

## Prey capture by the African lion

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The capture of prey by the African lion in Ngorongoro Crater, Tanzania, is examined. For analytic purposes the process is envisaged as a consecutive set of events: searching, stalking, attacking, and subduing prey.

Initiation of prey capture activity by the lion arises from the interaction of degree of stimulation presented by the prey, timing of the activity cycle of the lion (diurnal or nocturnal), and its level of hunger. These factors yield thresholds for initiation which result in kills being directly related to prey density at high and low densities and inversely density dependent at intermediate prey densities.

Success in stalking appears to depend primarily upon the failure of the prey to see the approaching lion until it is within its effective distance. Using data from actual stalks and contrived experiments, the probability is calculated of the lion being detected for a range of conditions.

The attack involves a matching of the sprinting abilities of the predator and prey. To analyze this aspect in detail, the velocity curves of running are defined for the lion and four prey species.

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On étudie ici la prédation du lion africain dans le cratère Ngorongoro, en Tanzanie. Pour des raisons analytiques, on examine le phénomène étape par étape: la recherche, l'affût, l'attaque et la maîtrise de la proie.

La déclenchement du processus est dû à l'interaction de plusieurs facteurs: l'intensité de la stimulation inhérente à la proie, le moment précis dans le cycle d'activité du lion (diurne ou nocturne), enfin l'intensité de la faim chez le lion. Ces facteurs donnent lieu à des seuils d'initiation de la prédation; il s'ensuit que les attaques sont directement proportionnelles à la densité des proies, lorsque cette densité est forte ou faible, et inversement proportionnelles à la densité, lorsque celle-ci est intermédiaire.

Le succès de l'affût semble dépendre surtout de ce que la proie reste inconsciente de la présence du prédateur jusqu'à ce que celui-ci atteigne une distance efficace. D'après des observations et des expériences sur l'affût, on calcule la probabilité de détection du lion par la proie dans une série de conditions.

Le succès de l'attaque, par ailleurs, dépend d'une combinaison des capacités de course du prédateur et de la proie. Pour analyser cet aspect, on a tracé la courbe de vélocité de la course chez le lion et chez quatre espèces de proies.

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### Introduction

The large mammalian predators are rarely considered with indifference. There are those who regard them vehemently as expendable competitors in the 'battle' for protein or trophies while on the other hand, there are those who champion them as desirable, if not necessary, links in the chain of life. Scientific studies have tended to support the latter view (Murie 1944; Cowan 1947; Thompson 1952; Stenlund 1955;

Rausch 1967; Pimlott 1967; Pulliainen 1965; Estes and Goddard 1967; Kruuk 1972; Hornocker 1969; Schaller 1972; McLaughlin 1970; Kruuk and Turner 1967; Pienaar 1969; Rudnai 1973). The identified positive aspect of these predators is the occurrence of a disproportionately high number of inferior (young, old, or weak) prey individuals in the observed kill. Under many circumstances this can have a desirable population effect on the survival of the prey species.

Studies have however tended to concentrate upon determining the composition of the kill rather than upon the manner in which the observed composition is derived. If the ultimate

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test of the usefulness of an approach is the power of the resultant theories to forecast or permit manipulation of events, then the success of these studies has been limited. Part of the problem derives from the fundamental complexity of the ecological process of prey capture. This complexity results from the number of simple events involved in this process plus the actions and interactions of the components operating at each event (Holling 1965, 1966). If this complexity can be adequately overcome then the expectation would be that new insight could be derived. The aim of this paper then is to probe the process of predation, specifically by the African lion (*Panthera leo*), to elucidate the strategies and tactics of prey capture.

Such a study required extensive observations of predation by lions under a variety of conditions. In this regard, the Ngorongoro Conservation Area, Tanzania, was ideal. A description of this study area and the lion population is given in Elliott (1975) and Elliott and Cowan (in preparation).<sup>3</sup>

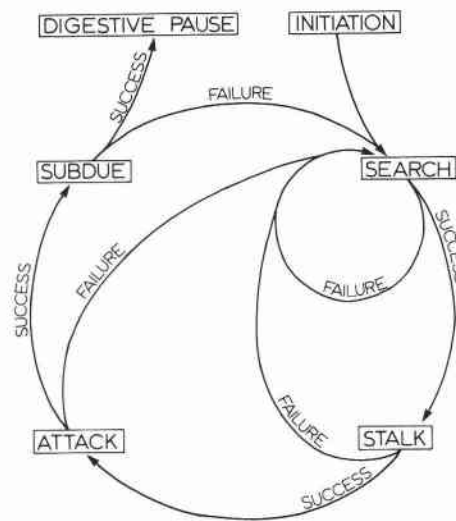
### Methods

Whenever possible basic data were gathered through measurement of the values of operative variables during actual prey capture situations. However, since only one successful kill was witnessed involving male lions, this study refers only to the values of constants for prey capture by female lions.

