectively. Expressions (1) and (2) can be combined to define a variable, STIM, which is equal to the product of the relative luminance of the object times its area and thus is constant at the visual threshold:

$$\text{STIM} = \frac{\text{AREA} * \text{SILLM} * |\text{RFPRD} - \text{RFCOV}|}{D^2} \qquad (3)$$

This equation applies only to short distances such as those of stalking. Greater distances introduce difficulties of atmospheric interference (Middleton, 1952).

The constancy of threshold STIM (equation (3)) is not strictly independent of the duration of exposure. Graham and Kemp (1938) studied this effect and found that as the duration increases the threshold stimulus drops. However, for exposure times greater than 0.1 seconds, the threshold is constant. This has been confirmed by a number of other studies (Woodworth, 1938; Barlow, 1952; Johnson and Bartlett, 1956; Pirenne, 1956; Barlow, 1958; Baumgardt and Hillman, 1961). Although the prey's scanning rate is not known, it is probable that it would be adjusted to maximum effectiveness such that a minimum of 0.1 seconds was spent scanning each sector. This would give a constant value for the threshold STIM.

The preceding and present state of illumination of the eye, affect its ability to respond to stimuli. This is termed adaptation and occurs in three ways: the iris acts to alter pupil size; the concentration of photochemical substances changes, and changes occur in the degree and types of inhibition and summation by neural units in the retina (Walls, 1963; Barlow, 1957). This feature of vision presents a difficulty in trying to define the visual response using the data of the pseudo-predator trials which were outlined in the methods section. The light recording equipment was only adequate for measuring diurnal levels of brightness. Furthermore, the need to detect the prey's response to the pseudo-predator would have necessitated being rather close to the animals at night which could alter their behaviour. As a result, only day-time trials were undertaken. This set of data is therefore, inadequate to define the effect of visual adaptation. Use of the data from actual night stalks by the lion allows this limitation to be overcome. Because there was often no solid cover involved in night stalks, the determination of the AREA variable (see section "The Lion Stimulus") is possible.

Since the nocturnal stalk is the run stalk, detection of a moving object must be considered. Orio (in Walls, 1963) has deduced a simple relationship which states that motion halves the angular diameter necessary for visual detection. This relationship is only valid for low angular velocities, but the direct approach of the lion does yield very low angular velocities. A halving of the angular diameter can be achieved by either reducing the exposed area of the stimulus or by doubling the detection distance. Schmid (in Walls, 1963) gives some corroborating data for dogs. The dogs could see moving objects at 810 to 900 meters, but could see stationary objects only at 585 meters.

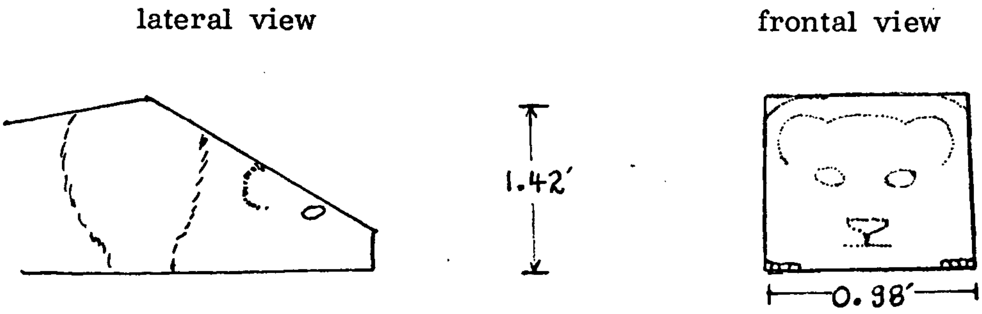
The application of the night stalk data to the problem of visual detection is not a simple one. Stalk success has not been defined in terms of a specific distance, but rather in terms of attack success. Thus, the validity of attack success for a given distance must be determined before the stalk data can be used. The discussion of visual detection will therefore be continued after the attack has been considered.

The Lion Stimulus

Equation (3) requires the determination of the exposed area of a crouching lion and also the manner in which cover affects the area.

Generality of application requires that the area be expressed in some simple manner. Figure 12 summarizes the stimulus shape of the stalking lion. This information has been derived from measurements made on photographs taken at known distances. The frontal view of a crouched lion is considered to be essentially a rectangle with the width and height being greatest at the shoulders. The total frontal area of the lion is 1.39 square feet. Excepting very short predator-prey distances, the effect of cover can be represented as subtracting area from the bottom of the frontal rectangle which represents the lion. That is, with cover height (COV) expressed in feet, the exposed area of a lion is:

Figure 12. Stimulus dimensions of a generalized stalking lion



$$\text{AREA} = 1.39 - (0.98 * \text{COV}) \qquad (4)$$

where AREA is the same as in equation (3). Equation (4) is negative if COV is greater that 1.42 feet. Field observations suggested, however, that this situation does not result. The lion tried to keep the prey always in view. If the cover was greater than would permit this with the head down, then the head was raised. It will be shown in a later section that the maximum value for COV is probably 1.3 feet for the crouch and sneak-crouch stalks.

The frontal area of a run stalk lion is considered to be the same as that of a crouched lion. The effect of cover is quite different, however. Measurements from photographs showed that the lion could vary in height from about 18 to 33 inches. Presumably faster stalk speed would necessitate greater leg extension. Cover greater than about 10 inches could reduce the exposed area of the lion. It was shown (Tables XXXVII and XXXVIII) that 17 inch cover did not give any increase in stalk success at night. Possibly increased noise offset any visual advantage to the lion. Although no specific data are available it is a reasonable assumption that taller cover adjacent to a lion on a short vegetation area, would provide an increase in stalk success.

The reflectivity of the lion was not known, It seems probable though that reflectivity per se may be an oversimplification as a scanning prey will be searching specifically for hidden predators. Thus it will be more receptive to a lion stimulus than a comparably reflective, featureless object. Since the pseudo-predator head was designed to mimic a lion's head as closely as possible in terms of features, the mean reflectivity difference found for the pseudo-predator head (12.5 per cent) is used in the following calculation as the best estimate of the reflectivity difference for the lion against its backgrounds.

A feature of this generalized lion stimulus model is the absence of a variable for prey eye height. This introduces negligible error for the usual eye height to predator-prey distance ratios observed for this study. However, a giraffe close to a hidden lion would exemplify a situation where the lion stimulus model would require modification.

Synopsis

Stalking success cannot be separated from attack success, which complicates the analysis of stalk tactics from direct observations of prey capture. Differences in approach technique by the lion suggest subdivision of stalks into three types. Two of these (the crouch and sneak-crouch) are however similar in terms of the prey's ability to detect the stalking lion.

Olfactory stimuli and the number of lions seem, in some cases, to affect stalk success but not in others. Auditory stimuli may be important in the run stalk. In any event, visual cues seem to be the prime influence upon stalk success.

It is possible to define the relation between the optical stimulus of a lion and the visual threshold value using standard photometric laws (equation 3). However, the effect of adaptation does not allow this to be related to specific prey until the attack has been considered. A simple approximation exists for the effect of motion of the lion and it is proposed that the size of a hidden lion be expressed by a simple formula (equation 4). Further analysis is postponed until the attack has been considered.

THE ATTACK

General

The attack for most prey species involves the matching of the sprinting abilities of the predator and prey. Thus a first stage in analysis is to define the velocity curve for each species. It will then be possible to determine the probability of attack success for various conditions.

Newton's Second Law of Motion states that the rate of change of momentum is proportional to the applied forces:

$$V(t) = \frac{FA * \Delta t}{M} + V(t - \Delta t) \tag{5}$$

where FA is the accelerating force, M is the mass accelerated, $V(t)$ is the velocity at time t, $V(t - \Delta t)$ is the velocity at time $t - \Delta t$, and Δt is the period of time during which the force acts. An animal does not continue to accelerate indefinitely, but instead shows a decreasing acceleration with time until an approximately constant maximum velocity (VMAX) is achieved (Ikai, 1968). Thus the accelerating force is being reduced as velocity increases. Various workers (Hill, 1922; Dickinson, 1934; Furusawa, Hill and Parkinson, 1928; Best and Partridge, 1928) concluded that the reduction in force increased in direct proportion to the velocity of movement. Later work suggested that the relationship was better described by a shallow hyperbola (Fenn and Marsh, 1935; Mashima and Kushima, 1971; Pertuzon and Bouisset, 1973; Sukop and Reisenauer, 1973). However, as Mashima and Kushima (1971) indicate, there is little error in assuming a linear relationship. The accelerating force at any time can thus be defined:

$$FA = \left(\frac{VMAX - V(t)}{VMAX}\right) * FR \qquad (5)$$

where FR is the force which an animal is capable of directing rearwards when its initial velocity is zero. Equations (4) and (5) can be combined and integrated to define the velocity at any time (t):

$$V(t) = VMAX \left(1 - e^{-\frac{FR * t}{VMAX * M}}\right) \qquad (6)$$

where e is the base of the natural logarithms. The constant fraction, $\frac{FR}{VMAX * M}$, can be replaced by a single constant, K, to give:

$$V(t) = VMAX \left(1 - e^{-kt}\right) \qquad (7)$$

Furusawa, Hill and Parkinson (1928) developed a numerically equivalent equation and tested it by timing trained runners exerting a maximum effort along a horizontal track. They observed many runs and found that the predictions of their equations were very accurate. Subsequently, Henry and Trafton (1951) used this equation and found it to give a statistically satisfactory fit for 50 experimental velocity curves of human runners.

Longer runs must include the effect of fatigue. In 1954, Henry considered the relation between fatigue and the velocity of a runner. Noting that many types of performance and biological functions follow an exponential curve (presumably since first order chemical reactions are frequently limiting), he suggested that fatigue be considered a reduction in the speed potentiality with time such that at any time, t, the speed potential is equal to some constant multiplied by the exponential term $e^{-K_2 t}$, where the exponent K_2 is a rate coefficient. This is equivalent to stating that the rearward force (FR) is reduced exponentially with time. Including this aspect in equation (7) yields:

$$V(t) = VMAX\ (e^{-K_2 t} - e^{-Kt}) \qquad (8)$$

Although the "VMAX" of equation (8) is slightly lower than the VMAX of equation (7), the small size of K_2 makes this difference negligible.

Henry (1954) tested equation (8) by recording distance specific times for a number of runs from each of 54 runners. He found that the distance reached at any particular time after the start of an all-out 900 foot run could be predicted within one per cent error. Furthermore, he found that the value of K_2 was the same as that of the reaction constant for human aerobic metabolism. The development of fatigue has been shown to be similar for isolated muscle fibres (Aljure and Borrero, 1968) and arm movements (Wilkin, 1952).

In a later paper, Henry (1955) extends his development of the distance-time equation to include distances up to 26 miles and then to 150 miles (see also Lietzke, 1954). These refinements are not necessary for the distance involved in attacks by lions.

The papers cited would seem to provide strong evidence, both in terms of human muscles in vivo and individual muscles in vitro, to describe sprinting by the predator and prey.

The Lion Velocity Curve

The first consideration in defining the velocity curve of the lion is the importance of fatigue for the time interval involved in an attack. Ideally equation (8) would be fitted by standard non-linear least squares techniques to the velocity data from the film analysis (see methods) and the value of the constant K_2 would be tested to determine whether it differed significantly from zero. Such an approach is not possible, however. Variance for a function of this sort (sum of exponentials) can be minimized by several quite different combinations of values for the constants unless the fit of the data is very close, and in this case, it is not. A less precise approach is therefore necessary. The technique adopted was to scan the velocity-time plots visually and note whether there was any indication of a reduction in the plateau velocity (other than at the termination of the attack). The longest attack (Figure 13) of 47 seconds showed fluctuations in plateau velocity, but remained fairly constant for the first 35 seconds or so after which there was an abrupt drop of about 10 feet per second. The remaining 12 seconds showed no further regular change prior to termination of the attack. Other lengthy attacks (Figure 14) of 15 to 30 seconds also indicate no major reduction in plateau velocity. It will be assumed for this analysis that fatigue has no significant effect upon velocity for at least the first 35 seconds. Most kills occur in far less time than this. Equation (7) can, therefore, be used to describe the lion's velocity curve.

Figure 13. Lion velocity curve, attack of 1050 21-11-70

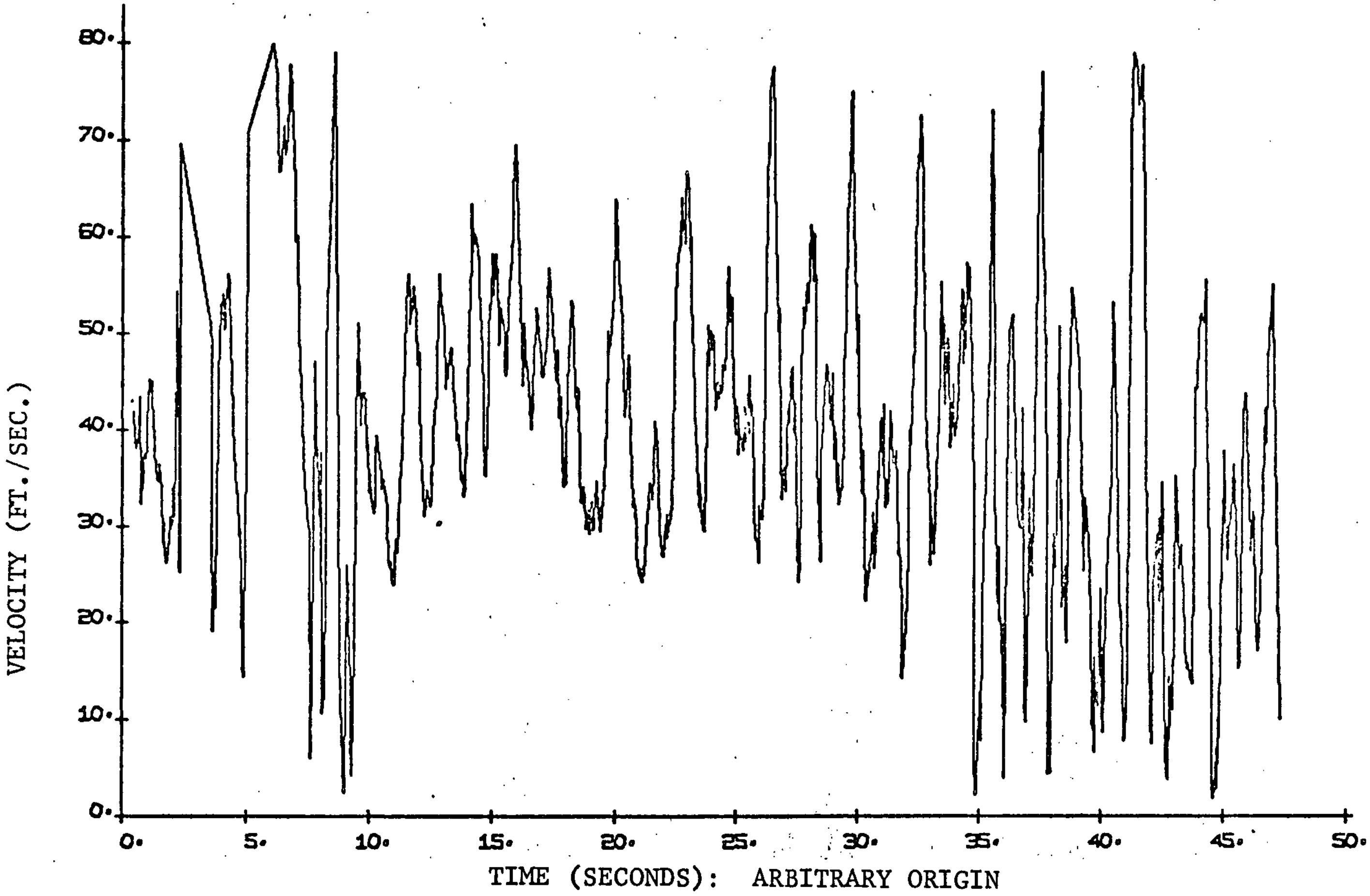
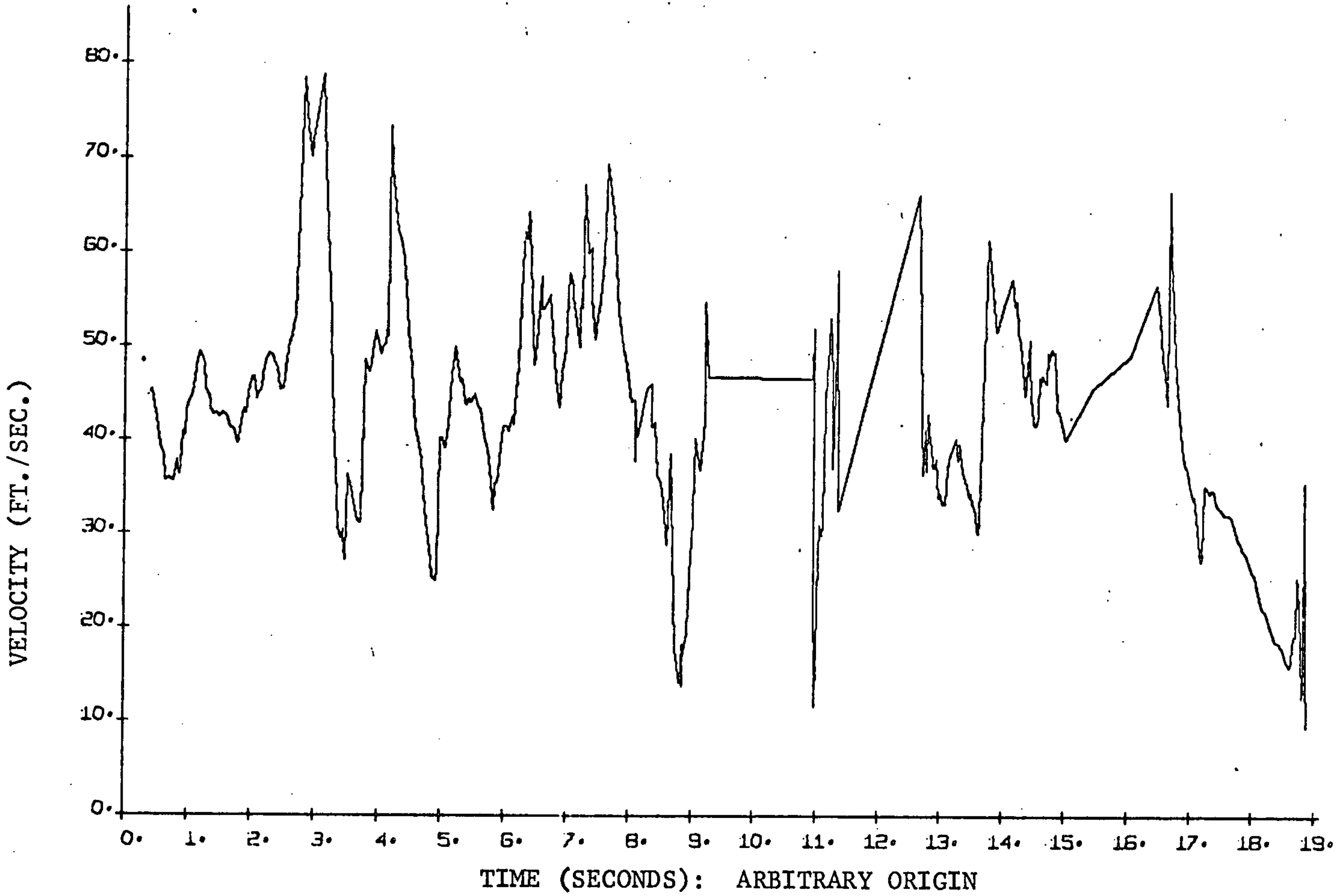


Figure 14. Lion velocity curve, attack of 1340 03-11-70



A feature of these film data is the lag (p) between the beginning of an attack and the commencement of filming. This necessitated the modification of equation (7) for curve fitting purposes:

$$V(t) = VMAX\ (1 - e^{-K(t-p)}) \qquad (9)$$

Since this lag eliminates some of the initial acceleration, calculation of the acceleration constant (K) is difficult. This is evident in Figures 13 and 14. As a result only three attacks were suitable for determining the value of the acceleration constant. One of these is shown in Figure 15, and the data relating to the calculation are given in Table XXXIX.

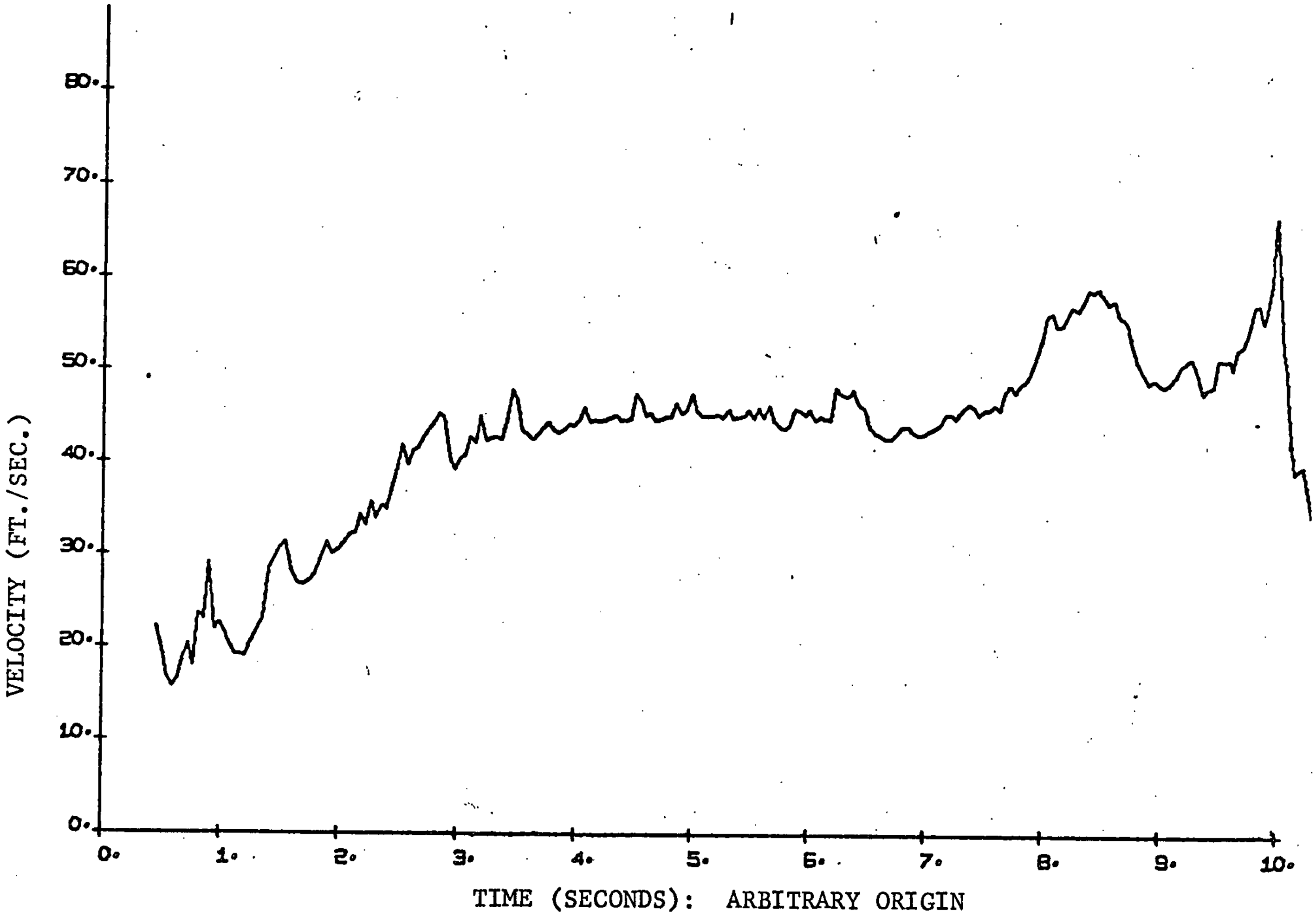
TABLE XXXIX. Acceleration constant (K) of the lion velocity curve

SET NUMBER	K ESTIMATE	STANDARD ERROR OF THE ESTIMATE K
1	0.603	0.0351
2	0.836	0.1508
3	0.596	0.0720

Probability of homogeneity of the sets < 0.001
Unweighted mean = 0.68
Unweighted variance = 0.019

The homogeneity of the parameter was examined using a chi-square test of the weighted deviation of the parameter estimates from the weighted mean (Gilbert, 1973). The low probability found indicates that the variation

Figure 15. Lion velocity curve, attack of 0845 22-10-70



between the different attacks is significantly greater than that resulting from the variability within attacks. The estimates should not be weighted in such a case (Gilbert, 1973). The unweighted mean and variance of the acceleration constant are found to be 0.68 and 0.019, respectively.

The value of the maximum velocity constant was also obtained for the same three attacks. An analysis similar to that used for the acceleration constant is summarized in Table XL.

TABLE XL. Maximum velocity constant (VMAX) of the lion velocity curve

SET NUMBER	VMAX ESTIMATE (feet/second)	STANDARD ERROR OF ESTIMATE OF VMAX
1	47.3	0.438
2	50.4	0.473
3	44.6	0.518

Probability of homogeneity of the sets < 0.001
Unweighted mean = 47.4
Unweighted variance = 8.42

This yields a mean of 47.4 feet per second for VMAX and a variance of 8.42.

It can be seen that if little of the acceleration phase is present then a small error in the value of the acceleration constant would have negligible effect upon the least-squares estimate of the value of the VMAX constant. Thus the value of K can be set at its best estimate (0.68) and attack data which has a large filming lag can then be analyzed to obtain the value of the VMAX constant. This allows a number of other runs to be analyzed, increasing the sample size for the VMAX estimate. Six attacks were sufficiently long to be useful for this and these estimates plus the previous three are shown in Table XLI.

TABLE XLI. Maximum velocity constant (VMAX) of the lion velocity curve including six values obtained by fixing the value of the acceleration constant

SET NUMBER	VMAX ESTIMATE (feet/second)	STANDARD ERROR OF ESTIMATE OF VMAX
1	47.3	0.438
2	50.4	0.473
3	44.6	0.518
4	46.4	0.538
5	44.0	0.322
6	47.4	1.393
7	44.4	0.640
8	44.5	0.667
9	42.2	0.486

Probability of homogeneity of the sets < 0.001
Unweighted mean = 45.7
Unweighted variance = 6.18

The mean value is 45.7 feet per second and the variance is 6.18. The effect of the value of K upon the value of VMAX was examined by undertaking the same analysis using a value of K which was twenty per cent less than the calculated mean. The mean increase in the estimate of VMAX was negligible (0.2 per cent or 0.1 feet per second).

The equation of the lion's attack is now complete:

$$V(t) = 45.7\ (1 - e^{-0.68t}) \qquad (10)$$

or integrated to yield distance (Y):

$$Y(t) = 45.7\ (t + \frac{1}{0.68} * e^{-0.68t} - \frac{1}{0.68}) \qquad (11)$$

where V and Y are in feet per second and feet, respectively. The mean velocity curve of the lion is shown in Figures 16, 17, and 18 together with prey velocity curves.

Equation (11) refers only to the mean distance which a lion can be expected to have traversed at a time, t, after commencing attack. It is equally important to know the variance associated with the distance. This can be approximated (Gilbert, 1973) from the variance of VMAX and K and their covariance (which can be calculated from Tables XXXIX and XL as 0.36):

$$\text{variance}(t) = \left[(\frac{dY}{dK})^2 * \text{variance}(K)\right] + 2 * \left[(\frac{dV}{dK}) * (\frac{dY}{dVMAX}) * \text{covariance}(K, VMAX)\right] + \left[(\frac{dY}{dVMAX})^2 * \text{variance}(VMAX)\right] \qquad (12)$$

where:

$$\frac{dY}{dK} = VMAX - \frac{1}{K^2}(e^{-Kt} - 1) - (\frac{t}{K} * e^{-Kt})$$

$$\frac{dY}{dVMAX} = t + \frac{1}{K} e^{-Kt} - \frac{1}{K}$$

Assuming a normal distribution, it is now possible to define the probability (P(YY,t)) of the lion travelling a distance YY or less in a time, t:

$$P(YY,t) = GAUS\ (\frac{YY - \bar{Y}(t)}{SD(t)}) \qquad (13)$$

where GAUS represents the normal cumulative probability function, SD(t) is the standard deviation of the distribution (calculated as the square root of the variance defined by equation (12)), and $\bar{Y}(t)$ is the mean distance travelled in time t as defined by equation (11).

The Zebra Velocity Curve[1]

The determination of the fatigue constant for the zebra suffered from the same limitations as was the case for the lion. Visual inspection of the velocity plots suggested that the value was rather low and could be ignored for the time range involved in attacks by the lions.

The value of the acceleration constant (K) is less than that of the lion and thus fewer data values relating to the period of positive acceleration are deleted by the time lag (p). More runs, therefore, proved suitable for direct analysis by the least squares method. Table XLII summarizes

[1] Only animals over one year are considered.

the data relating to the analysis of K.

TABLE XLII. Acceleration constant (K) of the zebra velocity curve

SET NUMBER	K ESTIMATE	STANDARD ERROR OF THE ESTIMATE OF K
1	0.152	0.0587
2	0.392	0.0318
3	0.183	0.0255
4	0.502	0.2086
5	0.366	0.1170
6	0.243	0.0250

Probability of homogeneity of the sets < 0.001
Unweighted mean = 0.31
Unweighted variance = 0.018

The mean is found to be 0.31 and the variance 0.018.

Table XLIII summarizes the corresponding values for the maximum velocity (VMAX), and also includes one further value obtained by fixing K at 0.31. The mean is 52.5 feet per second, and the variance is 88.49. The covariance can be calculated from the two tables, and is found to be 0.12.

TABLE XLIII. Maximum velocity constant (VMAX) of the zebra velocity curve including one value obtained by fixing the value of K

SET NUMBER	VMAX ESTIMATE (feet/second)	STANDARD ERROR OF ESTIMATE OF VMAX
1	52.9	2.866
2	67.2	2.057
3	42.3	0.655
4	48.6	3.795
5	46.1	2.919
6	63.5	4.595
7	46.8	3.872

Probability of homogeneity of the sets < 0.001
Unweighted mean = 52.5
Unweighted variance = 88.49

The equation for the flight of an average zebra is (figure 16):

$$V(t) = 52.5\ (1 - e^{0.31t}) \qquad (14)$$

or in terms of distance:

$$Y(t) = 52.5(t + \frac{1}{0.31} e^{-0.31t} - \frac{1}{0.31}) \qquad (15)$$

The variance can be calculated from equation (12) and the probability of running a given distance or less in time, t, by equation (13).

The Wildebeest Velocity Curve[1]

The velocity constants for the wildebeest are determined much like those for the zebra. Fatigue is assumed nil and least square fitting is applied to three complete runs. K is then set at the mean value and a further run is analyzed for VMAX. Tables XLIV and XLV summarize the results for K (mean of 0.39, variance of 0.005) and VMAX (mean of 46.9 feet per second, variance of 12.18).

TABLE XLIV. Acceleration constant (K) of the wildebeest velocity curve

SET NUMBER	K ESTIMATE	STANDARD ERROR OF THE ESTIMATE OF K
1	0.311	0.0209
2	0.456	0.1075
3	0.391	0.1554

Probability of homogeneity of the sets < 0.001
Unweighted mean = 0.39
Unweighted variance = 0.005

TABLE XLV. Maximum velocity constant (VMAX) of the wildebeest velocity curve including one value obtained by fixing the value of K

SET NUMBER	VMAX ESTIMATE (feet/second)	STANDARD ERROR OF THE ESTIMATE OF VMAX
1	50.5	0.398
2	46.8	1.188
3	42.2	3.719
4	47.9	6.704

Probability of homogeneity of the sets < 0.01
Unweighted mean = 46.9
Unweighted variance = 12.18

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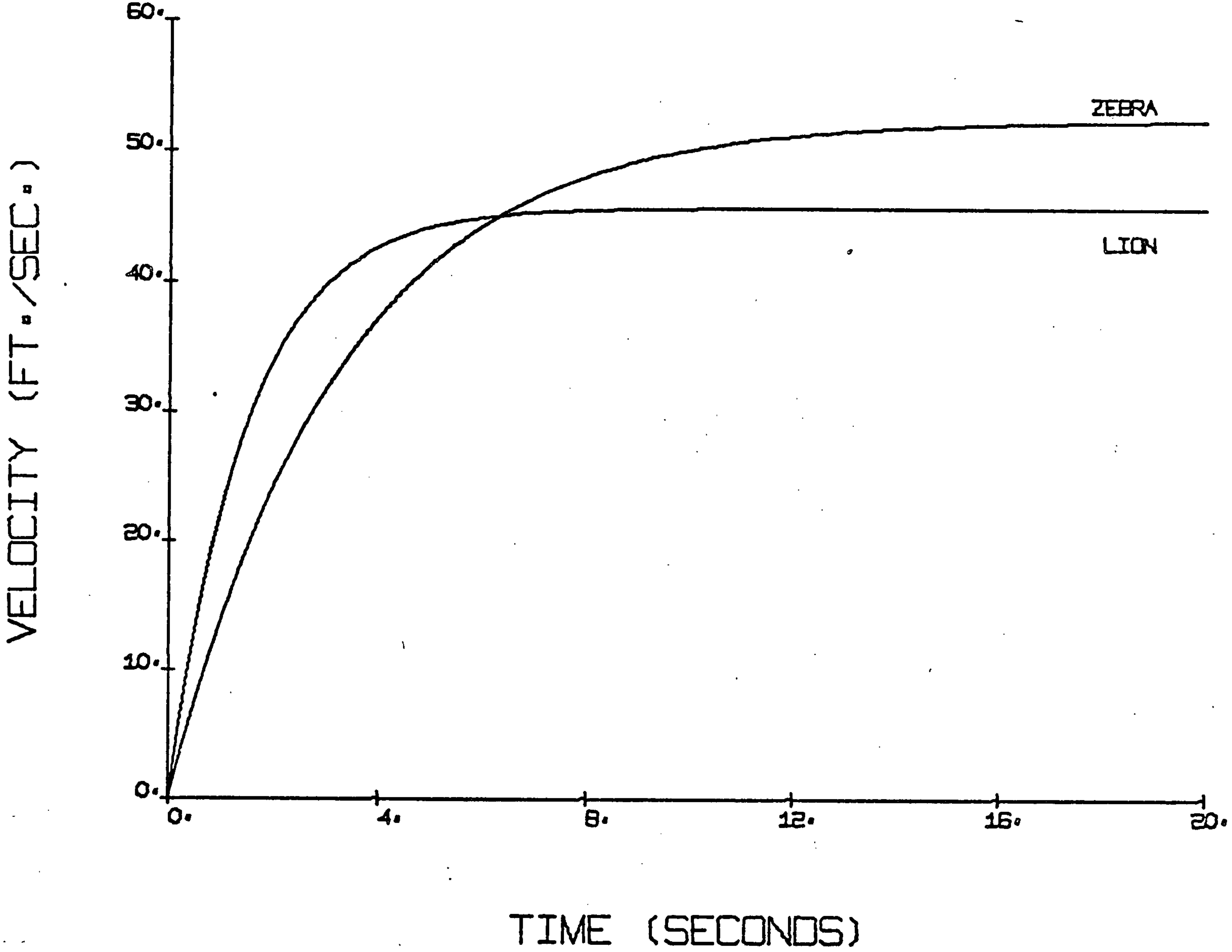
[1] Only animals over one year are considered.

Figure 16. Zebra and lion velocity curves



The covariance is found to be 0.18.

The equation for flight of an average wildebeest is (figure 17):

$$V(t) = 46.9\ (1 - e^{-0.39t}) \qquad (16)$$

or,

$$Y(t) = 46.9\ \left(t + \frac{1}{0.39} e^{-0.39t} - \frac{1}{0.39}\right) \qquad (17)$$

Equations (12) and (13) can be applied to determine the variance and probability associated with Y(t).

The Gazelle Velocity Curve

Insufficient attacks involving Grant's gazelle were observed to allow definition of the velocity curve for this species. Thomson's gazelle over eight months can however be considered. The similarity in body shape between the two gazelle species would suggest that the velocity curves are somewhat similar.

Following a technique of analysis similar to that of the previously discussed curves, fatigue is considered insignificant. Five runs are analyzed by least squares fitting. Tables XLVI and XLVII present the data for K (mean of 0.17, variance of 0.002) and VMAX (mean of 86.8 feet per second, variance of 4.36). The covariance is -0.0004.

Figure 17. Wildebeest and lion velocity curves

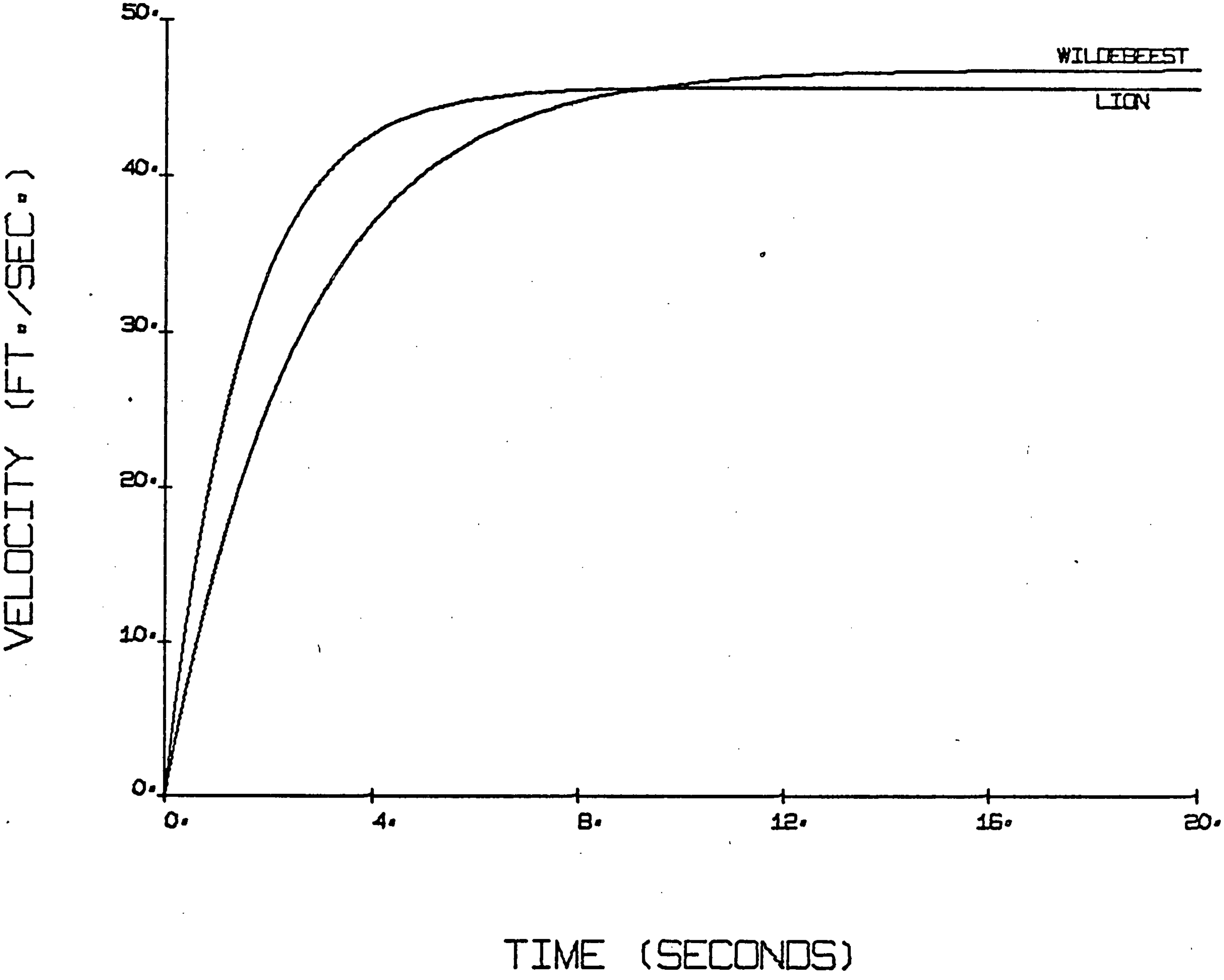


TABLE XLVI. Acceleration constant (K) of the Thomson's gazelle velocity curve

SET NUMBER	K ESTIMATE	STANDARD ERROR OF THE ESTIMATE OF K
1	0.182	0.0436
2	0.182	0.0128
3	0.147	0.0068
4	0.184	0.0070
5	0.173	0.0171

Probability of homogeneity of the sets ≐ 0.14
Unweighted mean = 0.17
Unweighted variance = 0.0002

TABLE XLVII. Maximum velocity constant (VMAX) of the Thomson's gazelle velocity curve

SET NUMBER	VMAX ESTIMATE (feet/second)	STANDARD ERROR OF THE ESTIMATE OF VMAX
1	86.0	6.460
2	84.0	1.680
3	87.0	1.698
4	89.8	1.427
5	87.2	2.295

Probability of homogeneity of the sets <0.01
Unweighted mean = 86.8
Unweighted variance = 4.36

The flight equation of an average Thomson's gazelle is (Figure 18):

$$V(t) = 86.0\ (1 - e^{-0.17t}) \qquad (18)$$

or,

$$Y(t) = 86.0\ \left(t + \frac{1}{0.17} e^{-0.17t} - \frac{1}{0.17}\right) \qquad (19)$$

The variance and probability associated with Y(t) can be determined from equations (12) and (13).

Effect of Age and Sex on the Velocity Curve

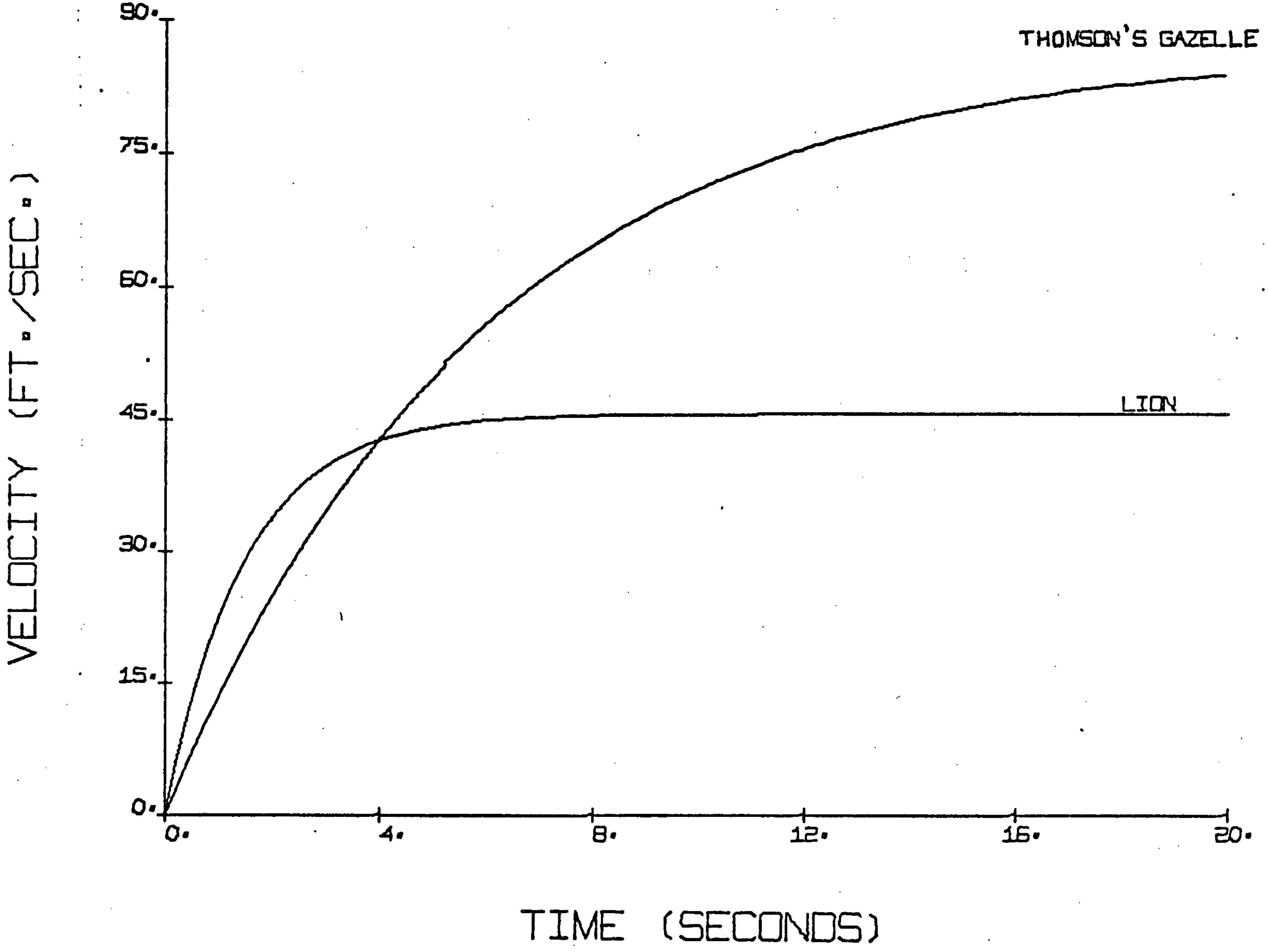
Ikai (1968) has considered the effect of age and sex upon the human velocity curve. He found that both acceleration and maximum velocity are affected. Presumably age and sex have the same effect for ungulates as well. However, there is insufficient attack data to consider these features for the prey velocity curves (although as indicated, runs by very young animals have been excluded for each species to avoid excessive variance). It will be shown in a later section that there is no significant selection for age (excepting very young individuals) and sex which suggests that velocity curve differences are minimal.