The quantitative approach chosen for analysis necessitated the subdivision of the predatory process into simpler segments. This basic partitioning is shown in Fig. 1 where prey capture is envisaged as a consecutive set of events or phases. The first or initiating phase of the process is prey searching. If this event is successful then the next event begins and so on until an event is unsuccessful in which circumstance the search phase begins again. Table 1 defines these prey capture events. It is important to realize that these are operational (modelling) events and need not be discrete behavioural sequences on the part of the lion. For example, any movement of predator and prey which reduces predator-prey distance (for prey not specifically located by the lion) classifies operationally as searching.

A difficulty arose in this study when measuring food intake for lions in that a number of individuals 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 lions eating was then of little use. An approximate measure of the portioning of available food was derived by assuming that individuals (of a given age, sex, and reproductive state) consume a given prey in proportion to their average

<sup>3</sup>Elliott, J. P., and I. McT. Cowan. Territoriality, density, and use of prey by the African lion in Ngorongoro Crater, Tanzania. In preparation.



### PREY CAPTURE

FIG. 1. Consecutive phases in prey capture by lions.

daily energy expenditure relative to that of other lions present at that kill (Elliott 1975).

To obtain a more precise evaluation of the visual aspects of the stalk than could be derived from strictly direct observation, an experimental situation was designed including many variables involved in an actual stalk. This involved the use of a pseudopredator constructed from wood fibre, cotton towelling, and cardboard. This pseudopredator was placed in vegetation and then undisturbed potential prey animals were observed as they approached the area. When the prey noted the pseudopredator the following variables were measured: (1) age, sex, and species of prey; (2) area of predator visible (this was accomplished by photographing a known area grid and the hidden pseudopredator from the eye position of the prey); (3) incident light and reflectivity of pseudopredator and background (using a Gossen meter, model Tri-Lux); (4) predator-prey distance; and (5) angle of orientation of the prey.

Four species were involved in these tests: wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), Grant's gazelle (*Gazella granti*), and Thomson's gazelle (*Gazella thomsonii*).

The salient features of the attacks (force-velocity) were measured by filming actual attacks. Two variations of this filming system were adopted. The more general technique involved two cameras, a known distance apart, filming the attack. A second technique used only one camera and was possible 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 precise grid was constructed at the site of the attack and filmed from the original camera location. All films were subsequently examined on a Vanguard motion analyser (model M-16 CW). The positions of predator, prey, and orientation marker were punched frame by frame into paper tape. This information plus knowledge of the film

TABLE 1. 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 reduces the probability of harm to the predator)
Subduing	The killing of prey which has been brought into contact with the lion

speed and the field parameters allowed the calculation of instantaneous predator and prey velocities.

## Results and Discussion

### The Initiation of Prey Capture

#### General

The factors which affected the initiation of prey capture activity by the lion are prey stimulus, hunt rhythm, and hunger. They are defined as follows. (1) Prey stimulus is the inverse of the amount of energy which must be used by the lion to place it in an attack situation (see Table 2). (2) Hunt rhythm is the activity cycle (diurnal or nocturnal) which the lion has been using for type III prey capture (see Table 2). (3) 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 aware of the lion's location. No 'dominance' was identified in the initiation of prey capture activity, and once the threshold for any of the lions in a group was reached the others would often adopt similar behaviour.

TABLE 2. Events involved in each of the three basic prey capture types

Type	Events or phases			
	Active search	Active stalk	Attack	Subdue
I			*	*
II		*	*	*
III	*	*	*	*

#### (1) Prey Stimulus

Prey stimulus 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 2.

'Active' refers to the lion having to move during the event. (A fourth capture type, type 0, could exist if carrion eating with no active attack were considered prey capture.) 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 this aspect.

#### (2) 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 stalk success is considered in detail under the section, Prey Stalking; however, direct observation of the lions while stalking showed that the gross difference between day and night was that during the day, vegetation or topography was essential for cover while during the night, darkness itself was adequate.

Generally prey animals showed a distinct avoidance of areas which had suitable lion cover. (Measurements of actual stalks suggested that this was vegetation, topographic irregularity, or a combination of both, 1.3 ft (1 ft = 0.3048 m) or greater in height.) The lions therefore had no option but to hunt at night when the cover constraint no longer applied.

No quantitative measure was derived for the



movement of prey to good cover areas diurnally; however, a qualitative estimate is obtained by examining the number of daytime kills made by lions as a result of type I and type II hunts. Successful hunts of these types depend upon prey being near cover in the same manner as do diurnal type III hunts and so an increase in the number of kills implies an increase in type III potential. The assumption here is that the non-actively searching lions were spending an equivalent amount of time 'resting' in suitable cover areas for the different periods. This indicator (Table 3) suggests that the February, March, and May period (wet season) yielded reduced prey diurnal vulnerability (location of prey in cover suitable for stalking within the home range of the lions). Nocturnal prey densities were high however (Table 4) and all type III hunts during this period occurred at night.