The lion data is based entirely upon adult female lions.

The Probability of Attack Success

The purpose of the velocity equations is the determination of the probability of attack success for various conditions. This involves matching the sprint characteristics of the predator and prey. Specifically, the probability of a successful attack is equal to the proportion of that prey

Figure 18. Thomson's gazelle and lion velocity curves



species an average lion (equations 10 and 11) could capture (Gilbert, personal communication). Lacking any specific measure, dodging by the prey is considered unimportant. This is probably valid for the short attacks used by the lion. Several situations were suggested by the field observations as being of interest. These are considered below.

Case One: Attack Success for Initial Predator and Prey Velocities of Zero, Zero Slope, and Direct Flight

This set of conditions was the most usual following a crouch or sneak-crouch stalk. For any initial predator-prey distance, it is possible to define using equation (13) the probability that the predator will overtake the prey within a time, t. The maximum distance (YY) the prey can traverse and still be overtaken is simply the distance travelled by the predator in time, t (equation 11) minus the initial predator-prey distance. Since VMAX for the prey species is greater than for the predator, increasing the attack time (t) will at first increase the calculated probability of success, but then will decrease the calculated probability. The decrease for longer times represents prey which had previously been overtaken passing the predator. The true probability of the attack success is the maximum value obtained. This can be found quite easily by iteration of the time variable. Since it was found that fatigue could have some effect upon velocities beyond 35 seconds, and since no successful attacks were observed lasting over 35 seconds, it was assumed that a capture must occur prior to that time. Thus the time iteration is restricted to the interval 0 to 35 seconds. The results of this analysis are shown in Figures 19, 20, and 21 for each of

Figure 19. Wildebeest attack success;
initial lion and prey velocities=0.0;
zero slope; direct flight

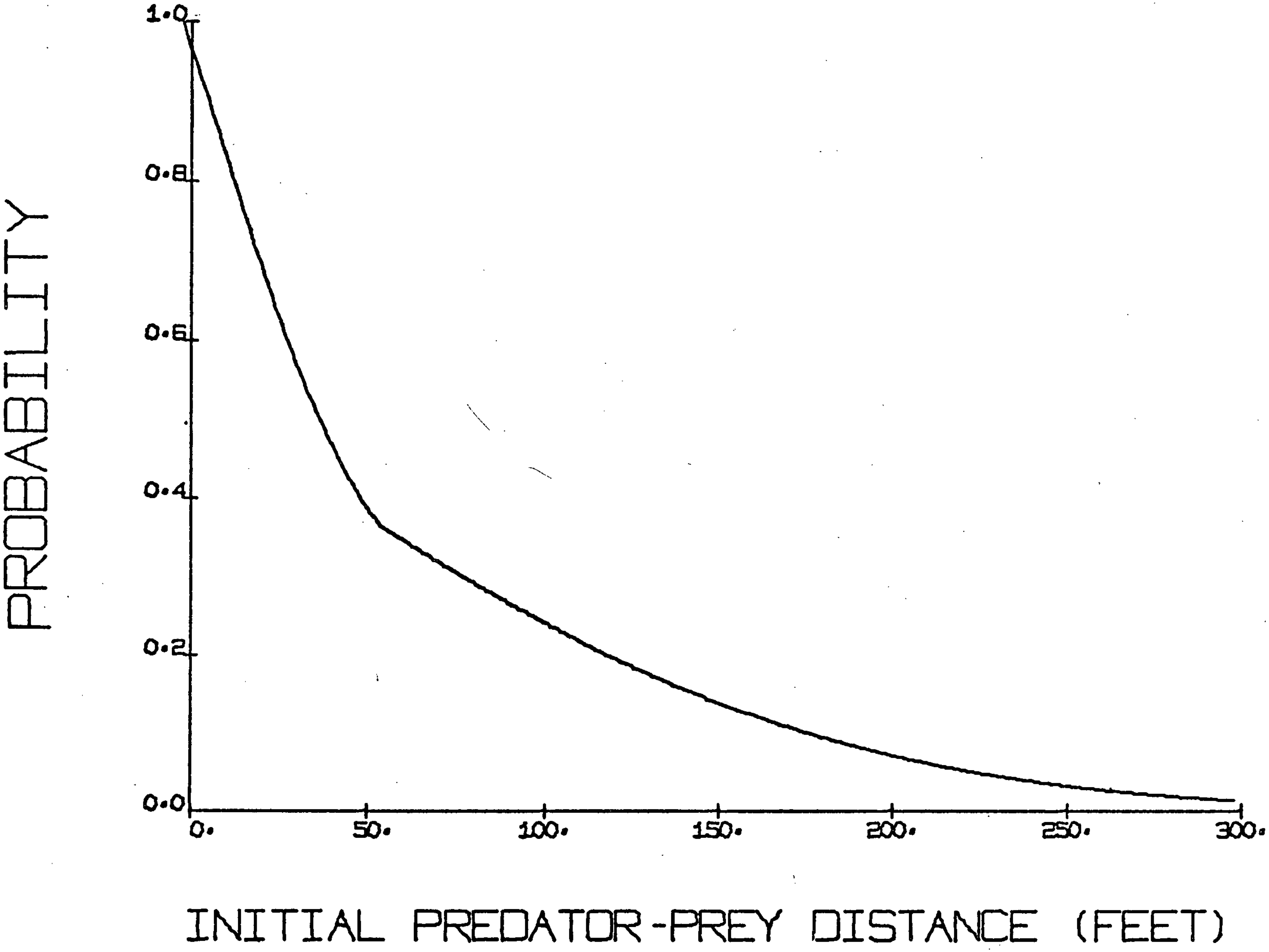


Figure 20. Zebra attack success; initial lion and prey velocities=0.0; zero slope; direct flight

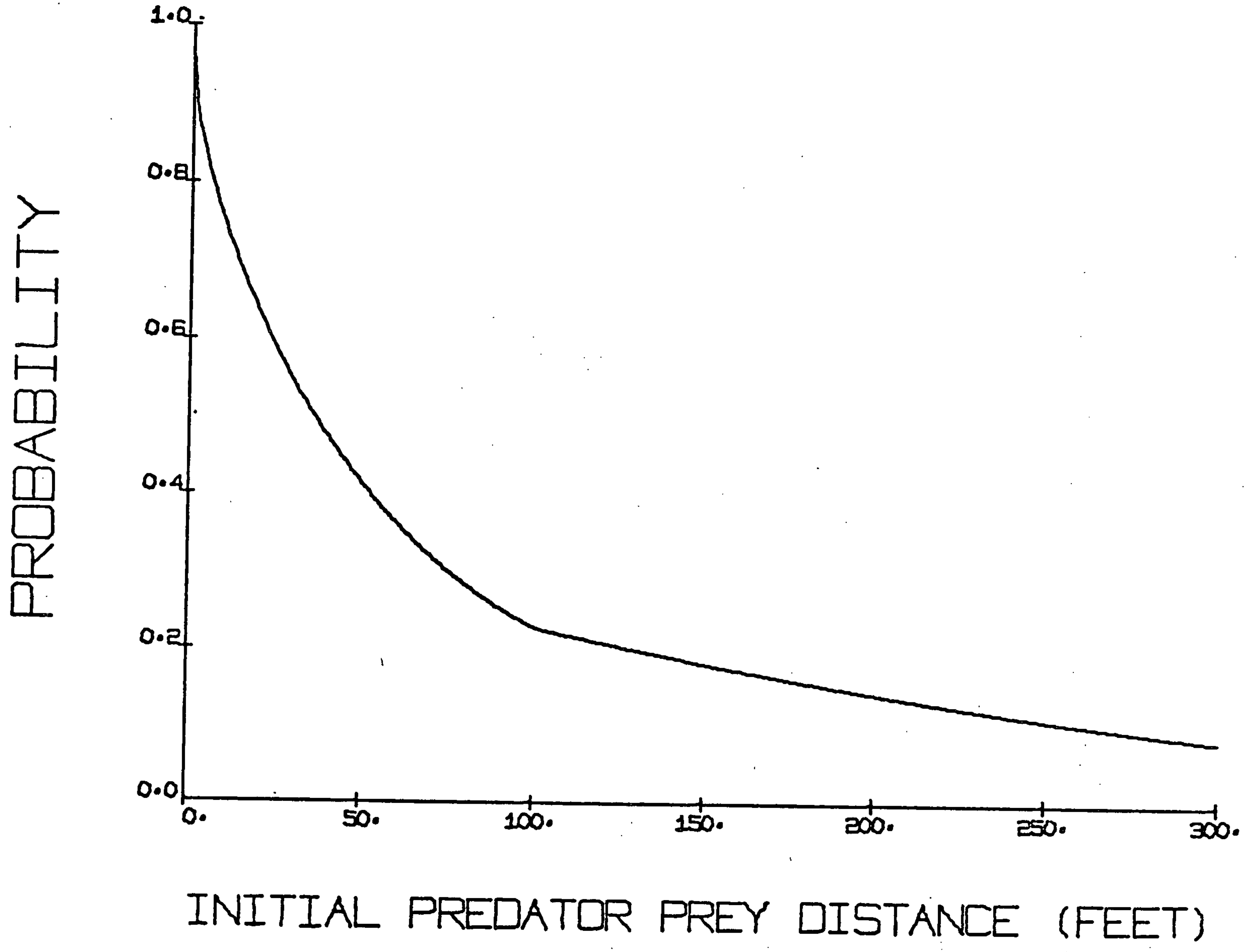
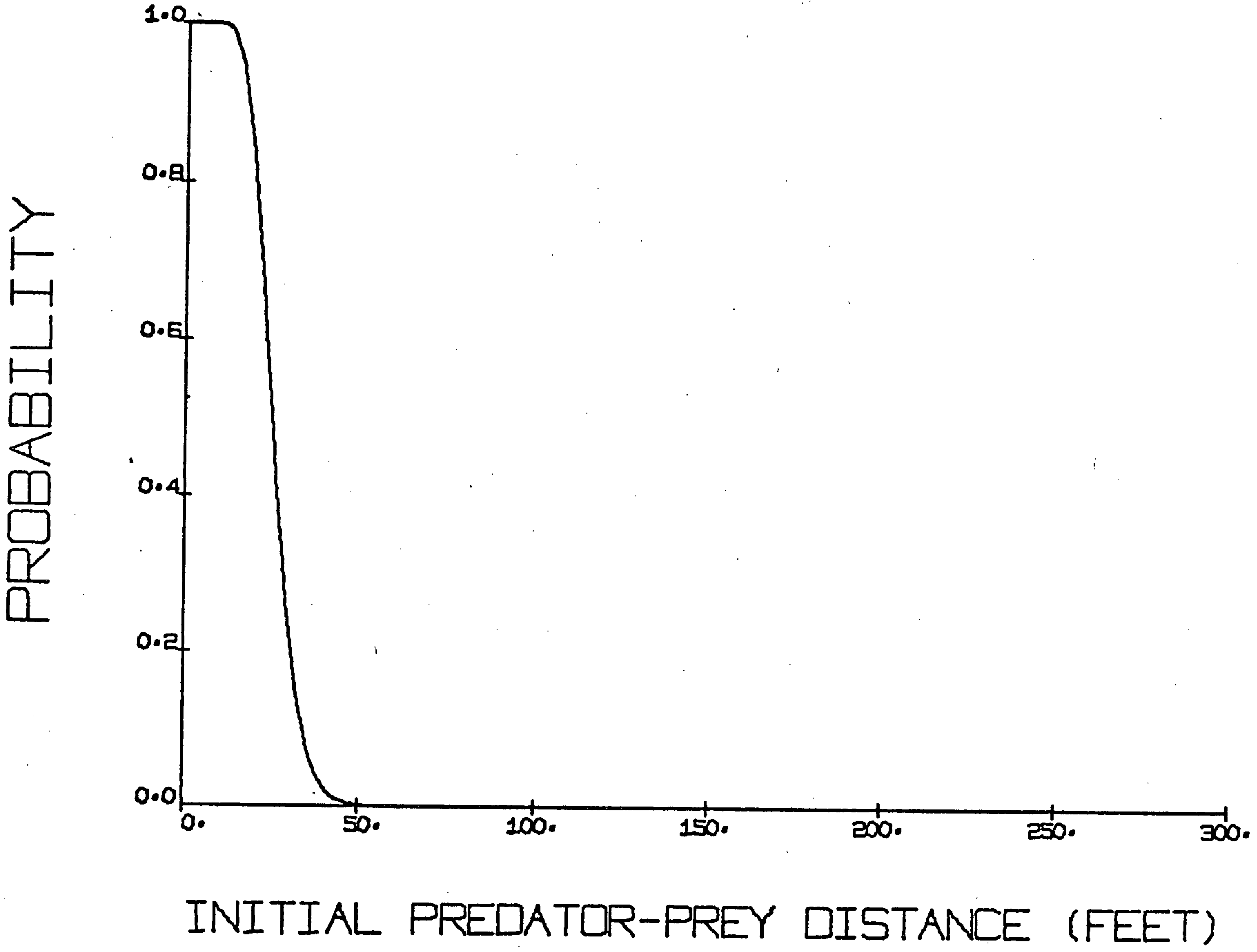


Figure 21. Thomson's gazelle attack success; initial lion and prey velocities=0.0; zero slope; direct flight

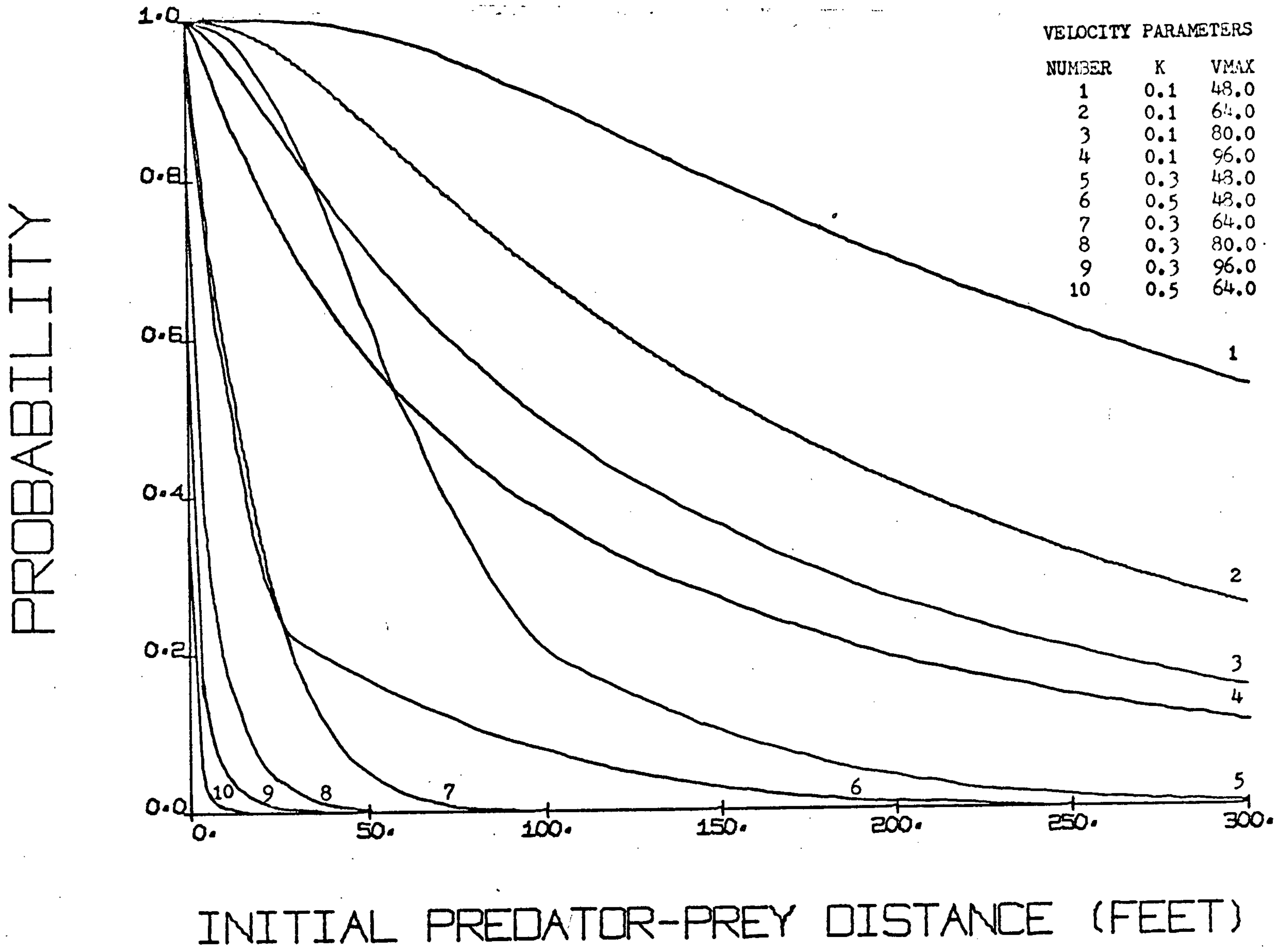


the three prey species. (The irregularity of slope in Figures 19 and 20 occurs when the time of maximum success reaches 35 seconds.

There are two features to note in these attack success plots. Firstly, there is the mean initial predator-prey distance at which prey can be successfully attacked. It can be seen that all three species are quite similar in this regard, although Thomson's gazelle are at a slight advantage. Secondly, there is the variance associated with the mean. As will be examined in the consideration of the stalk and attack combined, this aspect is of considerable importance, and it can be seen to differ for the three species examined.

The situation is confused by having different parameter variances for the different species. This difficulty is overcome by simulating prey which have differing velocity parameters (K and VMAX), but identical variances for the parameters. Four evenly spaced values of VMAX (48.0 to 96.0 feet per second) were chosen to cover the range of values found for the real prey. Likewise three values of K (0.1 to 0.5) were chosen. Two of the combinations require a nearly zero initial predator-prey distance to give a 0.5 probability of success, the remaining ten simulations are illustrated in Figure 22. The variance of K was set at 0.005 and that of VMAX at 10.0. The covariance was set at zero. In two cases (K = 0.1 and VMAX = 96.0 plus K = 0.3 and VMAX = 48.0; K = 0.3 and VMAX = 64.0 plus K = 0.5 and VMAX = 48.0) simulated prey with different parameter values yield the same mean initial predator-prey distance of successful attack. However, the effect of the variance is not the same. In each case the

Figure 22. Simulated prey attack success; initial lion and prey velociities=0.0; zero slope; direct flight



prey with the greater specialization (for either acceleration or speed) has the greater effective variance. It will be shown that the larger the prey variance, the larger the capture success; thus, excessive specialization seems undesirable. Indeed, it can be seen that the three prey analyzed in fact show a lack of extreme specialization.

Whereas the increase in effective variance reduces extreme specialization, various selective pressures will tend to favour rapid acceleration or speed. Since these two are mutually exclusive, favouring one reduces the other. Cheetah predation may, for example, have favoured improvement of maximum velocity in gazelle.

There may be some significance to the differences in the parameter variances between the three species, but this may simply be a result of the small sample sizes. If in fact there is true difference then either high speed and low acceleration is less prone to variation or there is a difference in the amount of selective pressure on the different species. The present data does not allow any investigation of these possibilities.

Case Two: Attack Success for Initial Predator Velocities Greater than Zero, Zero Initial Prey Velocity, Zero Slope, and Direct Flight

This set of conditions was the most usual following a run stalk. The determination of the probability of attack success is the same as that for case one, but a new equation for the distance-time relation (Y(t)) must be formulated for the predator. If VI represents the initial predator velocity, then from equation (7):

$$VI = VMAX\ (1 - e^{-K\emptyset})$$

where $\emptyset$ is the time span corresponding to when the predator would have to have begun maximal acceleration in order to achieve the velocity VI. Rearranging this gives:

$$\emptyset = \frac{-\ln\left(1 - \frac{VI}{VMAX}\right.}{K}$$

The distance equation based upon the time scale beginning at the commencement of attack (t) can now be defined:

$$\begin{aligned} Y(t) &= VMAX\left[(t + \emptyset) + \frac{1}{K}\, e^{-K(t+\emptyset)} - \frac{1}{K}\right] - VMAX\left[\emptyset + \frac{1}{K}\, e^{-K\emptyset} - \frac{1}{K}\right] \\ &= VMAX\left[t + \frac{1}{K}\left(e^{-K(t+\emptyset)} - e^{-K\emptyset}\right)\right] \end{aligned}$$

If VI and hence $\emptyset$ equal zero then this reduces to the original distance equation.

Figures 23, 24, and 25 illustrate the effect of initial lion velocity upon attack success for an initial predator-prey distance of 75 feet. Although the relative effect will vary for the prey species depending upon the initial predator-prey distance, the improvement in success will be greatest for Thomson's gazelle attacks. This is consistent with the observation (Table XXX) that run stalks are more frequent for gazelle as compared to wildebeest and zebra.

Figure 23. Wildebeest - effect of initial lion velocity upon attack success initial lion-prey distance=75'; initial prey velocity=0.0; zero slope; direct flight

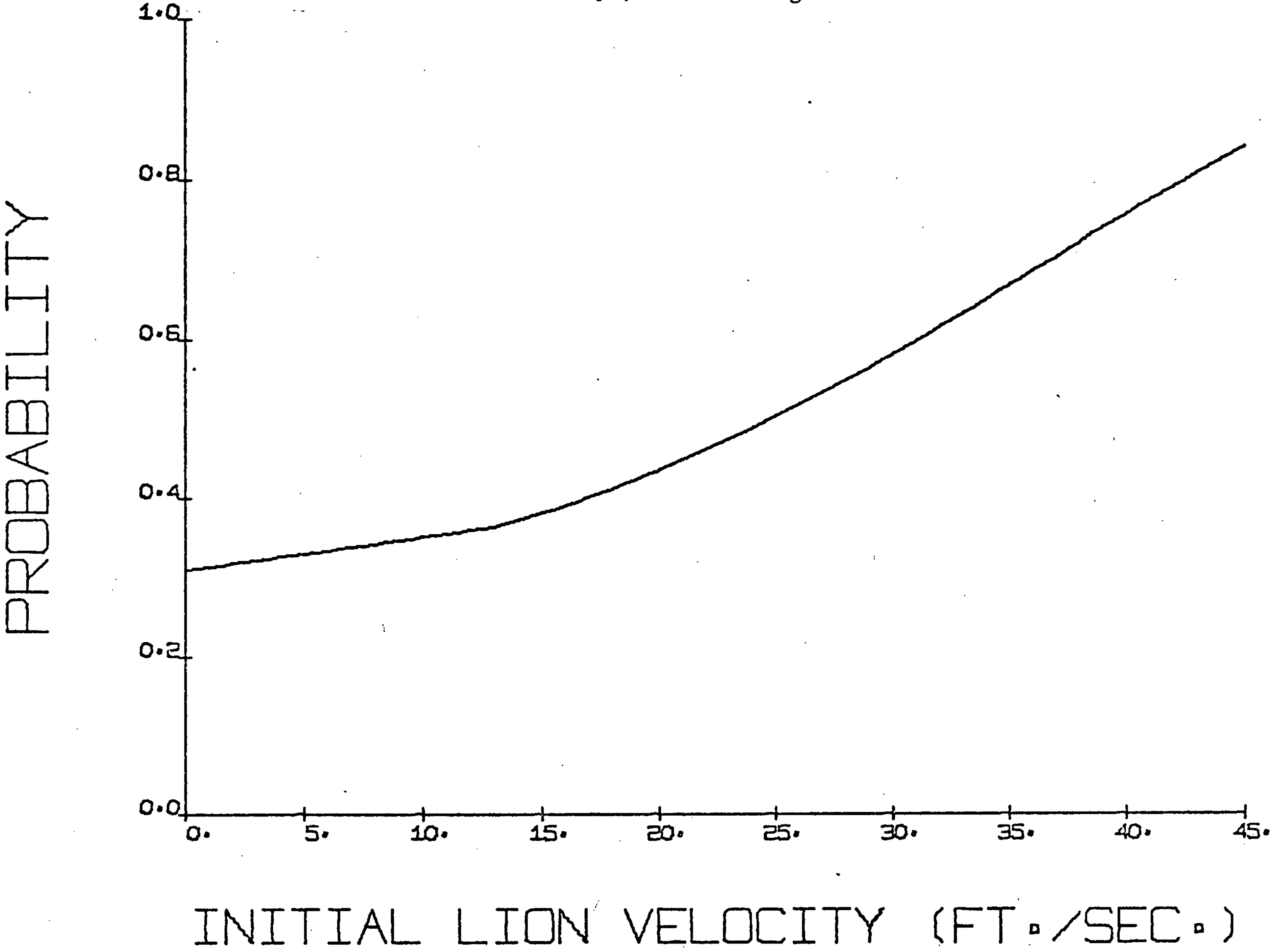


Figure 24. Zebra - effect of initial lion velocity upon attack success; initial prey velocity=0.0; zero slope; direct flight

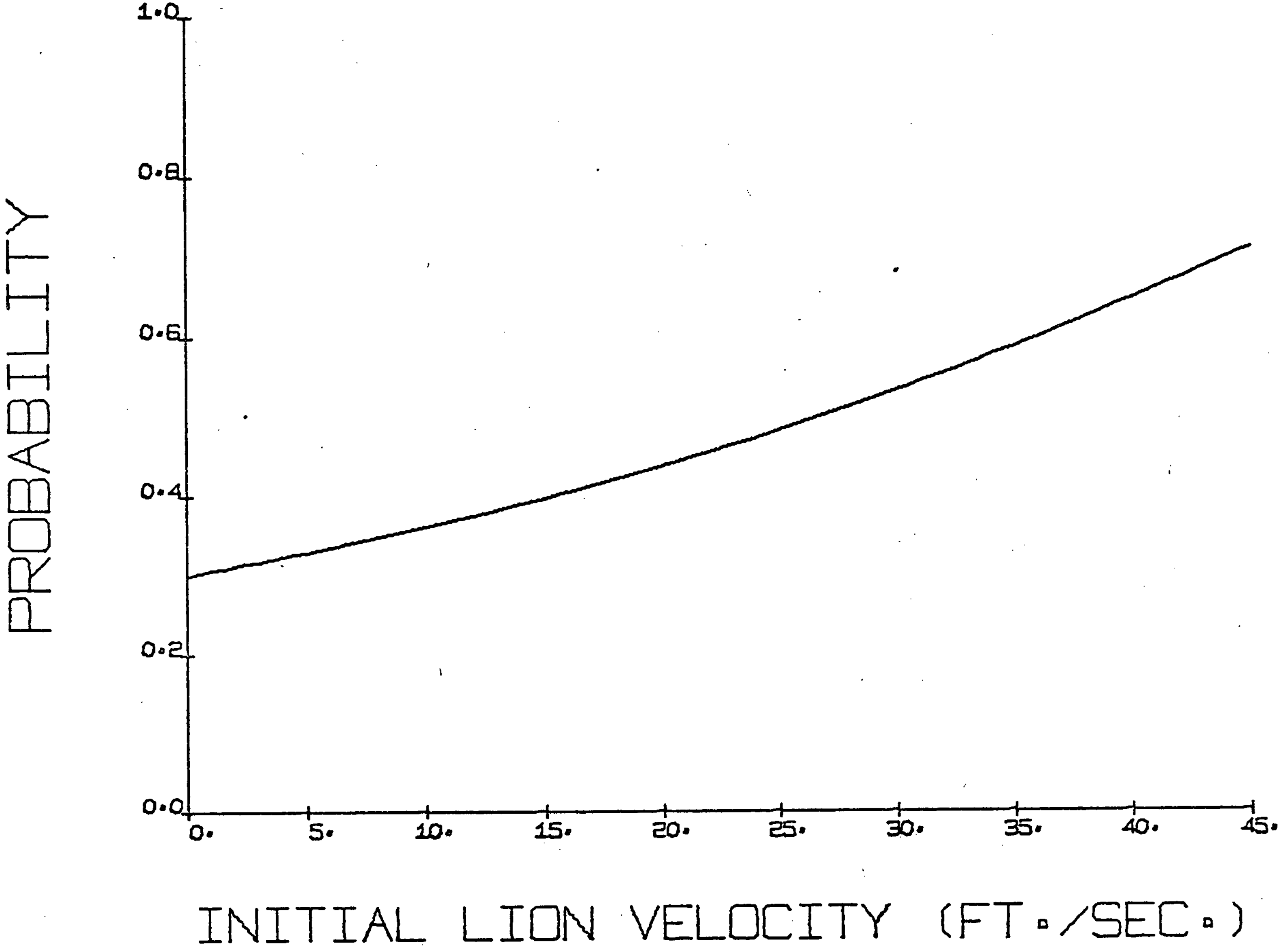
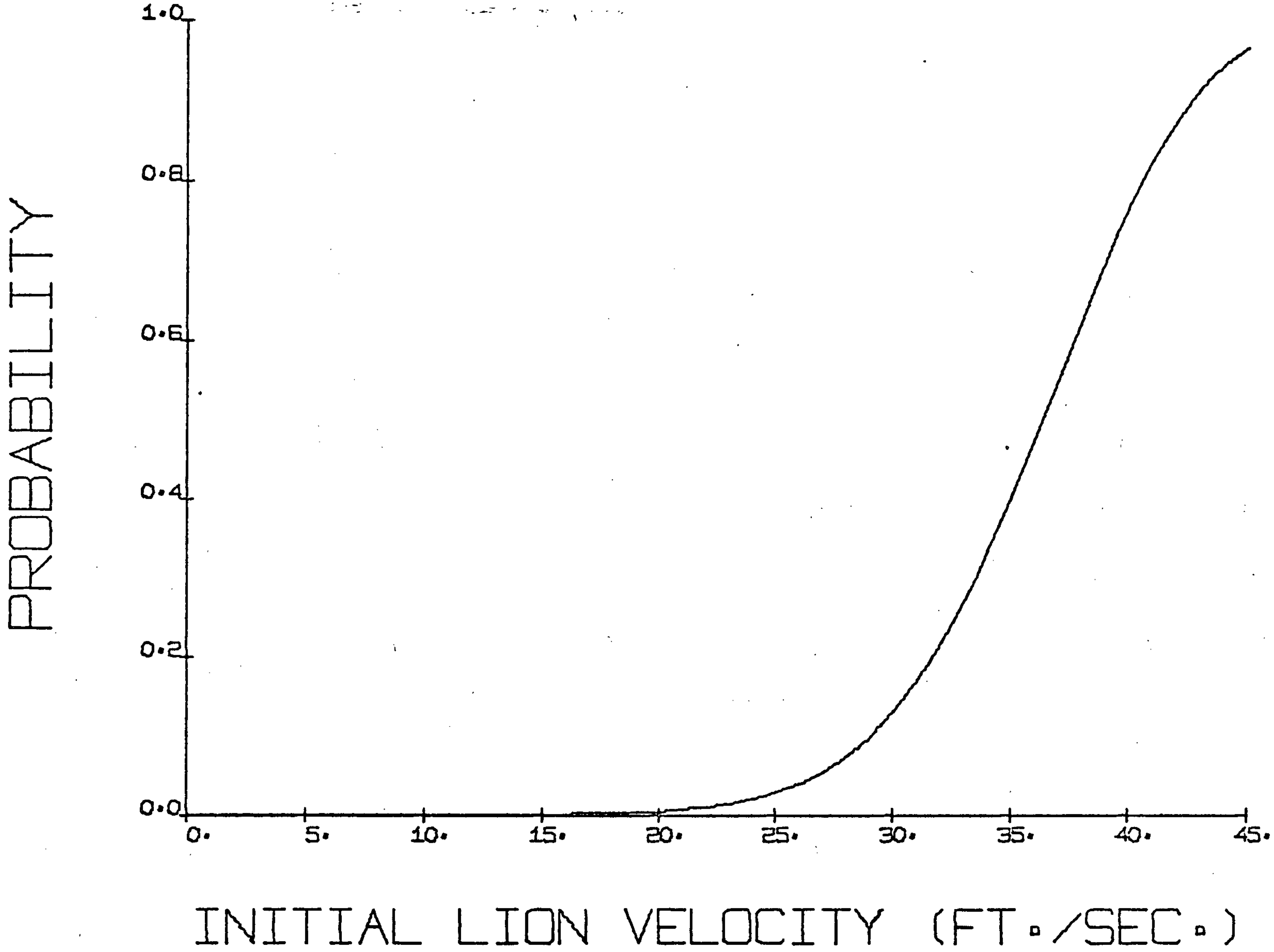


Figure 25. Thomson's gazelle - effect of initial lion velocity upon attack success; initial lion-prey distance =75'; initial prey velocity=0.0; zero slope; direct flight



Case Three: Attack Success for Initial Predator and Prey Velocities of Zero, Variable Slope, and Direct Flight

Consideration of the effect of the slope of the ground requires reference to equation (6) where the acceleration constant is given in its complete form. This allows the definition of FR (the force which an animal is capable of directing rearwards when its initial velocity is zero):

$$FR = K * VMAX * M$$

In the case of the lion, this force would be:

$$\begin{aligned} FR &= 0.68 * 45.7 * 330 \\ &= 10255 \text{ poundals} \\ &= 319 \text{ pounds} \end{aligned}$$

The calculated magnitude of FR is approximately what would be expected (Ikai, 1968).

It was noted that the resistance to motion (RES) increases in approximately direct proportion to the velocity:

$$RES \propto \text{velocity}$$

Since the resistance will be zero when there is no velocity:

$$RES = \text{constant} * \text{velocity}$$

Furthermore, RES equals FR at VMAX, thus:

$$RES = \frac{FR}{VMAX} * \text{velocity}$$

If locomotion is up or down a slope, the accelerating force (FR) is increased or decreased by the downward component of gravity. For a slope of OMEGA radians the downslope force due to gravity (DF) can be defined:

$$DF = M * SIN(OMEGA) * g$$

The constants of the velocity equation can now be redefined. Consider firstly downslope running. Maximum downslope velocity (VD) still occurs when RES equals the total propelling force (FR + DF) thus

$$DF + FR = \frac{FF}{VMAX} * VD$$

but since

$$FF = K * VMAX * M$$

it is found by rearranging that:

$$VD = \frac{DF}{K * M} + VMAX$$

$$VD = \frac{SIN(OMEGA) * g}{K} + VMAX$$

The value of the exponential constant K is unchanged by slope. The maximum upslope velocity (VU) is derived similarly to the downslope situation:

$$VU = VMAX - \frac{SIN(OMEGA) * g}{K}$$

As expected, the mass of the animal does not affect its running performance up or down a slope in a direct manner (assuming the force to mass ratio is constant for different sized animals of the same species). However, those animals which are the strongest runners (high force to mass ratio) and/or the least efficient runners (high force to maximum velocity ratio) are less affected by slope. Thus the prey animals studied would be at a disadvantage running upslope and at an advantage running downslope when attacked by a lion. Prey were never observed to flee upslope when attacked; however, other factors such as more open terrain downslope may well have been involved.

Figures 26 and 27 illustrate one downslope and one upslope example of the effect of slope upon attack success for wildebeest. Slopes to 60 degrees are shown, but those beyond approximately ten degrees are of more theoretical than practical interest. The expected effect of slope can be seen to be considerable although there were no field data to allow actual measurements of this feature. However, Best and Partridge (1928) explored an analogous situation. They provided a constant external resistive force to human runners by winding a light cord around a metal drum. Their experiments using external resistances of varying magnitude showed that maximum speed of a runner was decreased by the amount calculated from the velocity equations.

This effect of slope might be of some use in the design of waterholes or saltlicks in situations where one wished to increase or decrease attack success.

Case Four: Attack Success for Initial Predator and Prey Velocities of Zero, Zero Slope, and Restricted Escape Route

This set of conditions frequently arose for attacks following a diurnal run stalk although an initial predator velocity would often also exist. Analysis of the effect of a restricted escape route requires two simplifying

Figure 26. Effect of slope angle upon wildebeest attack success; initial lion-prey distance=75'; direct flight; downslope movement; initial prey and lion velocities=0.0

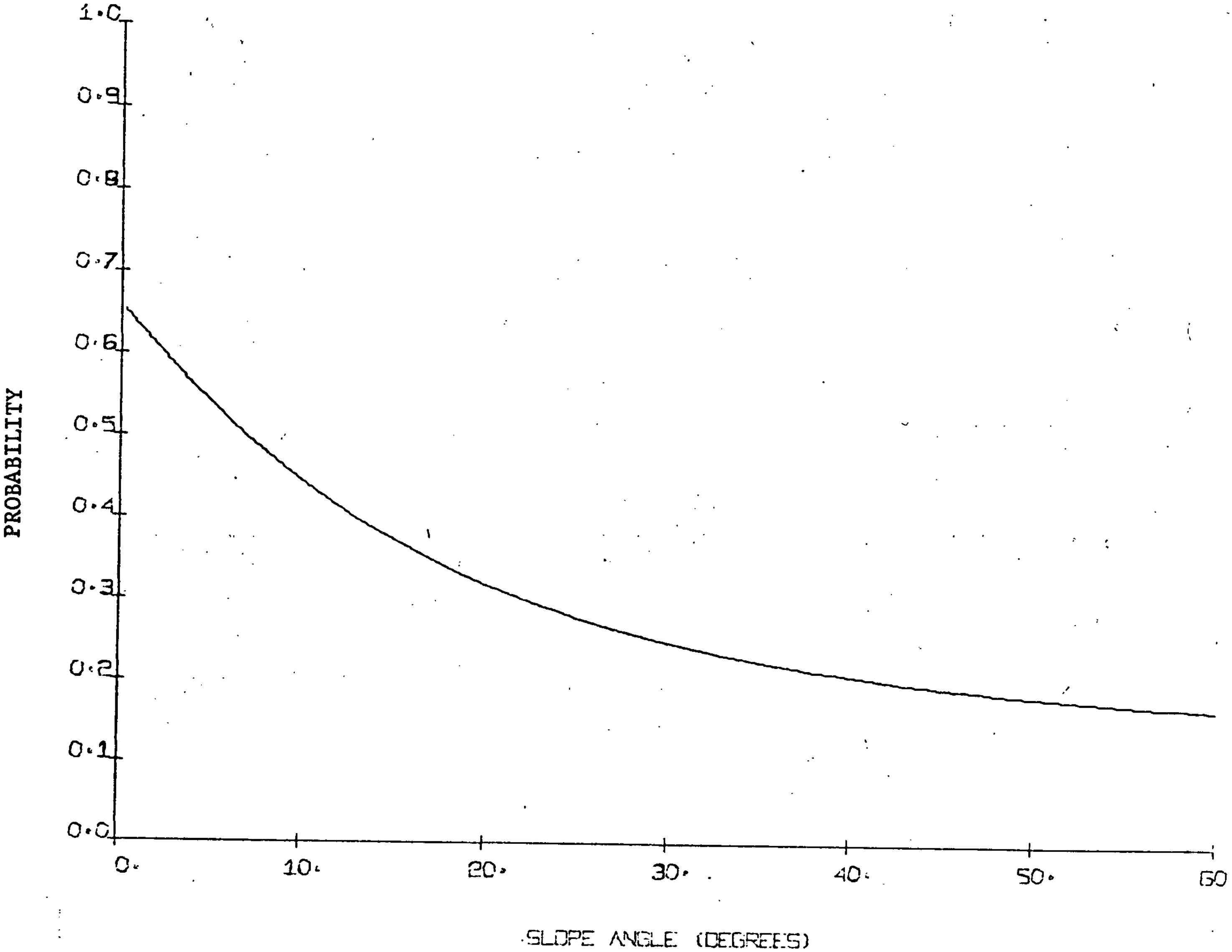
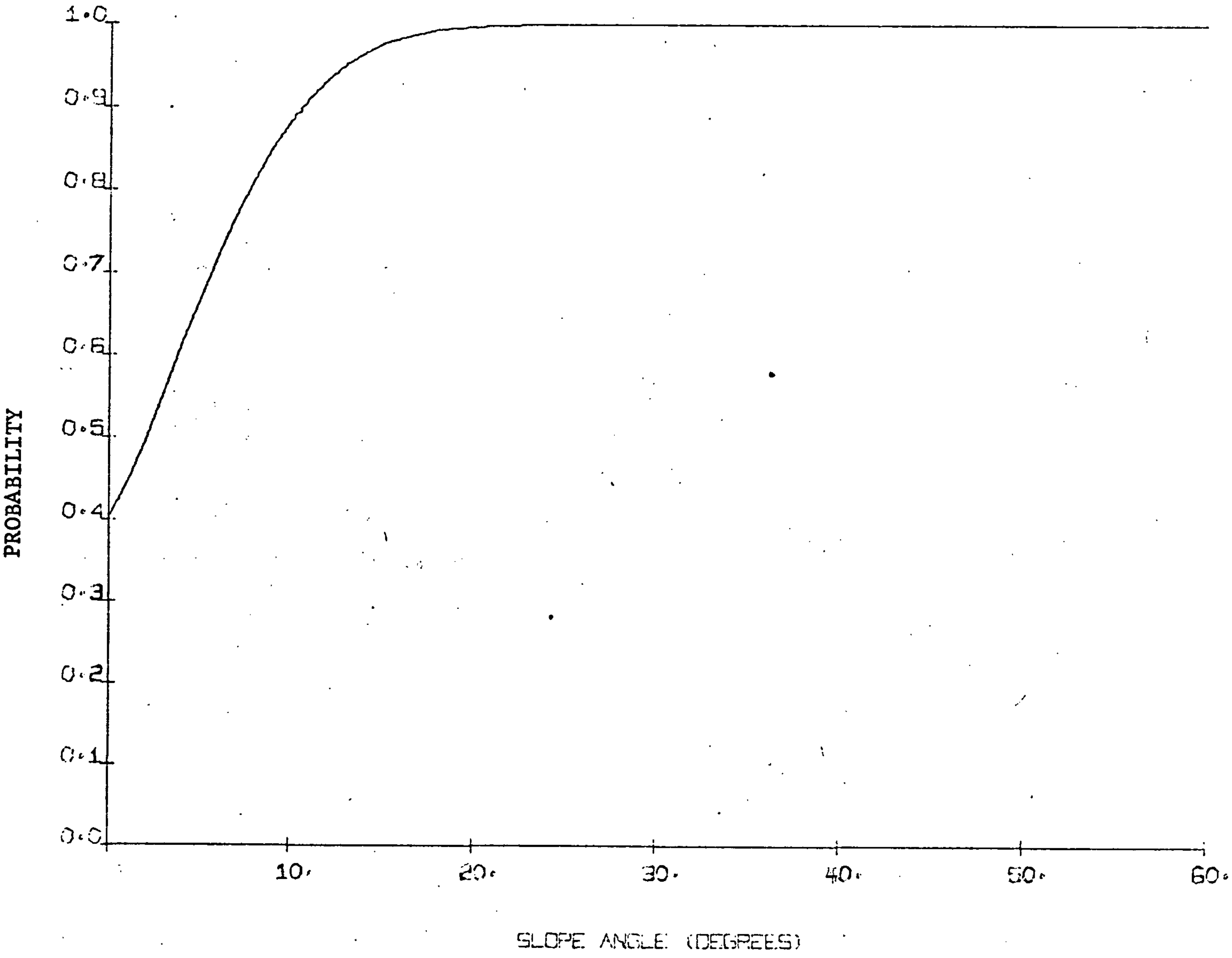


Figure 27. Effect of slope angle upon wildebeest attack success; initial lion-prey distance=75'; direct flight; upslope movement; initial prey and lion velocities=0.0



assumptions. Firstly, the prey is assumed to follow a non-manouvering straightline course at some angle (THETA) to the initial predator-prey axis. Secondly, the predator velocity is directed towards the location of the prey at each moment (or at the end of each integrating interval). This second assumption corresponds to what is termed the pursuit course in warfare ballistics (Dow, 1958).