The prey situation changed later in the dry season (August to November). At this time prey densities were low in the night hunting area (Table 4). Diurnally, the prey were moving into tall *Aeschynomene schimperi* swamplands and riverine bush to graze and obtain water, increasing their vulnerability (Table 3). During this period all type III hunts were diurnal.

It appears that the lion tends to continue to initiate type III hunts only during one phase of the day and not to expand its activity over the entire 24-h period. During 7 October 1970 a large number of wildebeest moved into the night-hunting area of the lions (Table 4). The lions

however did not change their activity pattern, but continued to use only diurnal type III prey capture. Reverse situations (which are, as noted, difficult to quantify) were also seen at times when the lions were on a nocturnal cycle, with similar results.

### (3) Hunger

Holling (1965) has conducted an extensive analysis of the effect of hunger on all aspects of predation using a mantid as an 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 initiation by large fissioned therefore seems to be upon search.

Hunger is a function both of the period of time since feeding and the amount consumed at that feeding. Holling's (1965) work showed an exponential relation between these two variables of hunger at the threshold of consumption. The least squares regressions of these two were compared for 18 diurnal searches and 21 nocturnal searches by lions. There was no significant difference and the combined data are presented in Fig. 2. It can be seen that a linear relation is suggested between initiation of active search (first phase of a type III hunt, Table 2) and caloric intake at the previous meal. (The amount of food consumed has been converted to kilocalories based upon 909 kcal (1 kcal = 4.1855 kJ) per pound (1 lb = 0.453 kg) of food.) The relationship at threshold is as follows: hours until initiation =  $0.00097 \times$  kilocalories consumed with the variance in the estimate of the slope being  $0.35 \times 10^{-8}$  and the standard deviation about the regression being 11.20 h.

We have few data for this relationship for type I and II hunts in phase (occurring during the established active search period, diurnal or nocturnal) or out of phase; however, the threshold was found to be very low with attacks occurring shortly after a meal involving con-

TABLE 3. Number of diurnal kills per day from type I and II hunts

Date	No. per day	Sample size
February, March, and May 1970	0.041	49
August to November 1970	0.347	101

TABLE 4. Mean densities of major prey in nocturnal type III areas (No./10<sup>6</sup> ft<sup>2</sup>)

Date	Prey densities	
	Wildebeest	Zebra
February, March, and May 1970	24.68	4.77
August and September 1970	0.40	0.22
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

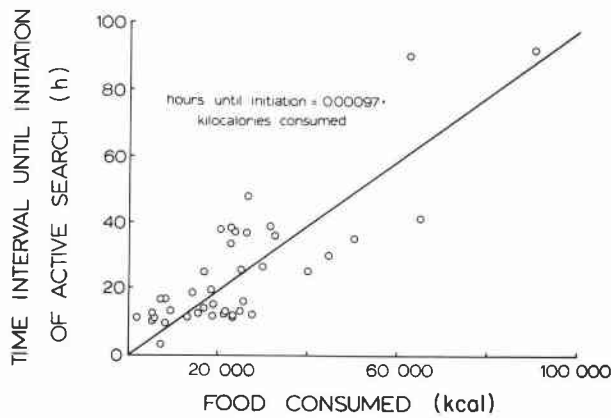


FIG. 2. Effect of hunger on active search initiation, nocturnal and diurnal, in the lion ( $n = 39$  sets).

siderable food intake. Conversely out-of-phase type III initiation was found to be very lengthy as compared with the inphase situation.

#### *Ecology of Prey Capture Initiation*

The multiple threshold nature of initiation (that is, the combination of three factors influencing initiation: prey stimulus, hunt rhythm, and hunger) would have considerable significance to the lions' role as a population-regulating factor for ungulate prey species. Very high prey densities would result in the lion obtaining all of 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 tend toward 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. However the lion needs simply to 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 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 is strictly functional and not numeric (Solomon 1949).

#### *Prey Searching*

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.

Since the methodology concentrated upon observation of the lion, the effect of prey activities upon prey searching was not analyzed by means of components analysis. Thus, only general features of prey activity will be noted here as reference for future study.

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.

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 (type III hunt) 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.

#### *Prey Stalking*

##### *General*

The stalking of prey is a phase in prey capture of major significance to overall capture success

TABLE 5. Effect of species upon diurnal stalking by lions

Species	Crouching stalk time (min)			Relative frequency of stalk types		
	Mean	Standard deviation	Sample size	Crouching type	Running type	Sample size
Wildebeest and zebra	31.6	26.4	88	96%	4%	159
Thomson's and Grant's gazelles	6.9	9.0	25	73%	27%	51

by the lion. Not surprisingly therefore, a complexity of action was found which resulted in many variants. However, in terms of the quantifiable factors affecting the stalk, it was possible to reduce all stalks to three basic types. (1) Crouch occurs when the predator adopts concealing posture and zero velocity; the prey unknowingly moves towards the predator. (2) Sneak-crouch is when 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. Approach speed is generally reduced as predator-prey distance is reduced. (3) Run occurs when 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. Furthermore, although the crouch and sneak-crouch stalks differed greatly in terms of necessary prey stimulus and requirements for stalking cover, functionally (time, visual stimulus to the prey, and success) they are very similar.

Thus only two groupings of stalks need be considered: the crouching stalks and the running stalks.

Diurnally, stalks of both groupings occurred; however, as seen in Table 5, the relative frequency and mechanics of occurrence varied with the two principal prey species groups. (Since wildebeest and zebra often grazed and travelled to water together, and similarly the two gazelle species, it was necessary to combine diurnal stalk data for each pair of species. Similarity of detection and flight abilities in each case reduces the error of this technique.) Wildebeest and zebra

required long crouching stalk times by the lion and were only infrequently stalked with running stalks. Conversely, the two gazelle species required far shorter crouching stalk times and over one-quarter of all stalks were running type. However, as seen in Table 6, the overall stalk success (diurnally) was not significantly different for the two species groupings. (Stalk success refers to the reduction of predator-prey distance sufficiently to permit a successful attack (Elliott 1975.))

McLaughlin (1970) noted for cheetah that percentage success tends to be similar for different prey and Kruuk (1972) made the same observation for hyaena. This consistency suggests that these carnivores have considerable tactical abilities and the question presented by the Ngorongoro lion observations is, Does the observed difference in stalk tactics used by the lion for the two species groupings relate to a tactical or to a strategic escape mechanism of the prey? As will be shown when the attack is considered, it is largely the latter.

Nocturnally the situation was less complex although the darkness did hinder observation. Firstly, stalks for gazelle did not occur nocturnally. This partially resulted from the tactical feature of gazelle that they generally lay prone during periods at night when the moon was not shining thus reducing search success for the lion. (Moonless periods were the only times when active (type III) search occurred.) A further reason for the lack of nocturnal gazelle stalks (based upon a strategic feature of gazelle escape) will be discussed under attack phase.

Night stalking for wildebeest and zebra was simplified in that all stalks were of the running type.

#### *A Quantitative Model of Stalk Success*

The first step in developing a model of stalking is the distinguishing of the variables controlling

TABLE 6. Effect of species upon success of crouching and running type diurnal stalks

Species	No. of successful stalks	No. of unsuccessful stalks	Totals
Wildebeest and zebra	34 (22%)	123 (78%)	157
Thomson's and Grant's gazelles	14 (27%)	38 (73%)	52
Totals	48 (23%) $\chi^2 = 0.61$	161 (77%) $0.5 > P > 0.3$	209

TABLE 7. Effect of the number of lions involved in a stalk

Stalk type	Time of day	Prey species	Stalk success for:		Probability of similarity
			One lion*	Two or more lions*	
Crouching	Diurnal	Wildebeest and zebra	20% (82)	25% (67)	0.3-0.5
Crouching	Diurnal	Thomson's and Grant's gazelle	29% (14)	25% (17)	0.7-0.8
Running	Nocturnal	Wildebeest and zebra	11% (35)	30% (23)	0.05-0.1

\*Sample sizes are given in parentheses.

stalk success for each species. One possibility is the number of lions involved in the stalk. Table 7 examines the effect of this variable and in no case was there a significant (less than 0.05 probability) improvement when more lions were involved. The indication of an improved success at night as opposed to daytime probably results from the removal of the specific cover constraint.

Since no significant effect can be demonstrated for the lion-related variable of number of lions, then stalk success must either depend upon the sensory abilities of the prey species or upon third party factors (human, other wild animal, or abiotic disturbance), which however can be assumed random. In the former instance there may be auditory, olfactory, or visual stimuli. No measure of sound was made; however, the crouching stalks produced very little noise and even the running stalk was very silent. Lacking any quantitative measure it must be assumed insignificant (or random) in the Ngorongoro situation. The effect of olfactory stimuli can be examined by comparing success for downwind and upwind stalks. Table 8 examines this feature for crouching type stalks against wildebeest and

TABLE 8. Effect of wind direction upon crouching type stalk success for wildebeest and zebra

	Wind source - prey - lion angle (degrees)		
	0 to 60 (predator upwind)	60 to 120 (crosswind)	120 to 180 (predator downwind)
No. observed	36	44	39
% success	19	18	18

zebra (insufficient sample size prevented us from analysing attacks on gazelles). It can be seen that the lion does not appear to consider wind direction nor does it affect success. Since running stalks are much shorter they are even less likely to involve an olfactory effect.