As with the basic situation, the probability of attack success for a given angle, species, and initial predator-prey distance can be readily determined by iteration. Figures 28 and 29 illustrate the expected effect for wildebeest and Thomson's gazelle with an initial predator-prey distance of 75 feet. It can be seen that the effect is minimal for smaller angles, but quite important for larger angles. Further more, although the relative effect will vary depending upon the initial predator-prey distance, the success will be most improved when Thomson's gazelle are the prey.

Restriction of the escape routes could also be incorporated into the design of a waterhole or similar, if it were desired to increase prey capture.

Synopsis

It is possible to develop theoretical equations (7 and 8) of sprinting based upon force-velocity characteristics of the runner. One of these equations (7) satisfactorily describes the flight of the lion and various prey during the attack situation (equations 10, 14, 16, and 18). For the prey studied, the lion's attack strategy is based upon the lion using its rapid

Figure 28. Wildebeest - effect of prey flight angle upon attack success; initial lion-prey distance=75'; initial prey and predator velocities =0.0; zero slope

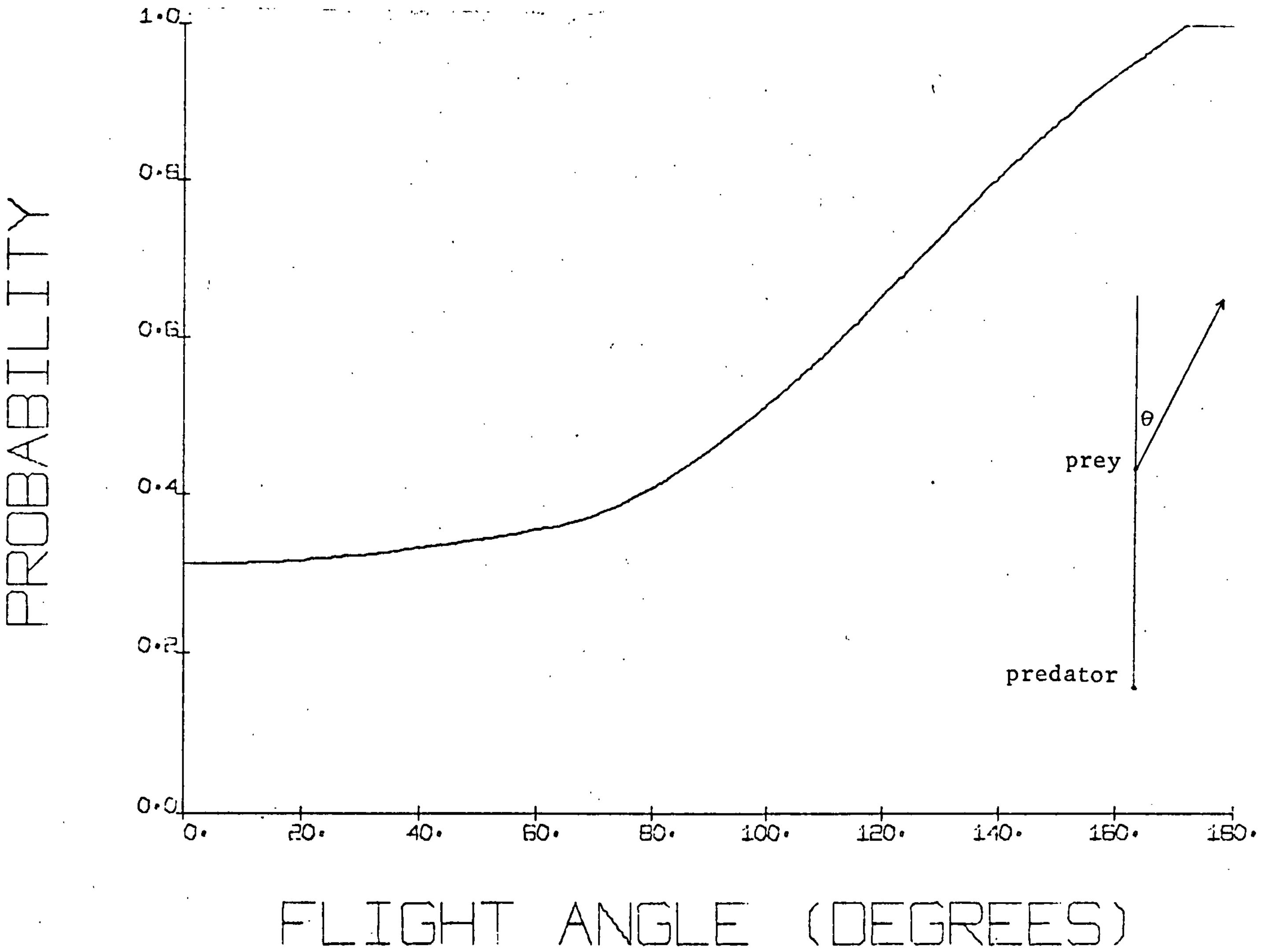
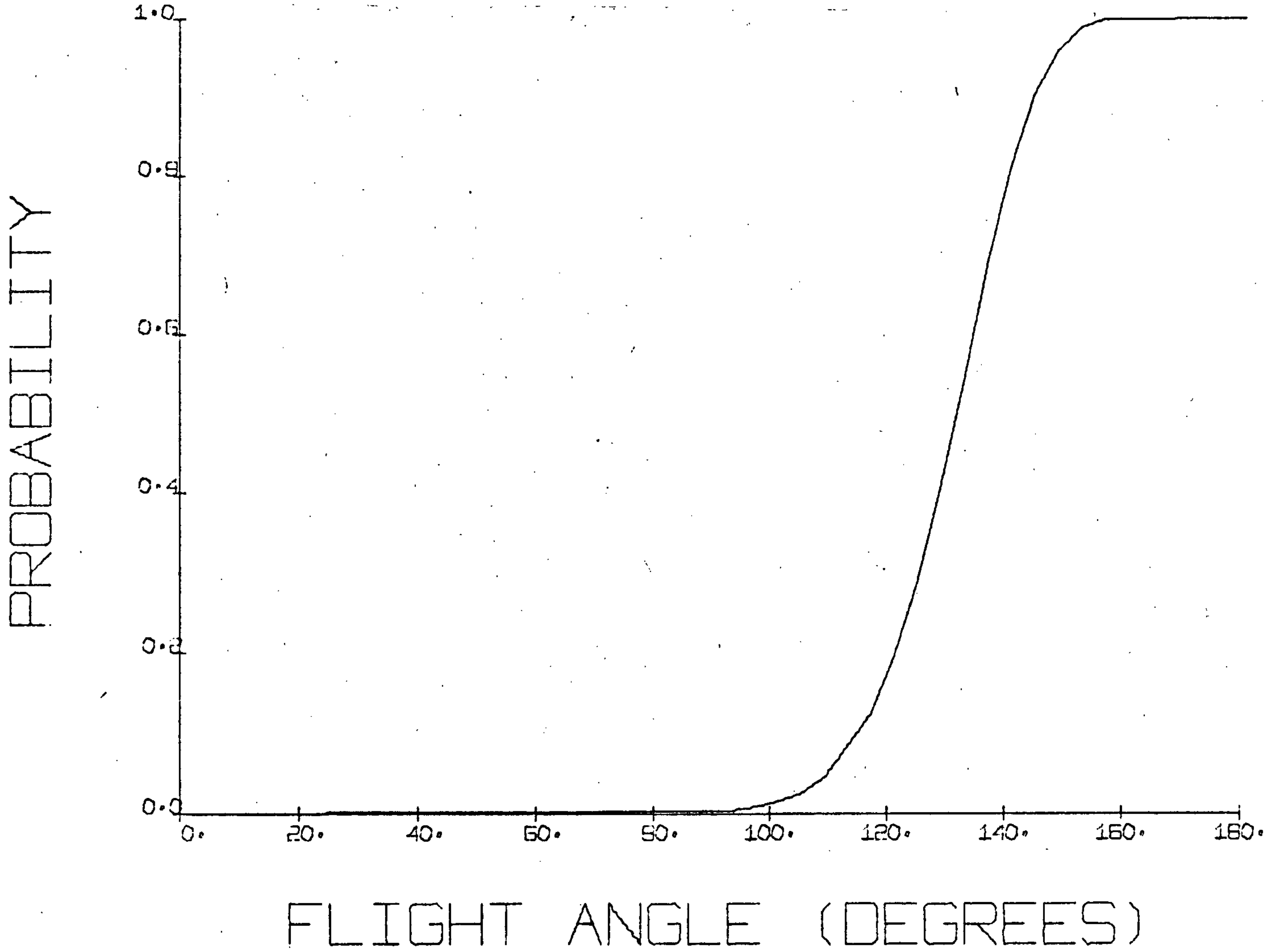


Figure 29. Thomson's gazelle - effect of prey flight angle upon attack success; initial lion-prey distance=75'; initial prey and predator velocities=0.0; zero slope



acceleration to overtake the more slowly accelerating prey before that prey can outdistance the lion. Simulated matching of the velocity curves of predator and prey (real and theoretical) elucidates the action and interaction of five tactical and strategic variables: initial predator-prey distance, slope, initial velocities, flight path restrictions, and prey species (that is, prey velocity curve parameters).

STALK AND ATTACK COMBINED

The Visual Detection Equation for the Wildebeest and Examination of the Validity of the Stalk and Attack Models

The intent of this section is to determine the effect of adaptation, the constant relating the optical stimulus of a lion to the visual threshold of the wildebeest (equation 3), and finally to examine the validity of the attack and stalk models. The first step is to define the mean detection distance for a lion run stalking at night. This prey capture situation involved the lion directly approaching the prey, and upon detection, the prey fleeing directly away (as shown for the case four attack, slight variation here will have little effect). Although it was not possible to see the precise mechanics of the attack at night, it is probable that detection of the predator by the prey (and its flight) is the initiating mechanism for the attack. This seemed to be true in the day, and would give the maximum attack success.

The probability of capture success (PC) for the nocturnal situation can be easily described knowing the probability of the prey detecting the predator and fleeing (PF(D)) and the probability of attack success (PA(D)) at a given distance (D):

$$PC = \int_{D=0}^{\infty} PA(D) * PF(D)\, dD \qquad (20)$$

In this instance PC can be calculated from the data, PA has been defined (case two), and PF is the unknown. The probability of detection (PF) is dependent upon two features, the mean and the variance. Furthermore, the initial attack velocity of the lion (estimated from field observations as 10 to 25 feet per second) was not known previously. The variance of PF is calculable from the pseudo-predator data, but only with some error prior to the determination of the effect of adaptation. An extensive series of iterations was necessary to account for all three unknowns, but eventually it was possible to derive best fit estimates. Starlight stalks of wildebeest led to 23.5 per cent capture success. This corresponds to a mean detection distance of 140 feet. Moonlight stalks of wildebeest led to 16.7 per cent capture success which corresponds to a mean detection distance of 177 feet. (The standard deviation of vision was taken as 37.9 feet and the initial lion velocity as 20 feet per second).

The above two values plus the pseudo-predator data provide a complete range of light conditions for wildebeest visual perception. In order to relate the two night values to the dirunal values, it is necessary to establish an equivalence between the illuminance readings of the foot candle-meter and changes in field brightness. Middleton (1952) gives the luminance of the sky near the horizon on a clear day as 10^4 candles per square meter. The foot-candle meter gave an illuminance of about 10^4 foot-candles. Middleton's other daylight luminances are also of similar magnitude to the illuminances recorded by the foot-candle meter. Thus from his tables, it can be determined that starlight would be expected to yield 10^{-4} foot-candles, and average moonlight (about half-moon) $5.0 * 10^{-3}$ foot-candles. The true value of field brightness (as the determinant of adaptation) is assumed to be directly related to the foot-candle values.

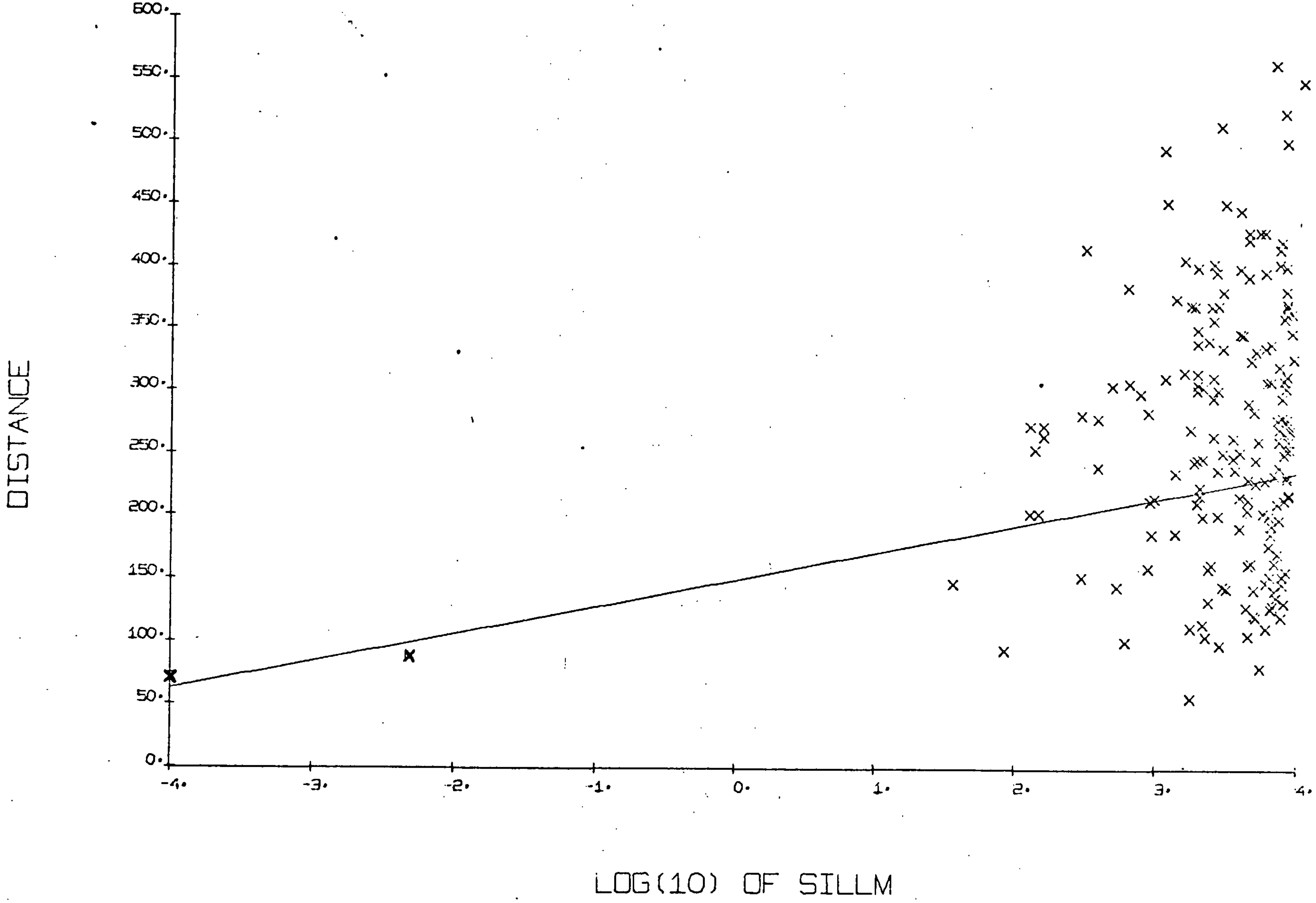
The stimulus equation (3) has four variables and this tends to obscure the relation between detection distance and field brightness. A first step then is to convert all the data to a common area and reflectivity difference. The frontal area and reflective difference of a lion in zero cover was arbitrarily chosen. This newly defined set of data (which has stimuli of similar magnitude to the old stimuli, but differently formed) is ideal to clarify the relationship between field brightness and threshold detection distance, although the variance is distorted by this procedure. These data are plotted in Figure 30 and it can be seen that the distance appears to be linearly related to the logarithm of the field brightness (ln(SILLM). A second feature to note is that the slope of the adaptation line (this is the line which will result from equation 21) is sufficiently shallow that including a possibly inaccurate affect for adaptation in the detection equation will introduce very little error into the predictions of the equation for diurnal conditions. In so far as adaptation is correctly represented, however, inclusion in the equation will allow investigation of what is happening during nocturnal stalking -- a case of nothing to lose and possibly considerable to gain.

A linear relationship suggests the following equation:

$$D = B * \sqrt{AREA * |RFPRD - RFCOV|} * (\ln(SILLM)) + CONS)$$

where B and CONS are constants and the other symbols are as previously defined. The unconverted wildebeest data were fitted with this equation using the least squares procedure, and the resultant equation was:

Figure 30. Effect of field brightness (SILLM) upon wildebeest vision - detection data



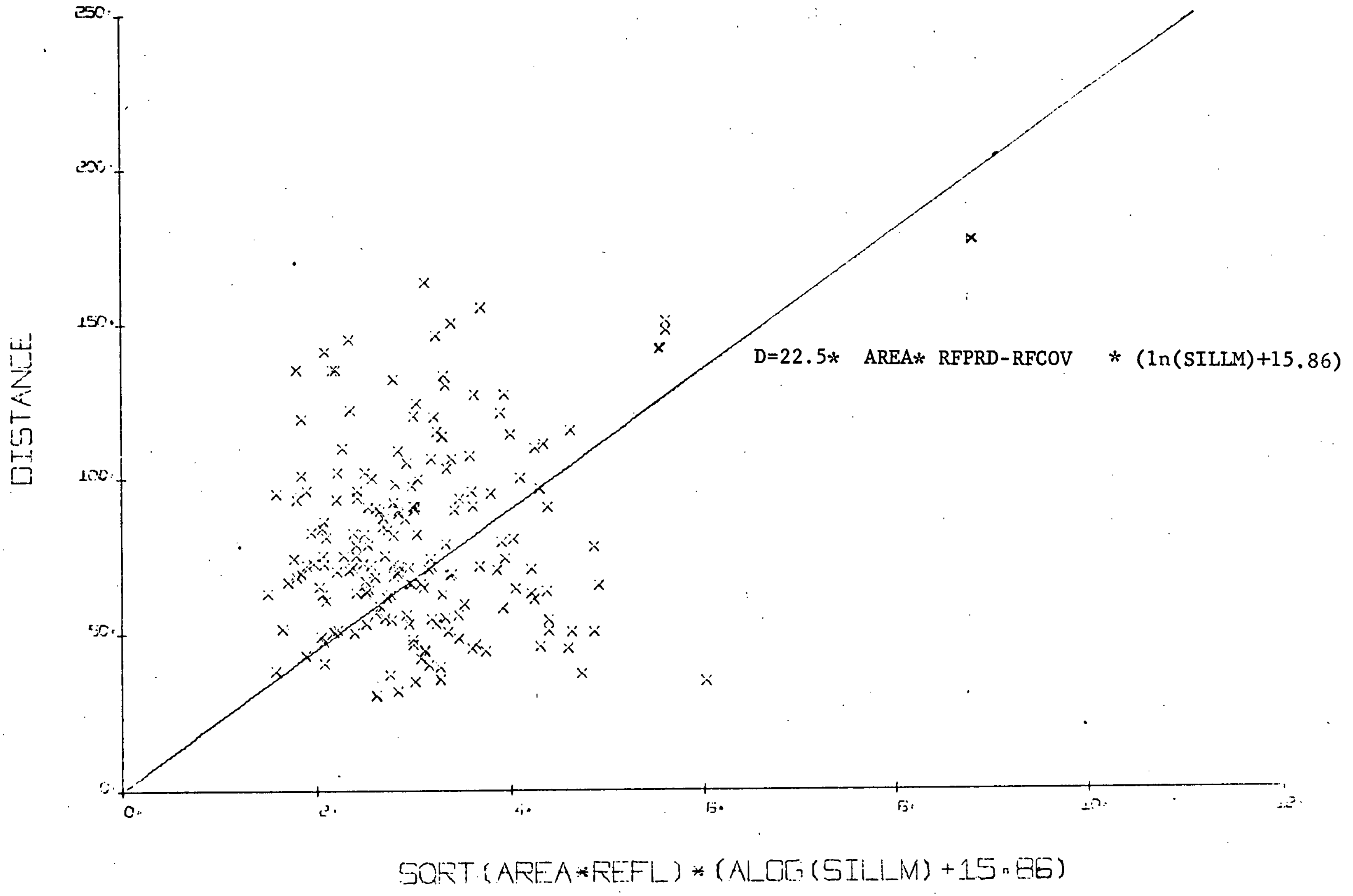
$$D = 22.5 * \sqrt{AREA * |RFPRD - RFCOV| * (\ln(SILLM) + 15.86)} \qquad (21)$$

with a standard deviation of 37.9 feet. There were 184 data points from the diurnal pseudo-predator data and only two from the nocturnal stalk data. These latter two involved 105 wildebeest stalks, and so should be weighted to increase their importance. Since they are less accurate than the other data, they were weighted (arbitrarily) only 40 times more than each pseudo-predator value. Equation (21) represents equation (3) rearranged with constants and the effect of adaptation for wildebeest included. Figure 31 illustrates the fit of the data to the line. While the range of the values on the abscissa is rather limited, the fit is satisfactory.

Variability of the visual threshold is a feature of all studies of vision (Hecht et al, 1942). Several workers (Mueller, 1950; de Vries, 1943; Blackwell, 1946) have used the normal distribution to describe this variability and this would appear applicable to the wildebeest data (PF(D)). However, where the mean value of D is low, it is necessary to use a truncated normal distribution (Hald, 1952).

It is desirable to compare the predictions of the detection equation (21) with the observed data from actual hunts. The nocturnal data can be seen from Figures 30 and 31 to be described quite well. Specifically, the expected probability of success for wildebeest in starlight is 28 per cent and in moonlight is 12 per cent, which are similar to the observed values of 23.5 and 16.7 per cent respectively. However, these data were used in the formulation of the equation and so do not represent a new test.