Visual stimuli remain as the possible (and probable) major inputs of sensory information to the prey and indeed the major nonrandom factor in stalk success. The simplest case of visual stimulation is that which occurs during the crouching stalks. In this circumstance the prey must detect a motionless predator concealed against and within a specific background. Since



the predator and background are not self-luminous, the difference in contrast ( $\Delta L$ ) between the two results from their reflectivity differences and the luminance, such as candles per square metre of incident light from the sun ( $SILLM$ ):

$$[1] \quad \Delta L = |RFPRD - RFCOV| \times SILLM,$$

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; this can be stated: stimulus area  $\times$  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 *et al.* 1939; Baumgardt 1948) such as the situation being investigated here. Furthermore for targets of less than a few minutes of arc, the shape of the area is not significant (Lamar *et al.* 1948). Since the functional area is an angular one, the predator's exposed area ( $AREA$ ) in square feet (or similar) must be converted:

$$[2] \quad \text{angular area} = AREA/D^2,$$

where  $D$  is the predator-prey distance (in the same basic unit as  $AREA$ ). Equations 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 is thus a constant at the visual threshold):

$$[3] \quad STIM = (AREA \times SILLM \times |RFPRD - RFCOV|)/D^2.$$

The procedure now would be to define the mean value of  $STIM$  for each prey species based upon the pseudopredator trials described under Methods, but a complexity is introduced through the effect of the preceding and present state of illumination of the eye. This effect 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).

The effect of adaptation is to alter the expected linear dependence of  $STIM$  upon  $SILLM$  (in Eq. 3). Since the pseudopredator trials were however restricted to the daytime they are poor for defining the effect of adaptation. Further trials should be undertaken at night although it would be difficult to observe animal reactions.

However to provide a complete picture of the process it is possible in the case of wildebeest to use the actual stalk data plus the attack model (see next sections) to determine a mean value for threshold night vision during moonlight and starlight conditions. This procedure allows the determination that the observed starlight capture success of 23.5% corresponds to a mean detection distance of 42.5 m and that the observed moonlight success of 16.7% corresponds to 52 m (Elliott 1975). (These are based upon the run stalk, initial lion velocity of 6.5 m/s and a standard deviation for vision of 11.5 m.)

Using the pseudopredator data (Fig. 3) plus the estimates for night vision it is now possible to define the effect of adaptation plus the variability of threshold vision in the case of the wildebeest. Lacking any a priori expectation as to the relationship of luminance ( $SILLM$ ) to the threshold (in this instance, distance), the data were plotted on various scales (after conversion to common area and reflectivity). Figure 3 presents the data with luminance expressed as a logarithm and it can be seen that this conversion appears to allow satisfactory linear description. (The line shown on this figure is the line which will result from Eq. 4.) A feature to note is that the slope of the adaptation line is sufficiently shallow that including a possibly inaccurate effect for adaptation in the detection equation will introduce very little error into the predictions of the equation for diurnal conditions.

A linear relationship suggests an equation of the form (derived from Eq. 3):

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

where  $B$  and  $CONS$  are constants,  $\ln$  refers to natural logarithm, and 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

$$[4] \quad D = 22.5 \times \sqrt{AREA \times |RFPRD - RFCOV|} \times (\ln(SILLM) + 15.86)$$

with a standard deviation of 37.9 ft and  $SILLM$  expressed in candles per square metre. Figure 4 illustrates the fit of the data to the lion. The variability of the visual threshold, expressed as distance, is considered to be a normal distribution (Mueller 1950; de Vries 1943; Blackwell



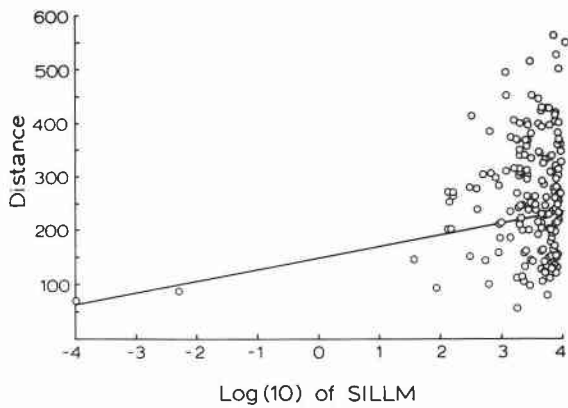


FIG. 3. Effect of field brightness (*SILLM*) upon wildebeest vision-detection data ( $n = 184$ ).

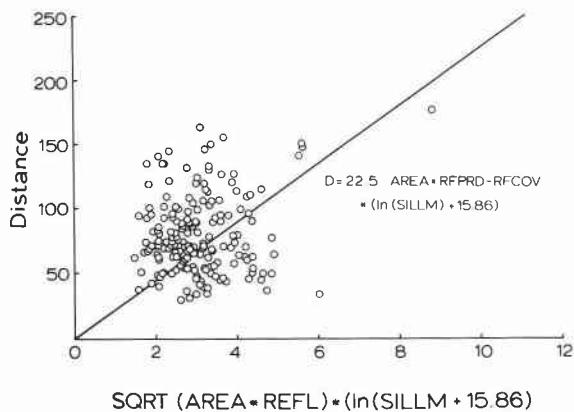


FIG. 4. Linearized form of wildebeest vision-detection data ( $n = 184$ ).