Figure 31. Linearized form of wildebeest vision - detection data



The diurnal crouch and sneak-crouch data are more interesting as it was not used in the previous formulation. Unlike the nocturnal run-stalk, these diurnal stalks do not involve such a distinctly direct stalk approach. The basic situation was one of the lion hidden in a good cover area and the prey approaching from outside of this area. The approach towards the cover (and the food or water resources generally associated with it) may or may not be directed at the point where the lion is hidden. Once the animals reached their objective in the cover, they tended to move laterally within the cover. Only in unusual circumstances did single wildebeest approach good cover areas, thus this lateral movement was not so much a single animal moving through the cover but was a spreading of a group of animals to facilitate utilization of resources. If the prey had not approached the predator directly, then the lateral spreading of the prey group served to reduce the predator-prey distance. Movements by the predator during the sneak-crouch stalk also serve to have this effect. There seemed to be two basic possibilities: either the prey moved to the cover but then moved out again soon thereafter, or the prey lateral movements were extensive. Since attack seemed to be initiated almost exclusively by flight of the prey (presumably after detecting the lion), the first case generally resulted in no attack unless the initial prey location happened to be near the lion's location. The result of these behaviour patterns of the prey is that there are some stalk situations which result in no attack and others in which the predator-prey distance becomes progressively less until eventually the prey detects the predator and flees. The stalk situation reduces, therefore, to approximately a direct approach situation plus some stalks which do not yield an attack situation. This was in fact the situation found (see Table XIII). The capture success which can be calculated from the detection and attack models as developed, refers only to those stalks resulting in decreasing predator-prey distance. It will not include those stalks failing due to what were previously termed random factors. It can be assumed to include the effect of cubs and other lions. These animals were near the stalking lion thus their effect would tend to have roughly the same distribution with distance as that due to detection of the stalking lion. In the case of mixed wildebeest and zebra herds where no extensive attack occurs, it must be assumed that the flight distance is due to the wildebeest alone. Subdivision of the field data using all of the above criteria gives an observed capture success of 38.9 per cent (sample size of 54).

The expected probability can be calculated from equation (20) where PF is based upon the truncated normal distribution of equation (21) and PA is determined as a "case one" attack. The effect of field brightness is slight for the range involved diurnally and is assumed to have been 5000 for all hunts. Cover is more difficult to derive.

It was never possible to measure the precise amount of lion exposed, but in many cases the approximate cover type could be ascertained. The cover height in the area was then measured as described in the methods. These measurements are of limited usefulness though since many of the cover heights are greater than 1.42 feet (the height at which "theoretically" the lion can never be seen). This feature was noted above in the section on the lion stimulus. It was indicated that the lion seems always to try to keep the prey in sight, and thus no matter how tall the cover, some of the lion is still visible. A number of stalks occurred in 15 inch and greater cover, but shorter cover yielded very few stalks. Although this could be an artifact of the study area, it does suggest that cover down to about 15 inches is quite satisfactory, and that this height is likely near to the "effective maximum cover". Presumably the "effective maximum" would be slightly higher than the lower limit of frequent cover, so it is assumed that 1.3 feet represents the true value and that this was the usual value for cover in the diurnal stalks observed. Figure 32 shows the expected probability of detection (and therefore flight) based on these assumptions.

The expected probability of capture can now be easily calculated, and is found to be 38.5 per cent (Figure 33). This is satisfactorily close to the observed value and supports the validity of the attack and stalk formulations. This also strengthens the notion that vision is the primary sense used by the prey to detect lions.

The Effect of Angle and Species upon Visual Detection

The discussion above was based upon the premise that the effect of the angle of orientation of the prey was insignificant to its ability to detect the prey. The best method of examining this feature would be to have data for the entire range of natural field brightnesses for each angle. Regression equations for each could then be determined and tested for similarity. Such a procedure is of little use for the restricted diurnal range available.

Figure 32. Average diurnal Munge conditions, cumulative probability of wildebeest detecting and fleeing lion

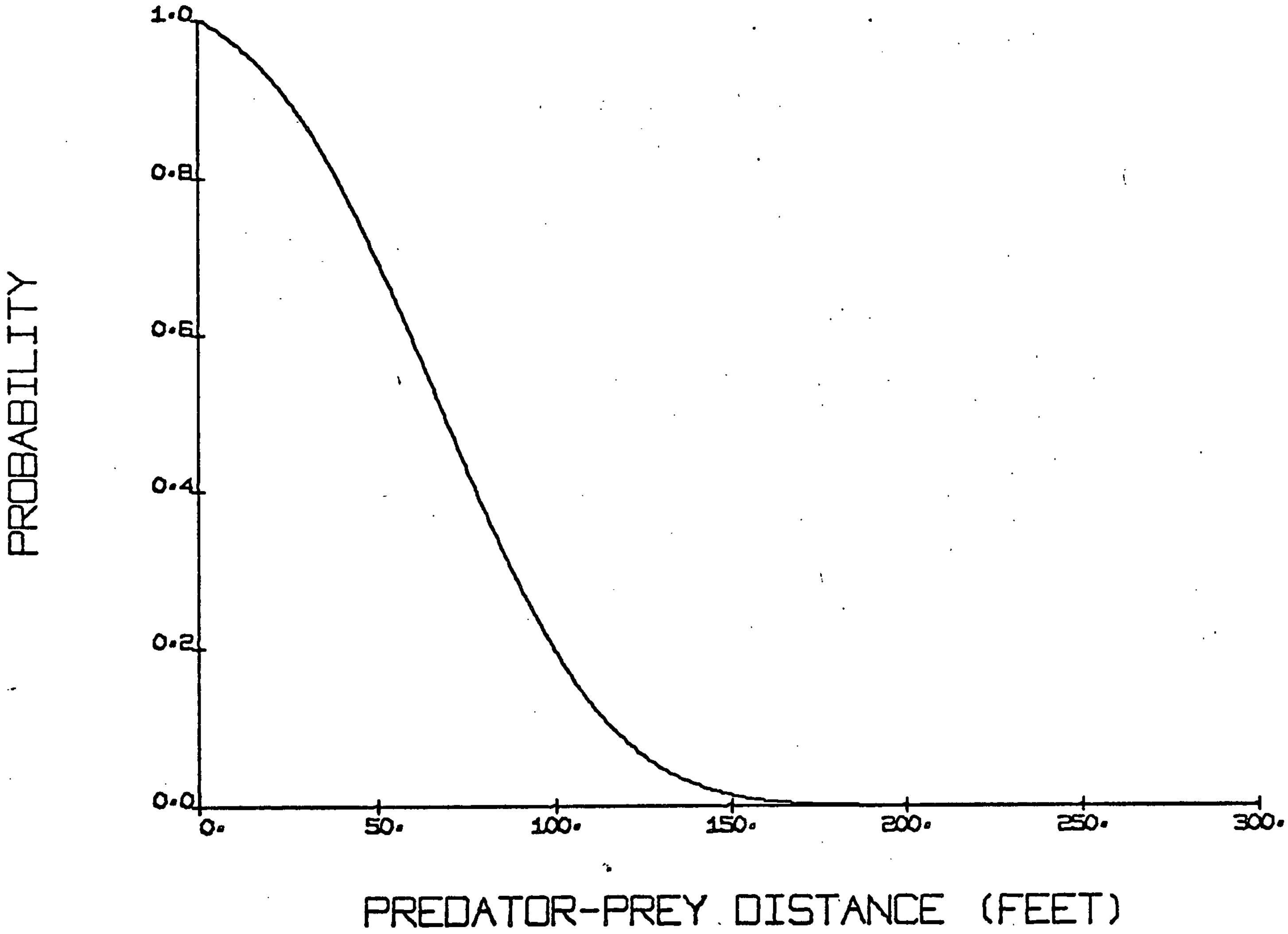
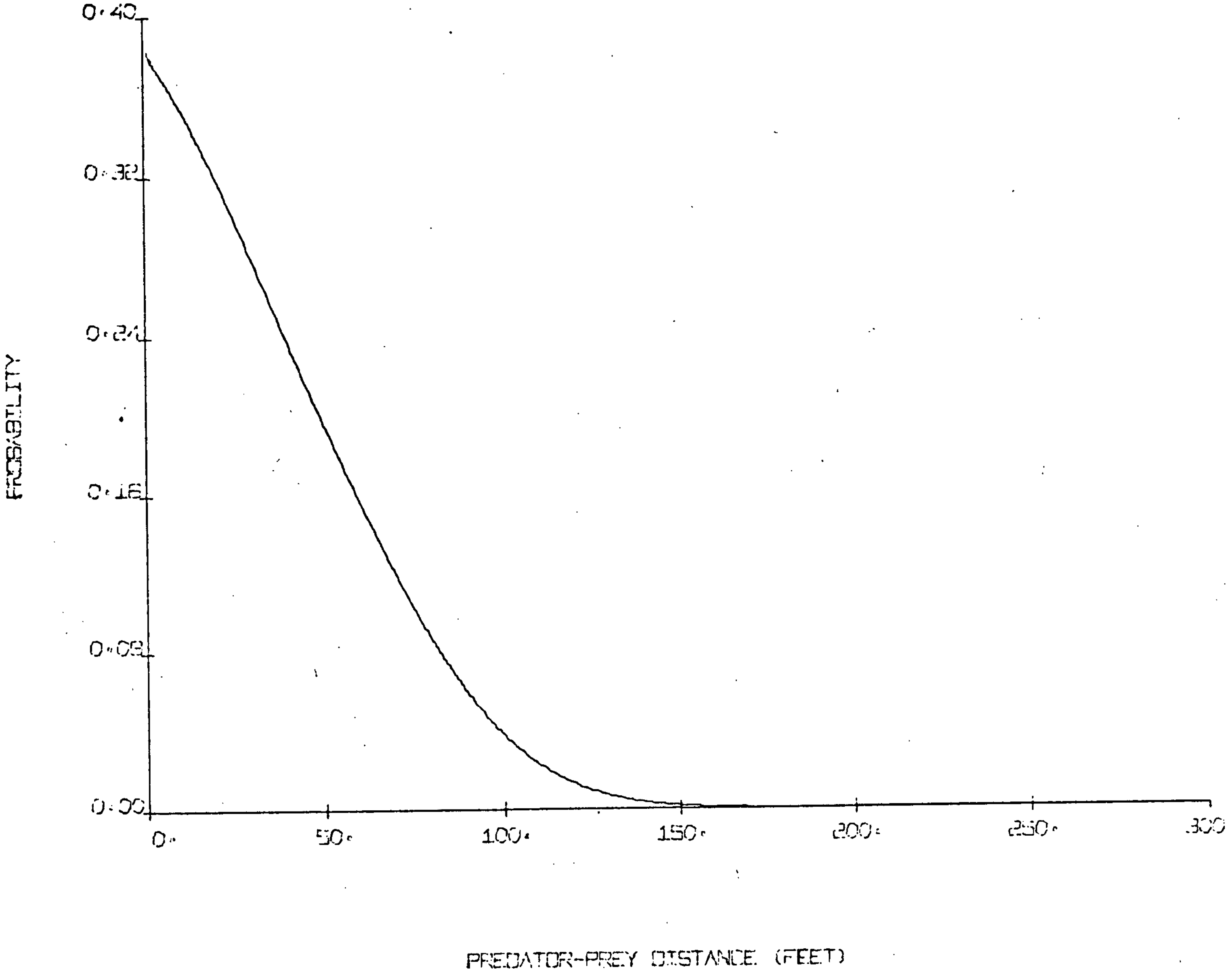


Figure 33. Average diurnal Munge conditions success probability cumulative ogive



All that can be done is to compare the diurnal abilities for each angle. Since the effect of field brightness is slight for the pseudo-predator data, the detection ratio ($\frac{D}{\sqrt{AREA * |RFPRD - RFCOV|}}$) should be nearly constant (except for the inherent variability of vision). The value of this ratio can, therefore, be compared for the different angles of orientation. Table XLVIII summarizes this analysis for the wildebeest and Tables XLIX, L, and LI give the same information for zebra, Thomson's gazelle, and Grant's gazelle, respectively. It can be seen that no species shows any significant effect in this regard. Furthermore, there is no consistent pattern for the four species.

Differences in the detection abilities of the different species can also be tested with the detection ratio (see definition above). This analysis is summarized in Table LII, and it can be seen that there is a significant effect due to species. It would also be expected (Walls, 1963) that adaptation to field brightness would differ from species to species. Since insufficient nocturnal stalk data is available for species other than wildebeest, this cannot be evaluated.

It is possible to use the pseudo-predator data for zebra to derive the probability of capture success for the diurnal situation as was done for the wildebeest. Because the effect of adaptation is not known, a modified approach is necessary. Table LII gave the diurnal detection ratios for the different species and since the mean diurnal detection ability of the wildebeest can be calculated from equation (21), it is possible to calculate the value for any of the other three species by proportions using the detection ratios.

TABLE XLVIII. Wildebeest: Effect of angle of orientation upon the diurnal detection ratio

ANGLE (degrees)	SAMPLE SIZE	MEAN RATIO	STANDARD DEVIATION
0.0 - 2.5	13	942.	520.2
2.5 - 7.5	6	692.	278.4
7.5 - 12.5	10	722.	225.9
12.5 - 17.5	21	679.	263.7
17.5 - 22.5	18	569.	233.9
22.5 - 27.5	8	659.	317.0
27.5 - 32.5	11	795.	324.5
32.5 - 45.5	46	622.	684.0
45.5 - 62.5	28	684.	294.8
62.5 - 72.5	11	634.	249.7
72.5 - 90.0	12	707.	235.4

F-ratio = 1.718

Probability of the angles being representative of the same population = 0.08

TABLE XLIX. Zebra: Effect of angle of orientation upon the diurnal detection ratio

ANGLE (degrees)	SAMPLE SIZE	MEAN RATIO	STANDARD DEVIATION
0.0 - 2.5	34	984.	406.1
2.5 - 7.5	9	849.	528.6
7.5 - 12.5	22	852.	361.8
12.5 - 17.5	24	946.	836.5
17.5 - 22.5	12	968.	445.9
22.5 - 27.5	10	982.	262.2
27.5 - 32.5	17	806.	308.2
32.5 - 45.5	33	926.	370.6
45.5 - 62.5	29	804.	348.7
62.5 - 72.5	14	812.	420.8
72.5 - 90.0	15	770.	426.4

F-ratio = 0.903

Probability of the angles being representative of the same population = 0.5317

TABLE L. Thomson's gazelle: Effect of angle of orientation upon the diurnal detection ratio

ANGLE (degrees)	SAMPLE SIZE	MEAN RATIO	STANDARD DEVIATION
0.0 - 2.5	14	736.	213.2
2.5 - 12.5	11	1062.	460.2
12.5 - 17.5	13	869.	257.4
17.5 - 22.5	12	934.	346.2
22.5 - 27.5	13	780.	286.0
27.5 - 32.5	17	844.	883.5
32.5 - 45.5	36	814.	357.7
45.5 - 62.5	31	770.	290.4
62.5 - 72.5	26	872.	358.4
72.5 - 90.0	13	1047.	543.2

F-ratio = 1.488

Probability of the angles being representative of the same population = 0.1556

TABLE LI. Grant's gazelle: Effect of angle of orientation upon the diurnal detection ratio

ANGLE (degrees)	SAMPLE SIZE	MEAN RATIO	STANDARD DEVIATION
0.0 - 2.5	17	746.	440.3
2.5 - 12.5	12	954.	400.5
12.5 - 17.5	10	651.	336.9
17.5 - 22.5	8	603.	281.7
22.5 - 27.5	11	778.	431.0
27.5 - 32.5	13	656.	535.0
32.5 - 45.5	39	667.	301.5
45.5 - 62.5	32	682.	271.5
62.5 - 72.5	22	792.	474.8
72.5 - 90.0	17	644.	285.3

F-ratio = 1.030
Probability of the angles being representative of the same population = 0.4180

TABLE LII. Effect of species upon the diurnal detection ratio

SPECIES	SAMPLE SIZE	MEAN RATIO	STANDARD DEVIATION
wildebeest	184	680.	302.2
zebra	219	888.	371.9
Thomson's gazelle	186	854.	347.4
Grant's gazelle	181	711.	371.9

F-ratio = 16.774
Probability of the species being representative
of the same population is less than 0.0001

Likewise, the variance can be calculated by proportions using Table LII. If this is done and an analysis similar to that for the wildebeest is undertaken, then it is found that the expected probability of success for zebra is 31.1 per cent (using the same criteria as outlined for wildebeest). The actual prey capture situation resulted in 29.2 per cent success (sample size of 48). This success is based upon those animals which were overtaken, and does not include subduing failures (see next section). The closeness of the expected and observed values lends further support to the theory developed.

The same calculation can be made for Thomson's gazelle, but would not represent the actual situation which occurred. It has been shown during the discussion of the stalk that a difference existed for gazelle as contrasted to zebra and wildebeest. This was shown to be evident in terms of the stalk time. The important question is, why were the stalk times different? The reason is that if the lion were to use the same strategy that it generally uses for the two larger prey, (that is, the case one attack -- direct approach, zero initial velocity, and direct flight), then it can be calculated (using the same technique as for the wildebeest and zebra) that the expected probability of success would be only 7.0 per cent. The case one attack involved a lot of waiting on the part of the lions while the prey gradually wandered into a suitable attack position. The lions were observed during this study to often ignore Thomson's gazelle which could have presented possible case one attacks had the lions remained hidden or sneak-crouch stalked. Case four attacks, however, take less time because the features restricting the prey's flight path also (generally) provide good stalk cover. As noted, case four attacks are particularly effective for the lion when gazelle are the prey and the field observations indicated that case four attacks were indeed quite frequent for gazelle. Important in this regard is the fact that the escape route of Thomson's gazelle was more easily restricted because they were less prone (probably due to their shortness) to flee through even medium length vegetation, than were the two larger prey. This explains both the increased success (39.1 per cent of a sample of 23 crouch and sneak-crouch diurnal stalks excluding random failures) and the reduced stalk time.

Another means by which the lion improved success for gazelle was to use the run stalk more frequently for the gazelle, and it has been shown -- case two attack, that this is most beneficial to the lion when gazelle are the prey.

Synopsis

It is possible to satisfactorily describe the lion-detection threshold (mean and variation) of wildebeest vision with a simple extension of standard photometric laws in order to include the effect of adaptation. This model when combined with the attack model (case one) satisfactorily predicts the observed diurnal stalk/attack success for wildebeest prey capture. Likewise when combined with the case two attack model, it predicts the observed nocturnal success for wildebeest (however this data was used in producing the detection model).

The angle of orientation of any of the four studied prey to the predator does not significantly effect the detection ability. Detection does vary with species however.

The detection and attack (case one) models satisfactorily predict diurnal stalk/attack success for zebra but at present cannot be extended to include the nocturnal stalk.

A basic difference in the tactics of the lion is noted for gazelle as opposed to wildebeest and zebra prey capture. This is essentially due to the need of the lion to counteract the strategic advantage afforded the gazelle by their high VMAX velocity curve. The result of the new tactics is to raise success from an expected 7 per cent, if wildebeest and zebra tactics were used, to an observed 39 per cent.

SUBDUING PREY

Success in subduing prey is largely dependent upon prey size. Indeed this feature alone can serve as an adequate defence strategy for certain prey species. The largest species: elephant (Pitman, 1945), rhinoceros (Goddard, 1967), and hippopotamus (Boulière and Verschuren, 1960) are rarely captured except for young individuals. Likewise, Hornocker, (1970) suggested that the size of an adult elk was responsible for the high proportion of calves taken by mountain lion. Medium large prey such as buffalo (Wright, 1960; Mitchell, Shenton, and Uys, 1965; Kruuk and Turner, 1967; Pienaar, 1969; Schaller, 1972) are frequently taken but probably require more than one lion in most cases. During this study a single male buffalo was seen to attack two hungry female lions, and several times small groups of three to five male buffalo scattered entire prides of lions. Day (1969) and others report lions killed by buffalo.

Lesser sized prey depend not upon their ability to outmatch the lion at the subduing stage, but instead attempt to evade the lion during the stalk, attack, and in some cases even search phases. The subduing phase can still be important, however. It may occur as with the larger prey due to a stopped individual temporarily outfighting the lion and escaping. One example involving a zebra (out of 14 successful attack contacts witnessed during continual diurnal observing) which had been knocked to the ground was of this type. Numerically more important is a subduing failure resulting from the lion being unable to down prey which is still fleeing after the attack has resulted in predator-prey contact. This situation is one where the lion has leaped at the prey, but is then shaken free. This was observed three times for zebra (out of the above 14 successful contacts). Likewise, an adult male wildebeest very nearly succeeded in dislodging a lion during one observed attack in this study. Eloff (1964) describes a case where a gemsbok (*Oryx gazella*, 450 pounds) successfully flung off a lion.

The above observations suggest that subduing prey is: unimportant for prey wildebeest and smaller in size; yields 28.6 per cent failure for otherwise successfully attacked prey of zebra size; and is of even more importance for larger prey.

It should be noted that the attack cases discussed under the section on the attack all calculated success in terms of overtaking the prey and did not include subduing.

INTRASPECIFIC PREY CAPTURE SELECTION

If sufficient information were available then the effect of age, sex, and condition of prey would have been incorporated at each phase of analysis of prey capture. In lieu of this, it has been assumed that in general all individuals of a species are equivalent or at least can be described by normal distributions. (Young individuals were excluded from the attack data). The validity of this can, to some extent, be examined from the final capture data (kills). This analysis is undertaken in the Appendix. It is found that for the present purposes: the age (excepting very young), sex, and condition (excepting very poor) of an individual does not have a major effect upon the probability of its being captured.