1946) or truncated normal (to zero) where the mean value of  $D$  is low.

A normal probability function with a mean based upon equation (4) and a standard deviation of 37.9 ft defines the probability of wildebeest detecting a stationary object against and within natural Ngorongoro cover. Furthermore this function was found to be independent (probability greater than 0.05) of the angle of orientation of the wildebeest (or other prey) for angles 0 to 90°. Unfortunately there were insufficient night stalks observed for other prey species to allow definition of the effect of adaptation. However since this effect is slight for the range of diurnal conditions a fairly accurate value can be obtained by assuming a constant mean threshold diurnally. A simple way of expressing this threshold is with a detection ratio

$$D / \sqrt{AREA \times |RFPRD - REFCOV|}$$

which excludes the effect of field brightness. Table 9 summarizes the daytime detection abilities of the four main prey species based on the pseudopredator data. It can be seen that detection ability does vary with species.

This ratio can be used to define the diurnal probability of detection curves for the zebra and the two gazelle species. Although the effect of adaptation is not known, the wildebeest adaptation response can be used with little error diurnally for the other species. In this case the mean and standard deviation of the normal probability function are determined by proportions (based upon the detection ratios) of the wildebeest values from Eq. 4 with *SILLM* set at 5000 candles per square metre.

The next stage in analysis must involve the definition of the numeric value of the visual stimulus produced by the lion, exclusive of distance. That is, definition of values for the size of a lion and the reflectivity difference. Generality of application requires that these be expressed in some simple manner. It was found by reference to photographs taken at known distances that a crouched lion could be envisaged as a rectangle of width 0.3 m (0.98 ft) and height 0.44 m (1.42 ft). Expressing this with a variable for cover height (*COV*, in feet) yields:

$$[5] \quad AREA = 1.39 (0.98 \times COV)$$

Equation 5 is negative if *COV* is greater than 0.44 m (1.42 ft). Field observations suggested, however, that this situation does not result as the lion tried to keep the prey always in view. If the cover was greater than would permit this with the head down, then it was raised. Indeed in cases where cover was easily measured (such as uniform depth grass on level ground) it appeared that the minimum cover used by lions was generally 1.3 ft and that higher cover tended to yield the same exposure, as noted and thus *AREA* can usually be fixed at 0.01 m<sup>2</sup> (0.12 ft<sup>2</sup>). For the running stalk the exposed area would be 0.4 m<sup>2</sup> (1.4 ft<sup>2</sup>) and to take approximate account of the effect of motion upon vision this is doubled (Walls 1963) to give a value for the *AREA* variable of 0.72 m<sup>2</sup> (2.78 ft<sup>2</sup>). The reflectivity difference ( $|RFPRD - REFCOV|$ ) for all stalk types was taken as 0.125 for Ngorongoro.

The above information allows for each of four prey species, the designation of a probability function (model) for diurnal detection of a stalking lion. Detection of a lion and subsequent

TABLE 9. 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
<i>F</i> ratio = 16.774			
Probability of similarity less than 0.001			

\*See text.

flight was found to be the trigger initiating attack by the lion (given a reasonably low predator-prey distance) thus this model also defines the probability of attack initiation. This in itself tells little of the probability of successful capture as this must be tied to attack success, which is considered in the next section.

#### The Attack

##### Theory

The attack involves a matching of the sprinting abilities of the predator and prey. Thus a first stage in analysis is the numeric definition of the velocity curve for each species.

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

$$[6] \quad V(t) = (FA \times dt)/M + V(t - dt),$$

where *FA* is the accelerating force, *M* is the mass accelerated, *V(t)* is the velocity at time *t*, *V(t - dt)* is the velocity at time (*t - dt*), and *dt* is the period of time during which the force acts. However 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 *et al.* 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:

$$[7] \quad FA = [(VMAX - V(t))/VMAX] \times FR,$$

where *FR* is the force which an animal is capable of directing rearwards when its initial velocity is zero. Equations 6 and 7 can be combined and integrated to define the velocity at any time (*t*):

$$[8] \quad V(t) = VMAX \times (1 - e^{-(FR \times t)/(VMAX \times M)}),$$

where *e* is the base of the natural logarithms. The constant fraction, *FR/(VMAX × M)*, can be replaced by a single constant, *K*, to give:

$$[9] \quad V(t) = VMAX \times (1 - e^{-Kt})$$

or integrated to yield distance, *Y(t)*:

$$[10] \quad Y(t) = VMAX \times \left[ t + \left( \frac{1}{K} \times e^{-Kt} \right) - \frac{1}{K} \right].$$

Furusawa *et al.* (1928) developed a numerically equivalent equation and tested it by timing trained runners exerting a maximal 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.