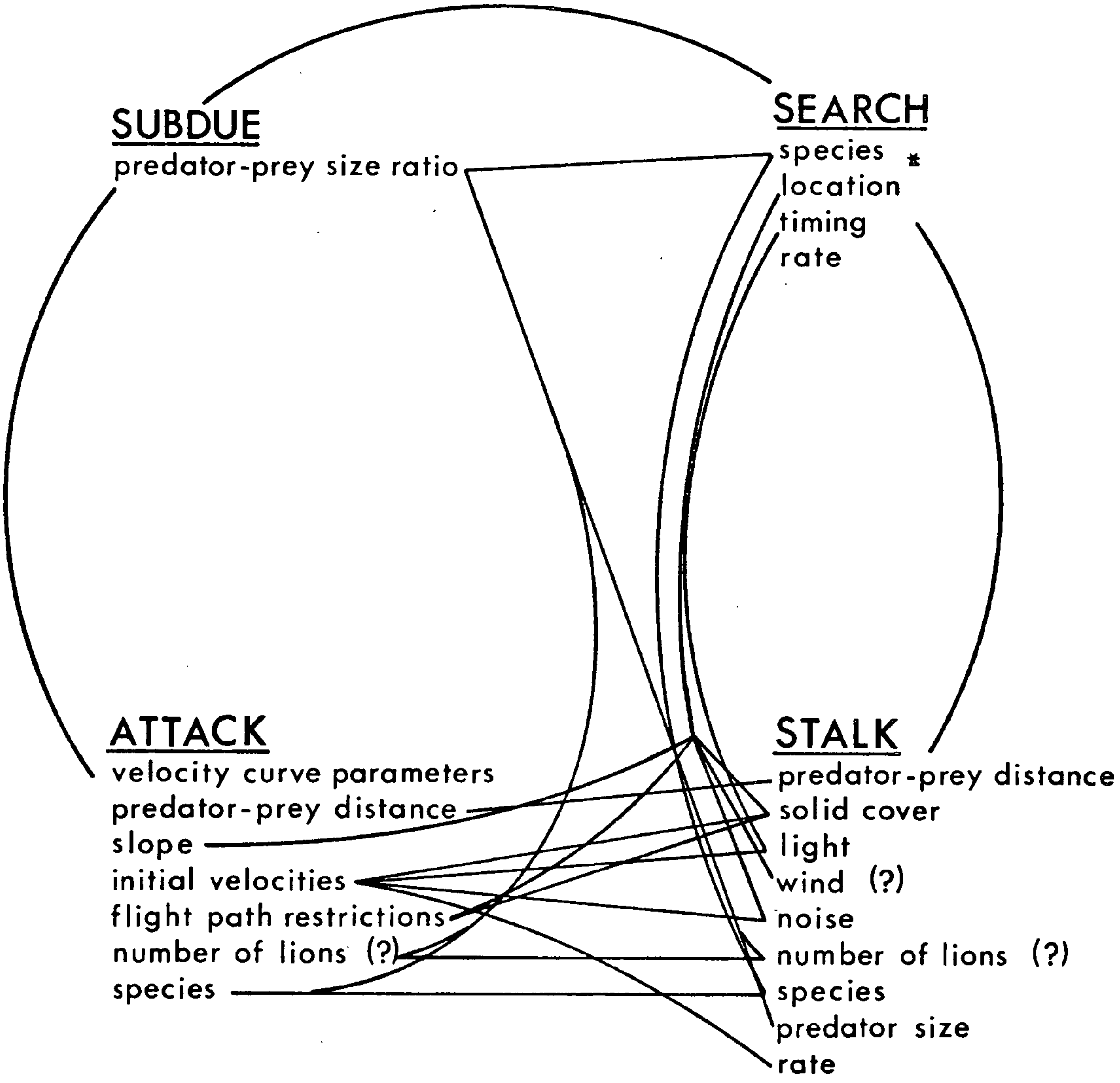
CONCLUSION: THE LION AS A STRATEGIST AND TACTITIAN

The aim of this study has been to define the strategy and tactics of prey capture by the lion. Lack of detailed analysis of prey activities does not allow the use of these to simulate the complete prey capture cycle; however an interesting pattern has been revealed. It is found that the lion is able to adjust its strategy and tactics at each phase of prey capture so as to achieve a consistently high overall capture success with different prey and conditions.

Figure 34 summarizes the strategic and tactical variables which affect the success of each event of prey capture by the lion. In addition, the central mesh of lines in the Figure (34) join variables which are related (or identical) in different events. Since improvement for one event may reduce success for another, the values of these variables for the different events must be "balanced" by the lion so as to provide maximum overall success.

Two of the variables, predator size and the velocity curve parameters, in Figure 34 differ from the others. While most of the variables can take a wide range of values, these two take only a very limited range for a given predator (species and especially individual). As a result, these two define the basic strategy of prey capture by the lion. Firstly, prey is only captured within a specific size range with the upper limit defined by the ability to subdue prey (although the number of predators can be increased to allow some raising of this limit) and the lower limit defined by

Figure 34. The strategic and tactical variables affecting the success of prey capture events.*


SUBDUE
predator-prey size ratio
SEARCH
species *
location
timing
rate
ATTACK
velocity curve parameters
predator-prey distance
slope
initial velocities
flight path restrictions
number of lions (?)
species
STALK
predator-prey distance
solid cover
light
wind (?)
noise
number of lions (?)
species
predator size
rate

*internal lines join related or identical variables in different events.

* within the pride area

energetic efficiency. Secondly, most prey capture involves the lion utilizing its high acceleration to overtake more slowly accelerating prey before that prey can outdistance it. For a given prey capture situation, specific tactics based upon adjusting the values of the remaining variables are employed in order to achieve maximum or at least "satisfactory" success for the basic strategy as defined by the velocity curve and within the prey size limitations. (A third variable, search rate, could be considered basic; however, for the lion much of the searching is dependent upon movement by the prey. Also the length of halts during active searching causes the search rate to vary considerably).

In addition to the usual velocity curve strategy of the lion, two other velocity curve strategies have been identified. Pursuit by lions of very young or enfeebled prey (also the usual hyaena and hunting dog attack situation; unpublished data) involves the greater stamina of the predator allowing it to overtake a fatiguing prey. A second type, not specifically identified for the lion (although possible for some young prey) but common for the cheetah (unpublished data) involves a greater VMAX for the predator allowing the predator to overtake the prey before fatigue slows the predator. In general, it would be expected that any sympatric large fissipeds would differ in body size and/or velocity curves, with the possible addition of differences in search rate.

If body size and velocity curve parameters are the basic capture strategies of the lion, then it follows that the basic escape strategies of the prey are likewise body size (for example, buffalo) and/or velocity curve parameters (and possibly anti-search features). As regards its velocity curve parameters, the prey uses a variety of tactics to keep it beyond the range or situation where its velocity parameters would result in it "losing" in a race with a lion.

The interrelationships of the variables have been discussed in the previous sections. Briefly, search variables depend considerably upon prey characteristics and have been inadequately quantified; stalk variables (those identified as significant to success) operate as per equation (21); attack variables are complex and examples have been given in discussing attack cases one to four; and the subduing variable (relative prey size) has been considered in a general manner (see SUBDUING PREY). Because the lion must undertake activities other than prey capture, two associated variables are imposed upon prey capture: pride area restricts searching potential but reduces conflict for food and reproduction, and hunger-based thresholds serve to allot specific time intervals to these non-feeding activities.

The analysis presented here has been specific to adult lions. However the identification of the variables involved and hierarchical structuring of the prey capture process provide a useful framework for studies of prey capture by other large fissipeds.

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APPENDIX

CALCULATION OF INDIVIDUAL FOOD CONSUMPTION OF LIONS

Because the lion is not a common laboratory animal, there is little or no specific bioenegetic data available. This necessitates using values derived for other species, especially domestic livestock.

The majority of the energy losses of an individual can be grouped into five categories (Maynard and Loosli, 1962). These are listed below:

1. resting metabolism
2. growth by the individual
3. reproductive growth
4. activity, temperature regulation, and other environmental interactions
5. specific dynamic action

Age and sex have a strong effect upon the amount of energy loss for each of the five categories. The first step then is to derive the growth curve of the lion. Because only live, free-ranging lions were available during this study, no direct weights were obtained. Using adult lion weights obtained from elsewhere in East Africa (Meinertzhagen, 1938 and Schaller, 1972), the average weight for a female is 330 pounds and for a male 380 pounds. Visual observations of known age Ngorongoro lions indicated that they were near to full adult size at four years, and about two-thirds of adult size (220 pounds for females and 254 pounds for males) at two years. Schaller's (1971) estimates for the Serengeti lions are similar. Cubs born in zoos have an average birth weight of 2.9 pounds. At six weeks their average weight is 13.4 pounds (Crandall, 1964; Carvalho, 1968).

Beyond six weeks, weights of zoo raised animals are probably not applicable to wild lions.

Lacking a series of precise age and weight values for the lion, there is little point in developing an elaborate mathematical analysis for growth. A plot (see Figures A-I and A-II) of the four approximate values for each sex shows weight increasing with age up to a maximum -- first at a progressively increasing rate and then at a progressively decreasing rate. The inflection point in the curve occurs nearer to birth than adulthood. One of the simplest means of yielding this effect would be to assume that the rate with which the logarithm of weight changed with age was proportional to the difference between the logarithm of the present weight and the logarithm of the adult weight. That is,

$$\frac{d\ (\ln W)}{d\ t} = K'(\ln(W_{max}) - \ln(W))$$

where W is the weight, W_{max} is the maximum weight, t is time, and K' is the rate constant. Integrating yields

$$\ln(W) = \ln\ (W_{max}) * (1 - e^{-K't-C})$$

where "-C" is the constant of integration. This equation can be written in linear form, facilitating calculation of the two constants:

$$\ln\ \left(\frac{\ln(W_{max})}{\ln(W_{max}) - \ln W}\right) = K' * t + C$$

Figure A-1. Lion growth curve - Male

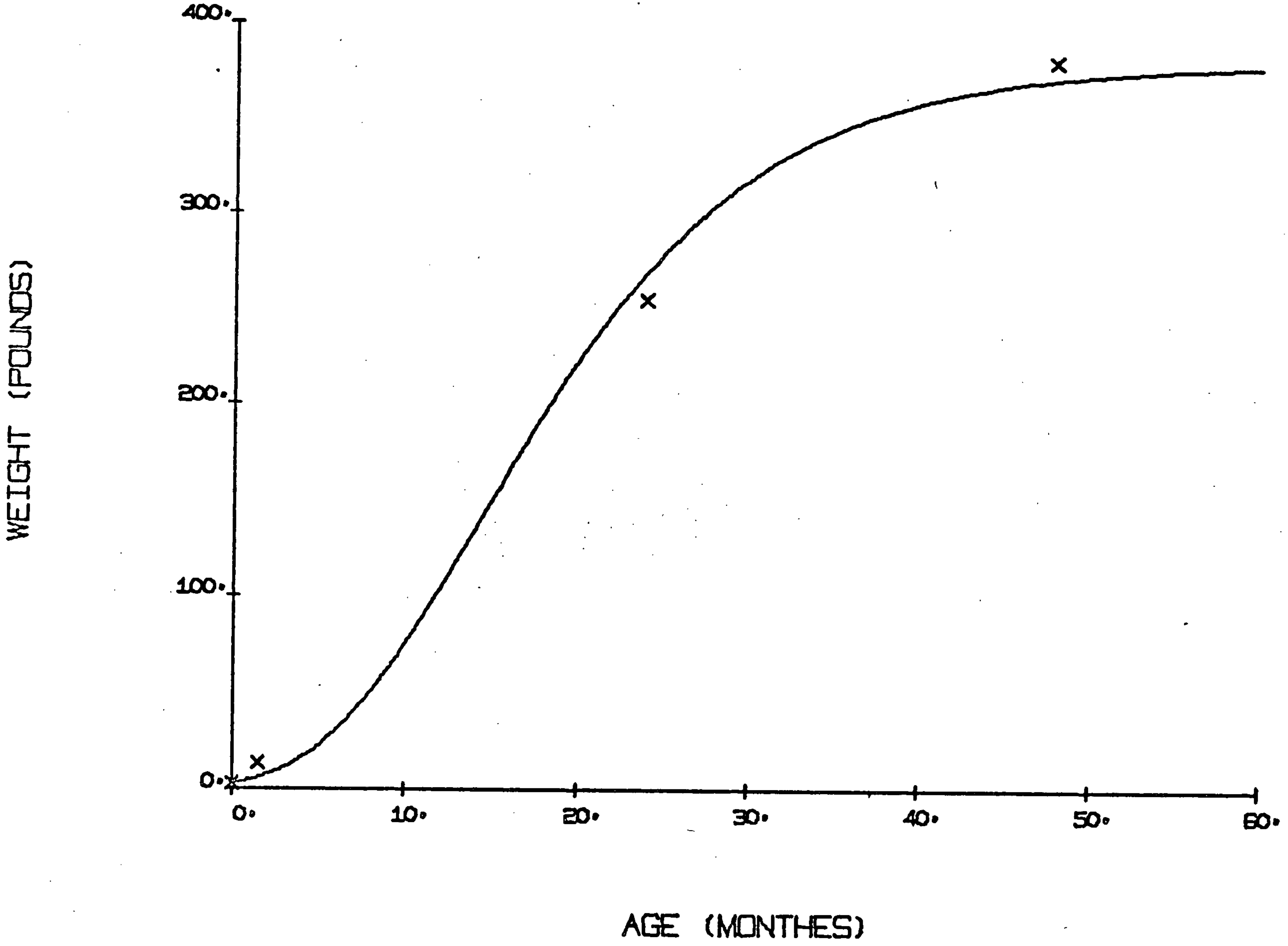
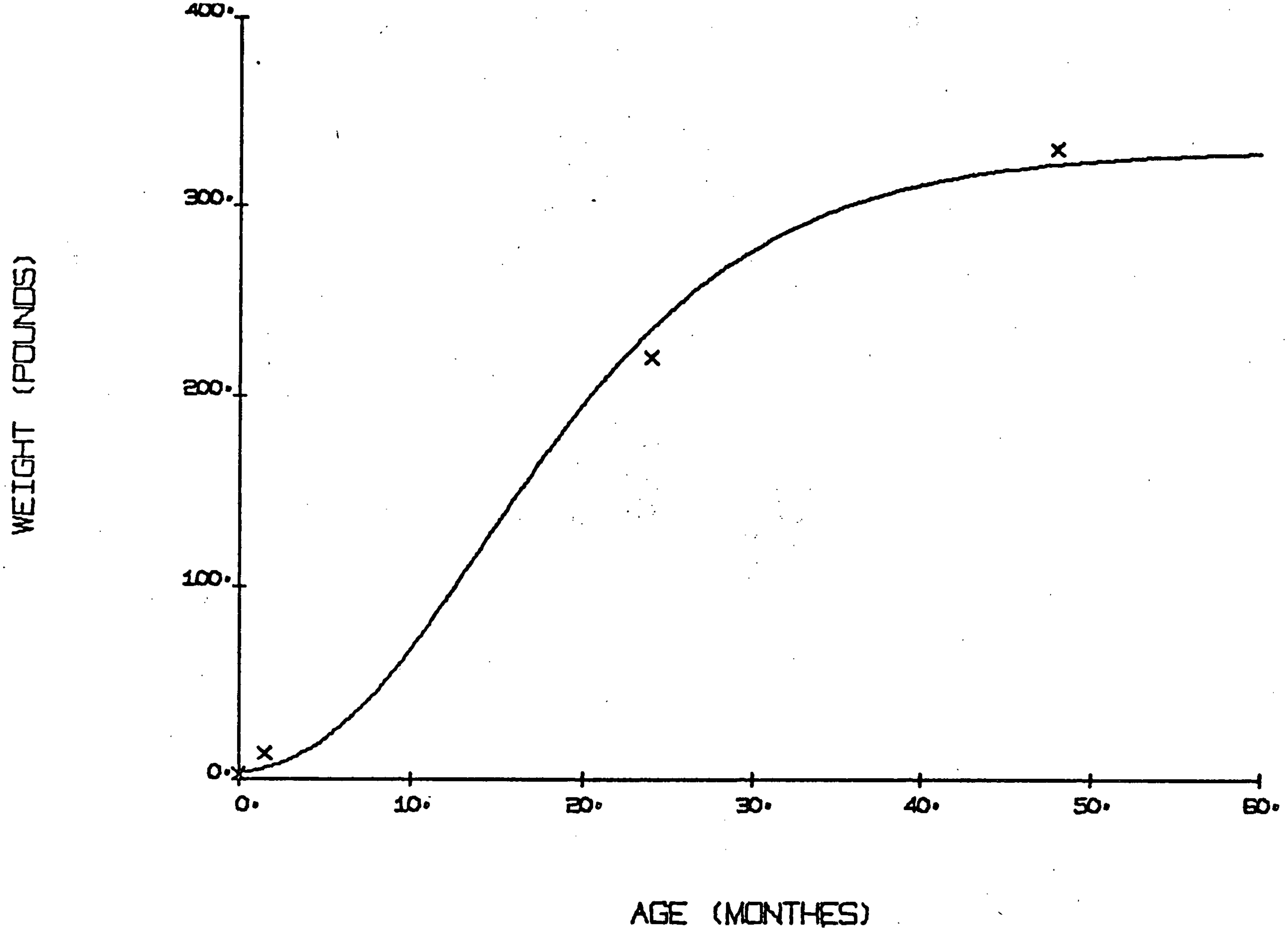


Figure A-11. Lion growth curve - female



This linearized equation is undefined if the weight equals the maximum weight. The fit must therefore be done with only the three submaximal weights. The values of K' and C for both the male and the female are then found to be 0.11 and 0.2 respectively: thus,

$$\ln (W) = \ln (W_{max}) * \left[1 - e^{-(0.11t + 0.2)}\right]$$

with weight in pounds and age in months.

Solving for weight yields,

$$W = W_{max}\left[1 - e^{-(.11t + 0.2)}\right]$$

This becomes for the male lion (Figure A-I),

$$W = 380\left[1 - e^{-(.11t + .2)}\right] \qquad (1)$$

and for the female (Figure A-II),

$$W = 330\left[1 - e^{-(.11t + .2)}\right] \qquad (2)$$

Now, as noted, these two equations are rather imprecise, but lacking better information for this aspect they must suffice. (The findings of Wood and Cowan (1968) for ungulate growth curves highlight the difficulties of trying to describe mathematically even well documented growth curves). An indication of possible validity is shown by the growth curves for the domestic cat which are similar in form to that predicted for the lion. (Gershoff, 1972; Scott and Scott, 1967; da Silva, 1950; Latimer and Ibsen, 1932).

Kleiber (1961) has found that a very consistent relationship exists between the weight of a mammal and its basal metabolic rate, that is, the resting metabolism of a non-growing, non-digesting animal in a thermoneutral environment (Brody, 1964). For such a case, the mathematical relationship between weight and basal metabolism is (Kleiber, 1961):

$$BMR = 70 * (WK)^{3/4}$$

or,

$$BMR = 39 * (WL)^{3/4} \qquad (3)$$

where BMR is the basal metabolic rate in kcal per day, WK is the body weight in kilograms, and WL is the body weight in pounds. This formula (3) will rarely ever describe the total metabolic expenditure of the lion. However, it should represent the category "resting metabolism" (a non-growing, non-pregnant, and non-lactating lion) (Brody, 1964). In terms of the various classes of lions, one obtains:

adult male: $BMR = 3357$ kcal/day (4)

adult female: $BMR = 3019$ kcal/day (5)

or in general for all ages,

$$\text{(male):} \quad BMR = 39 * 380^{3/4*\left[1-e^{-(.11t+.2)}\right]} \qquad (6)$$

$$\text{(female):} \quad BMR = 39 * 330^{3/4*\left[1-e^{-(.11t+.2)}\right]} \qquad (7)$$

where the symbols are as previously defined.

Forumlae (6) and (7) will, of course, never describe the total component of resting metabolism of young lions since these lions were assumed to be steadily growing, and in addition to the energy equivalent of growth, there is an associated growth metabolism which must be included in the resting metabolism. This is difficult to evaluate since the causal factors are multiple, but it can be assumed that the level of growth metabolism is directly proportional to the amount of growth occurring (Brody, 1964). There is no available value for the proportionality constant relating these two phenomena; however, using Brody's (1964) values relating metabolism of calves (Bos) and growing rats (both of which were fitted with a smooth growth curve similar to the one derived for the lion) to that of the adult, the maximum growth metabolism plus the basal metabolism is found to be approximately twice the value of the basal metabolism of an adult mammal of similar weight. The growth rate for lions under four years can be obtained by differentiating equations (1) and (2):

$$\text{(male):} \qquad \frac{dW}{dt} = .11 \ln (380) * 380^{\left[1-e^{-(.11t + .2)}\right]} * e^{-(.11t + .2)} \qquad (8)$$

$$\text{(female):} \qquad \frac{dW}{dt} = .11 \ln (330) * 330^{\left[1-e^{-(.11t + .2)}\right]} * e^{-(.11t + .2)} \qquad (9)$$

Both sexes show a maximum growth rate at 14 months.

The basal metabolism of an adult mammal with weight corresponding to that of each sex at the time of maximum growth can be calculated from the earlier formula (3):

(male: 14 months): BMR = 1536 kcal/day (10)

(female: 14 months): BMR = 1406 kcal/day (11)

The approximation noted above relating growth metabolism and basal metabolism at the time of maximum growth then leads to a similar pair of values for growth metabolism. That is, 1536 kcal per day for the male lion and 1406 kcal per day for the female lion at 14 months of age. Now the growth rate at 14 months can be determined from (8) and (9):

$$\text{(male):} \quad \frac{dW}{dt} = 15.4 \text{ lbs/month} = 0.51 \text{ lbs/day} \tag{12}$$

$$\text{(female):} \quad \frac{dW}{dt} = 13.4 \text{ lbs/month} = 0.45 \text{ lbs/day} \tag{13}$$

By comparing the values determined above for (10) and (12), and also (11) and (13), it is possible to define an approximate coefficient (CGM) relating growth metabolism to growth rate for the lion.

$$\text{(male):} \quad \text{CGM} = 3012 \text{ kcal/lb} \tag{14}$$

$$\text{(female):} \quad \text{CGM} = 3124 \text{ kcal/lb} \tag{15}$$

Combining the relations described by (6), (7), (8), (9), (14) and (15), the resting metabolism (RM, in kcal per day) for lions can now be determined. That is,

$$\text{RM} = \text{BMR} + \left[\text{CGM}\left(\frac{dW}{dt}\right) \div 30\right] \tag{16}$$

In addition to the energy required to formulate new growth, there is also the energy equivalent of the growth itself. Using Brody's (1964) value derived for cattle (909 kcal per pound of gain), the direct rate of energy of growth (GE) for lions is:

$$\text{GE} = 909 \frac{dW}{dt} \div 30$$

The energy requirement predicted by RM and GE (and taking account of SDA) shows reasonable agreement to the energy requirements found for growing domestic cats (Scott and Scott, 1967).

The adult female lion may have increased energy output associated with production of cubs. As with growth for young lions, this increased energy takes two forms: the work of gestation which increases with resting metabolism and the energy equivalent of foetal growth.

It seems to be true for all mammals that the total energy associated with the work of gestation can be described by a single formula (Brody, 1964):

$$Q = 4400\ M^{1.2}$$

$$= 1708\ WB^{1.2} \qquad (17)$$

where Q is the work of gestation in kcal, M is the birth weight in kilograms, and WB is the birth weight in pounds. Assuming an average litter size at birth of 2.5 (Schaller, 1972) and an average birth weight of 2.9 pounds (as previously noted) the value for the average work energy of gestation can be determined from (17):

$$Q = 18{,}410 \text{ kcal}$$

The gestation length for the lion is 110 days (Schaller, 1972) thus the average daily energy required for the work of gestation is 167 kcal.