#### The Velocity Curves

It is a straightforward procedure to apply standard nonlinear least squares fitting to the velocity data from the film analysis to determine the values of the constants, *VMAX* and *K*, of Eq. 9 for the predator and each of three prey for which adequate data were gathered. The results of this exercise for adult lions, zebra, and wildebeest over 1 year and Thomson's gazelle over 8 months are given in Table 10. It can be noted that the sample size is larger for the calculation of *VMAX* than *K* for some species. This results

TABLE 10. Rate constants of the velocity curves\* of maximal running for the African lion and three prey

Species	Rate constant	Value	Sample size	Variance	Covariance
African lion	$K$	0.68	3	0.019	0.36
African lion	$VMAX$	45.7	9	6.18	
Wildebeest	$K$	0.39	3	0.005	0.18
Wildebeest	$VMAX$	46.9	4	12.18	
Zebra	$K$	0.31	6	0.018	0.12
Zebra	$VMAX$	52.5	7	88.49	
Thomson's gazelle	$K$	0.17	5	0.0002	-0.0004
Thomson's gazelle	$VMAX$	86.8	5	4.36	

\*Refers to Eq. 9 (velocity in feet per second, time in seconds).

from a time-dependent feature of the parameters. The determination of  $K$  is largely derived from the initial seconds of acceleration and this was not always adequately recorded;  $VMAX$ , in contrast is largely derived from the velocities subsequent to this and thus was more regularly recorded. The fixing of  $K$  at its best estimate in these cases still permits an accurate estimate of  $VMAX$  and increases sample size.

Figure 5 illustrates the mean velocity curves of each of the three prey plus the lion, based upon Eq. 9 and the values given in Table 6. It can be seen that for each of these three prey, the attack strategy of the lion involves the lion, with its faster acceleration, overtaking prey before that prey can achieve maximum velocity and escape.

#### Application of the Velocity Equations: General

The value of the velocity equations for predator and prey lies in their usefulness for the prediction of the probability of attack success under various conditions. This procedure involves the matching of the sprint characteristics of the predator and prey. Specifically, the probability of a successful attack for a given prey species is equal to the proportion of that prey (assumed to have a normal distribution) which an average lion could capture. This procedure requires the determination of the variance associated with the value,  $Y(t)$ , of Eq. 10. Gilbert (1973) gives the procedure for determining this from the variance of  $VMAX$  and  $K$  and their covariance.

Several situations suggested by field observations are considered in the following sections.

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

Case one conditions (both lion and prey beginning from stationary positions on level ground, with the prey fleeing directly away from

the lion) were the most usual after crouching type stalks. In this case, for any initial predator-prey distance, it is possible to define with a normal cumulative probability function, the probability that a lion will overtake a prey within a time,  $t$ . In other words one defines the proportion of the prey population which the lion could overtake in that time. The results of this exercise for wildebeest, zebra, and Thomson's gazelle are illustrated in Fig. 6. (An irregularity of slope can be noted in the figure which results from an assumption (based on maximum length of observed attacks) that an attack would not exceed 35 s.)

The case one attack situation is useful for testing the predictive accuracy of the stalk (detection) and attack models as the probability ( $PC$ ) of capture success (excluding subduing success) for stalked prey can be defined:

$$[11] \quad PC = \int_{D=0}^{\infty} PA(D) \times PF(D) dD,$$

where  $D$  refers to distance,  $PA(D)$  the probability of attack success (based in this instance on a case one attack), and  $PF(D)$  the probability of the prey detecting (visually) and fleeing the lion at distance  $D$ . In this instance field data for diurnal stalks of wildebeest, which yielded case one attacks, gave an observed capture success of 38.9% ( $n = 54$ ). Equation 11 based upon the models derived, gave an expected probability of success of 38.5%. The same calculation can be undertaken for zebra. Here the calculated (expected) probability of capture success is 31.1% while the observed probability was 29.2% success ( $n = 48$ ). The closeness of the predictions of the model lends strong support to the validity of the formulations.

As was noted when discussing the stalk, the lion did not often use stalks for gazelle which