The energy equivalent of the foetal growth itself must also be estimated. Assuming a further ten percent for the energy equivalent of the placenta and then utilizing the same factor as was used for postnatal growth, the total energy requirement will be 7250 kcal. The mean daily energy requirement for growth material is thus 66 kcal in the case of an average litter. There is little value in attempting to extend values for cows and the like to lactating lionesses. It is found for domestic cats that their energy requirement for lactation is very high (Scott and Scott, 1967) being about 7.5 times that of gestation. For the lion, this would yield a value of 1750 kcal per day.

The energy cost of activity and related aspects of environmental interaction cannot be estimated directly as has been attempted above for pre- and post-natal growth and resting metabolism. It will be necessary to consider this energy category as being equivalent to the residual energy after all other energy uses have been determined. The effect of age and sex upon energy requirements can only be generally determined. For the first year the activity of the cubs is largely related to that of the maternal lionesses and it will be assumed that the extra prey capture exercise by the adult females is balanced by the exercise in the form of play by the cubs. Adult males however are considerably more active than females and will be assumed to be twice as active. The energy cost of locomotion varies directly as the weight of the animal (Brody, 1964), thus:

$$\begin{aligned} A &= H * W * L \\ &= C * W \end{aligned}$$

where A is the energy expended for activity in kcal per day, L is the average level of activity, H is a rate constant relating A to L * W, and C is a constant equivalent to H * L when L is assumed constant for an extended period. This formula can be expressed for each age and sex of lion,

(adult female): $A = 330 * C$

(adult male): $A = 760 * C$

(cubs under one year): $A = W * C$

where C is taken as the constant for the female and the other symbols as before.

The final factor in the energy losses of the lion is the energy expenditure associated with food utilization (SDA). Brody (1964) referring to Rubner (1902) and Murlin and Lusk (1915, 1936) reports SDA values of 40 percent of intake energy for lean meat and 15 percent for fat in the case of canine nutrition. The prey animals observed were generally low in fat and so a figure of 35 percent will be used for SDA.

All forms of energy loss have now been evaluated. The final values are summarized in Table A-I. The sum of all energy losses for any given class of lion (sex, age, and reproductive condition) can be calculated from these values. The result will be an equation of the form:

$$\text{energy losses} = a + b * C$$

where a and b are constants specific to that class of lion (and determinable from Table A-I) and C is the activity coefficient as previously defined. Using this information and the kill data observed during the study, the value of C can be determined. It was assumed that the energy losses of an individual lion equalled its energy input. If all classes of lions have access only to

TABLE A-I. Lion energy losses in kcal. per day

+ $W = W_{max}(1 - e^{-(0.11t + 0.2)})$	+ $\frac{dW}{dt} = 0.11 \ln (W_{max}) * W * e^{-(0.11t + 0.2)}$

Sex and age	SOURCES							
	Resting Metabolism			Growth of Individual (GE)	Growth by Reproduction (RG)	Activity et al (A)	Lactation (L)	Specific Dynamic Action (SDA)
	Basal (BMR)	Individual Growth (GM)	Reproductive Growth (RM)					
adult male	3357					760*C		35% of Intake
x adult female	3019		167		66	330*C	1750	
young male	$39*W^{3/4}$	$100.4*\frac{dW}{dt}$		$30.3*\frac{dW}{dt}$		W*C		
young female		$100.4*\frac{dW}{dt}$						

+ see text for explanation of symbols

x exclude RM, RG, and L if female is neither pregnant nor lactating
exclude L if female is pregnant
exclude RM and RG if female is lactating

food available to the others (this was generally true for this study), then for each kill, the amount consumed by each individual will be, on average, proportional to its need. Thus for any extended period of time:

$$\text{time period} * \begin{array}{l}\text{energy loss equation}\\ \text{for individual}\end{array} \sum_{i=1}^{n} \left[\frac{\begin{array}{l}\text{energy loss equation}\\ \text{for individual}\end{array}}{\begin{array}{l}\text{energy loss equations}\\ \text{of all lions present}\\ \text{at the kill}\end{array}} * \begin{array}{l}\text{energy available}\\ \text{from the i'th kill}\end{array} \right]$$

where n is the number of kills at which that individual was present. This expression reduces to:

$$\text{time period} \sum_{i=1}^{n} \left(\frac{\text{energy available from the i'th kill}}{\text{(energy loss equations of all lions present)}} \right)$$

The energy available from a kill must be calculated. Live weight estimates were discussed in the methods section; the proportion of inedible material must however be determined. Table A-II gives the values obtained for the uneaten bones and attached flesh of nine large prey which had been consumed by lions.

TABLE A-II. Proportion of uneaten bones and attached flesh from large prey

SPECIES	AGE/SEX	POUNDS UNEATEN	EXPECTED LIVE WEIGHT	PERCENT UNEATEN
Eland	adult female	95.	661.0	14.4
Zebra	adult female	51.	481.9	10.6
Wildebeest	adult female	52.5	358.6	14.6
Wildebeest	adult female	67.	358.6	18.6
Wildebeest	adult female	38.	358.6	10.6
Wildebeest	adult male	76.	442.5	17.2
Wildebeest	adult male	79.5	442.5	18.0
Wildebeest	adult male	77.5	442.5	17.5
Wildebeest	adult male	80.	442.5	18.1
Average				15.5

The residue from smaller prey (calves and gazelle) was too scattered to permit accurate assessment, but it was a very small amount and was estimated at about 5.5 percent of the live weight. Ledger, et al (1967) give values for the weight of gut contents of various African ungulates. These average about 15 percent of live weight. Maynard and Loosli (1962) and Brody (1964) give values for the proportion of body weight due to blood. Assuming about three-quarters of the blood is uneaten, then a further approximately 8.2 percent of the total body weight is not used by the lions. These combined losses result in 61.3 and 71.3 percent of the live weight of large and small prey killed, respectively, being used by the lions. The resultant net consumption can be converted to kilocalories per pound (Brody, 1964).

Expression 18 can now be evaluated in order to determine the value of the activity constant (C). This has been determined from the feeding data of three different lionesses for several different periods and is summarized in Table A-III. The food consumed by an individual lion at a kill can now be calculated:

$$\begin{array}{c}\text{food consumed by}\\ \text{an individual}\end{array} = \frac{\text{energy loss rate for that individual}}{\begin{array}{c}\text{energy loss rates for all lions}\\ \text{present}\end{array}} * \begin{array}{c}\text{total}\\ \text{available}\\ \text{food}\end{array}$$

where food can be in any unit.

TABLE A-III. Value of the activity coefficient

LIONESS	DATE	HUNT RHYTHM	NUMBER OF DAYS	ACTIVITY COEFFICIENT
MF2	Feb. 1970	nocturnal	18	13.19
MF2	Mar. 1970	"	16	13.62
MF2	May 1970	"	15	20.99
MF2	Feb.-May 1970	"	49	17.65
MF3	Feb. 1970	"	18	11.97
MF3	Mar. 1970	"	16	13.63
MF3	May 1970	"	15	21.20
MF3	Feb.-May 1970	"	49	15.34
MF4	Feb. 1970	"	18	11.97
MF4	Mar. 1970	"	16	13.63
MF4	May 1970	"	15	21.20
MF4	Feb.-May 1970	"	49	15.34
Average	Feb.-May 1970	"	--	16.11
MF1	Aug.-Nov. 1970	diurnal	101	17.60
MF2	Aug.-Nov. 1970	"	101	16.32
MF4	Aug.-Nov. 1970	"	101	18.97
Average	Aug.-Nov. 1970	"	---	17.63

ANNUAL FOOD CONSUMPTION OF THE NGORONGORO LIONS

The result of prey capture can be expressed as the number of prey killed per year. By making several simplifying assumptions, this feature can be examined for the Ngorongoro lions. These assumptions are listed below:

1. The mean consumption of each lion is on average that of a non-reproducing, adult female.
2. All crater lions eat the same prey proportions as did the Munge lions during the study. (Diurnal hunt rhythm: wildebeest/zebra/eland/Grant's gazelle/Thomson's gazelle/reedbuck/buffalo = 23/11/1/1/16/3/1. Nocturnal hunt rhythm: wildebeest/zebra/eland = 34/3/1.)
3. There are 70 lions in the crater.
4. Five months follow a diurnal hunt rhythm and seven a nocturnal hunt rhythm.
5. Kill ratios are equivalent to those resulting if scavenging does not affect the ratios.
6. The wildebeest population is composed of 40.5 percent adult males, 40.5 percent adult females, 7.1 percent yearlings, and 11.9 percent calves. These values are based on a census of 2978 animals.
7. The average weight of a wildebeest is equal to the average weight of an animal based on the above population structure where all animals are born February 1 (although calves are calculated for both January and February as being one month old). All other prey are considered to be equivalent in weight to a female of the species, except for buffalo which have been shown (Sinclair, 1970) to be killed primarily as adult males.

Weights are based on those of Sachs (1967) and the wildebeest growth curve on that of Talbot and Talbot (1963). Wildebeest are treated in greater detail because they were the most important food source and also calving is peaked

(Estes, 1969) which permits easy calculation of the effect of age. Reedbuck are assumed to be the same weight as Grant's gazelle.

Table A-III in the appendix gives the estimates of the activity coefficient. A mean value for both diurnal and nocturnal hunt rhythm periods would be 16.87. The net consumption can be calculated from Table A-I:

$$\begin{aligned}\text{net consumption (Kcal)} &= 4649 + (16.87 * 508)\\ &= 13220 \text{ per day}\\ &= 4{,}825{,}322 \text{ per year}\end{aligned}$$

This corresponds to a net annual consumption of 5308.4 pounds which would result from a gross consumption of 8659.6 pounds of large prey or 7445.0 pounds of small prey. The gross annual consumption of 70 lions would be 606172 pounds of large prey or 521150 pounds of small prey per year.

The procedure for calculating the number of each prey species killed is straightforward. Firstly, the total number killed per month (TOTNO) is calculated:

$$\text{TOTNO} = \text{PPM} \;/\; \sum_{i=1}^{n} (\text{PROP}_i * \text{SPW}_i)$$

where PPM is the net number of pounds required by all the lions for one month, n is the number of kinds of prey species taken for that month, PROP is the proportion of the total kill comprised by each prey species, and SPW is the net number of pounds which an average animal of that species would provide to the lions. The number of each species (SP_i) taken per month is then simply:

$$SP_i = TOTNO * PROP_i$$

The results of this exercise are summarized in Table A-IV. The values for each month are based upon a 30 day month and the full year values are then corrected to 365 days.

It is desirable to examine assumption 5 (scavenging) more thoroughly. The proportions of prey taken annually (Table A-IV) are very similar to the proportions taken by hyaenas (Kruuk, 1972). Thus if scavenging from hyaenas is not of major importance and is random, then no significant effect upon the ratio of prey eaten will result. The continuous observations of feeding activity of the Munge pride revealed that only 6.9 percent of the food intake on a nocturnal hunt rhythm and 7.4 per cent of the food intake while on a diurnal hunt rhythm of the adult females was derived from hyaena killed prey. Limited observations suggested that this figure was probably much greater for males (15 to 75 per cent). The proportion of hyaena scavenged food for the whole lion population would thus probably be about 10 to 40 per cent. Kruuk (1972) estimated, however, that most of the crater lions' food during his study period was derived by scavenging from hyaena. His estimate is likely too large. If 50 lions on average were present in the crater at that time, then their annual food requirements would be about 400,000 pounds. Kruuk estimated that the lions were getting 10 to 20 per cent of the annual kill by hyaenas (690,580 pounds) which would be 69058 to 138116 pounds. It can be seen that this is only 17 to 35 per cent of the lion's requirements suggesting that the situation at that time was similar to

TABLE A-IV. Estimated annual kill of Ngorongoro lions

	NUMBERS TAKEN						
MONTH	WILDEBEEST	ZEBRA	ELAND	GRANT'S GAZELLE	THOMSON'S GAZELLE	REEDBUCK	BUFFALO
JANUARY	123.68	10.917	3.593	0.0000	0.000	0.0000	0.0000
FEBRUARY	123.47	10.899	3.587	0.0000	0.000	0.0000	0.0000
MARCH	122.46	10.810	3.558	0.0000	0.000	0.0000	0.0000
APRIL	121.47	10.722	3.529	0.0000	0.000	0.0000	0.0000
MAY	120.49	10.636	3.500	0.0000	0.000	0.0000	0.0000
JUNE	119.53	10.551	3.472	0.0000	0.000	0.0000	0.0000
JULY	55.93	26.738	2.455	2.4555	39.015	7.3665	2.4555
AUGUST	69.79	33.364	3.064	3.0640	48.684	9.1921	3.0640
SEPTEMBER	69.55	33.247	3.053	3.0533	48.514	9.1599	3.0533
OCTOBER	69.86	33.158	3.045	3.0451	48.988	9.1353	3.0451
NOVEMBER	69.23	33.095	3.039	3.0393	48.292	9.1180	3.0393
DECEMBER	116.57	10.289	3.386	0.0000	0.000	0.0000	0.0000
ALL 12	1197.94	237.679	39.828	14.6573	232.888	43.9718	14.6573

TOTAL NUMBER OF INDIVIDUALS TAKEN PER YEAR = 1781.6207 that of this study. Thus, although scavenging was important, it probably is not sufficiently major to effect the ratios of prey consumed.

Table A-V expresses the annual kill of the crater lions as a percentage of the prey population (see Table I in main text) for each of the three main prey species. It also shows the proportions taken by hyaenas (from Kruuk, 1972). Jackals and eagles would also be important predators of Thomson's gazelle. Without knowing the response which the prey populations would show in the absence of this predator, there is no certain means of determining whether the prey numbers are being limited by the lion and hyaena. If the numbers of hyaenas (Kruuk, 1972) and lion are ultimately being controlled by the prey numbers then a tendency towards an unstable balance would exist if prey numbers were in turn being limited by predation. This paradox would be resolved if the degree of vulnerability of the prey is controlled by some other feature. For example, the plane of nutrition of the prey may determine the proportion of the population which can be captured by subadult lions. Study must be concentrated upon this age group if the population interactions of the lion are to be fully understood.

TABLE A-V. Annual percentages of the major prey populations killed or scavenged by the Ngorongoro lions and hyaenas

PREY SPECIES	PERCENTAGES LION	HYAENA*	TOTAL
Wildebeest	7.0	7.6+	14.6
Zebra	4.3	6.5	10.8
Thomson's Gazelle	6.2	1.6	7.8

* adapted from Kruuk (1972)
+ considered an underestimate by Kruuk

EFFECT OF AGE, SEX, AND CONDITION UPON THE PROBABILITY OF CAPTURE

This section examines the kill data for indications of any major overall selection by the lion based upon age, sex, and condition of the prey individuals.

Table A-VI presents the age composition of 25 wildebeest killed during the period of continuous diurnal observations.

TABLE A-VI. Age of wildebeest killed by lion during the day

APPROXIMATE AGE (YEARS)	NUMBER KILLED
0 - 1	5
1 - 2	3
2 - 3	0
3 - 4	1
4 - 10	13
10 - 14	3
14 - 18	0
Total	25

The ages are based on Talbot and Talbot (1963). Since no sampling (killing or capturing) was done of the live population these data cannot be satisfactorily evaluated. Certainly, there are no obvious irregularities in the age composition of the lion kills. The proportion of calves in the kill can be compared to the proportion present in the census counts taken in the kill area. Table A-VII shows that there is no significant difference.

TABLE A-VII. Proportion of wildebeest calves killed by lions during the day

	CALVES	NON-CALVES	TOTALS
Observed	5 (20%)	20 (80%)	25
Expected	142 (11%)	1148 (89%)	1290
Totals	147	1268	1315

$x^2 = 0.552$
$0.5 > P > 0.3$

The nocturnal wildebeest data must be separated into two sets since it was found that the stage of the reproductive cycle was a significant feature of the search. Tables A-VIII and A-IX give the age structures of the kill and population.

TABLE A-VIII. Age of wildebeest killed by lions in February during the night

	CALVES	YEARLING	ADULT	TOTALS
Observed	5 (38.5%)	2 (15.4%)	6 (46.1%)	13
Expected	608 (15.4%)	408 (10.4%)	2925 (74.2%)	3941
Totals	613	410	2931	3954

$x^2 = 6.13$
$0.05 > P > 0.02$

TABLE A-IX. Age of wildebeest killed by lions in March and May during the night

	CALVES	YEARLING	ADULT	TOTALS
Observed	1 (7.1%)	1 (7.1%)	12 (85.7%)	14
Expected	410 (14.3%)	127 (4.4%)	2335 (81.3%)	2872
Totals	411	128	2347	2886

$x^2 = 0.764$
$0.98 > P > 0.95$

It can be seen that during the calving season (February) there is strong indication that an excess of calves were taken. This did not occur later (March and May). Probably increased attack success was most important in young calf capture. Schaller (1972) found no major selection for age in the total wildebeest kills by lions in the Serengeti except for an increase in the importance of the oldest age classes.

Table A-X gives the sex ratio of the 20 wildebeest (older than one year) killed by lions during the day. It can be seen that there is no significant effect of sex upon success.

TABLE A-X. Sex of wildebeest (over one year of age) killed by lions during the day

	MALES	FEMALES	TOTALS
Observed	9 (45.0%)	11 (55.8%)	20
Expected	680 (59.2%)	468 (40.8%)	1148
Totals	689	479	1168

$x^2 = 1.65$
$0.2 > P > 0.1$

Tables A-XI and A-XII present the same information (but refer to animals older than two years) for the two nocturnal time periods. Although there is an indication that females were killed more during the calving period and males more during the rut the sample is insufficient to demonstrate a significant difference. Schaller's (1972) total data showed a preponderance

TABLE A-XI. Sex of wildebeest (over 2 years of age) killed by lions in February during the night

	MALES	FEMALES	TOTALS
Observed	1 (16.7%)	5 (83.3%)	6
Expected	1555 (53.2%)	1370 (46.8%)	2925
Totals	1556	1375	2931

$x^2 = 3.20$
$0.1 > P > 0.05$

TABLE A-XII. Sex of wildebeest (over 2 years of age) killed by lions in March and May during the night

	MALES	FEMALES	TOTALS
Observed	9 (75.0%)	3 (25.0%)	12
Expected	1104 (47.3%)	1231 (52.7%)	2335
Totals	1113	1234	2347

$x^2 = 3.68$
$0.1 > P > 0.05$

of male wildebeest in the Serengeti kills whereas Pienaar (1969) found no selection in Kruger Park kills.

Selection based upon condition cannot be evaluated since no sample is available for the wild population of wildebeest. Sixty-four per cent (of 14) diurnally killed wildebeest showed marrow with the highest category of fat content, and none showed the lowest category. Furthermore, no obvious debilities were present. This at least suggests that poor condition is not essential to successful prey capture, although it does not discount it. Schaller (1972) considers condition to be of some importance to prey capture by lions in the Serengeti.

Insufficient nocturnal zebra kills were recorded, but diurnal kills can be examined. Table A-XIII gives the age distribution of 13 diurnal kills. Again, no estimate is available for the live population so it can only be noted that older age classes seem to have been important. The ratio of animals under one year to those over one year in the live population average 5 to 19 per cent during the sample period, which encompasses the observed kill of 15.4 per cent first year individuals.

TABLE A-XIII. Age of Zebra killed by lions during the day

AGE (YEARS)	NUMBER KILLED
0 - 1	2
1 - 4	1
4 - 7	2
7 - 11	6
greater than 11	2
Total	13

Tables A-XIV and A-XV summarize the data relating to diurnal sex selection for zebra over one year of age. It can be seen that there is no significant effect for sex.

TABLE A-XIV. Sex of zebra (over one year of age) killed by lions in August during the day

	MALES	FEMALES	TOTALS
Observed	2	2	4
Expected	20	96	116
Totals	22	98	120

$x^2 = 2.77$

$0.1 > P > 0.05$

TABLE A-XV. Sex of zebra (over one year of age) killed by lions in September and October during the day

	MALES	FEMALES	TOTALS
Observed	6	2	8
Expected	238	57	295
Totals	244	59	303

$x^2 = 0.16$
$0.8 > P > 0.7$

Bone marrow as an estimate of condition in zebra is less straightforward than for wildebeest. Two types of marrow were found for zebra during this study: red with loose consistency, and yellow with loose consistency. No fat analyses of the marrow were made, but yellow marrow corresponded to animals generally appearing less fit. No zebra kills by lions showed this yellow marrow.

One zebra (marrow not examined) was in extremely emaciated condition and virtually ignored the presence of the lions as it approached a drinking site (where it was readily killed). This was the only individual of any species during this study which had grossly increased vulnerability due to its condition. Low incidence of animals of this sort is one of the features of the Ngorongoro ecosystem (Kruuk, 1972). In contrast, Schaller (1972) found that 23 per cent of wildebeest and zebra killed by lions in the Serengeti were markedly debilitated. There is little usefulness in including such animals in the calculation of success (stalk, attack, and subdue) because their frequency in the population is likely to be subject to considerable variation from season to season and year to year. In terms of the approach used for this study, the frequency of this class of prey should be determined (preferably defined by causal factors) and then combined with an analysis of the success of each of the four phases of prey capture. The low incidence of this form of capture did not allow such an evaluation for this study.

Table A-XVI gives the data relating to diurnal age selection in lion kills of Thomson's gazelle. It can be seen that there is no significant effect for age.

TABLE A-XVI. Age of Thomson's gazelle killed by lions during the day

	LESS THAN 4 MONTHS	MORE THAN 4 MONTHS	TOTALS
Observed	5 (29.4%)	12 (70.6%)	17
Expected	105 (28.7%)	461 (71.3%)	566
Totals	110	473	583

$x^2 = 1.27$

$0.3 > P > 0.2$

TABLE A-XVII. Sex of Thomson's gazelle (over 4 months old) killed by lions during the day

	MALES	FEMALES	TOTALS
Observed	11 (91.7%)	1 (8.3%)	12
Expected	162 (35.1%)	299 (64.9%)	461
Totals	173	300	473

$x^2 = 16.11$
$P < 0.001$

The sex of an individual (Table A-XVII), however, does show a significant effect with males being killed 2.6 times more frequently than expected. Although no quantitative measure was made, general observations suggested that the males (non-territorial) moved into good cover areas more readily than did females, thus increasing search success. Walther (1969) also found an increased tendency for males to be near cover areas.

The long bones of the Thomson's gazelle were generally chewed, therefore, marrow samples were not obtainable. No obviously poor condition prey were killed, as was also found by Schaller (1972) in the Serengeti.

In view of the above analysis of the kill data, the assumptions made during the prey capture analysis are found to be satisfactory at this stage. Further study might allow more detailed subdivision within species. For example, the subduing success for zebra is almost certainly affected by the age of the individual.