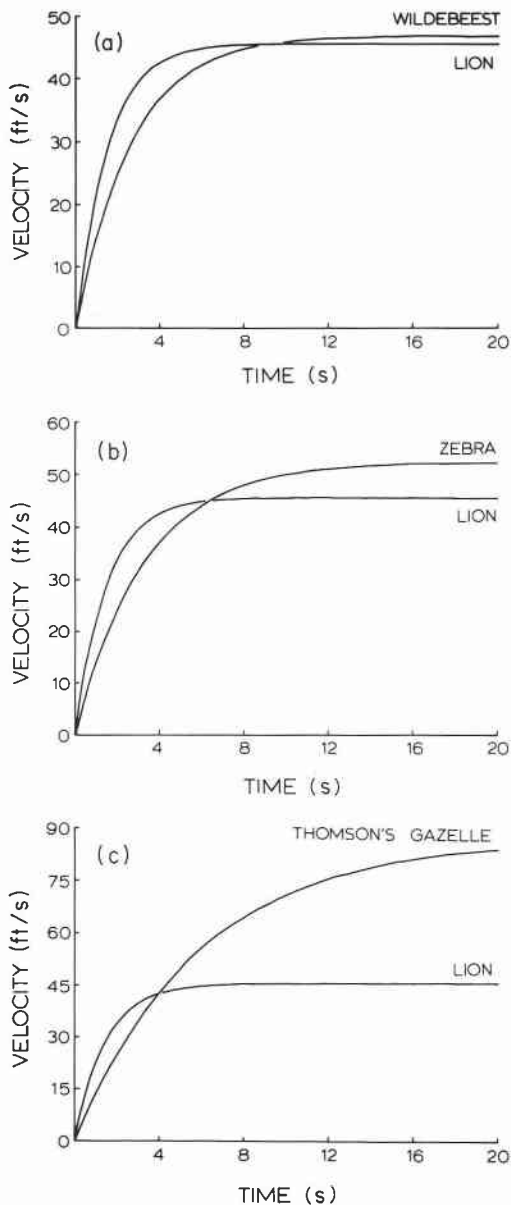


FIG. 5. (a) Wildebeest and lion velocity curves. (b) Zebra and lion velocity curves. (c) Thomson's gazelle and lion velocity curves.

would place it in a position for a case one attack diurnally or nocturnally. The probable reason for this is that the expected probability of success of such a tactic is only 7.0%.

The reason for the difference in success against Thomson's gazelle as opposed to wildebeest and zebra can be seen by further examination of Fig. 6. There are two features to these curves,

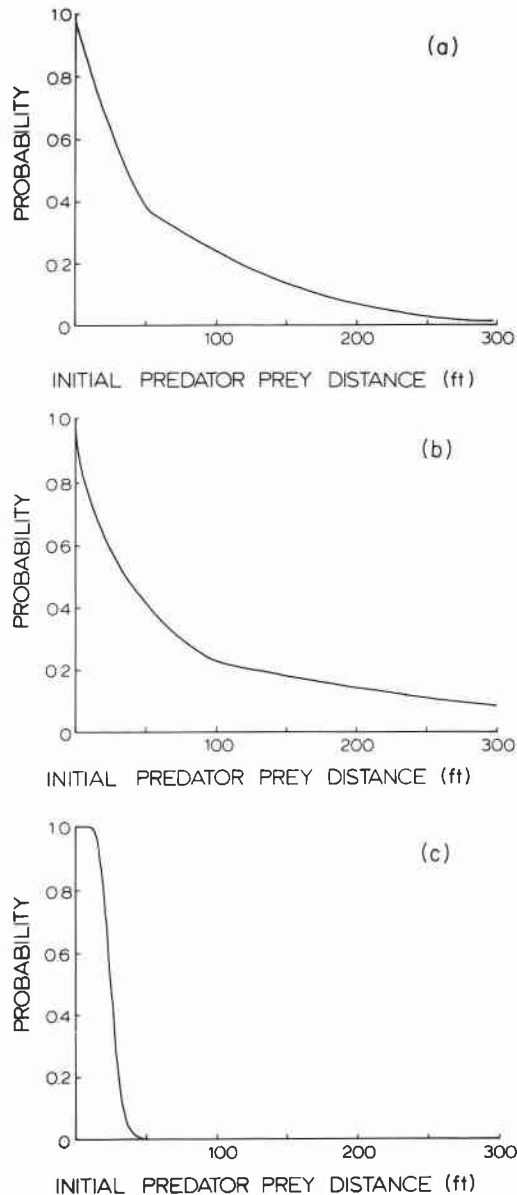


FIG. 6. (a) Wildebeest attack success; initial lion and prey velocities = 0.0; zero slope; direct flight. (b) Zebra attack success; initial lion and prey velocities = 0.0; zero slope; direct flight. (c) Thomson's gazelle attack success; initial lion and prey velocities = 0.0; zero slope; direct flight.

firstly there is the mean initial predator-prey distance at which prey can be successfully attacked. These points are indicated in the figures. 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. This aspect is the primary one causing the difference in prey capture success because the slightly below average, average, and above average individuals (in terms of their velocity curve parameters) are rarely captured. Thus the higher the proportion of the population which has decidedly below average parameter values, the higher the capture success. This is an important example of the role of physical condition in the success of prey escaping from a cursorial predator.

In view of the significance of the variance in the case one situation, it is worthwhile to examine this aspect further for possible generalities. A variety of attacked prey species can be simulated with differing velocity parameters and the influence on mean capture distance and the variance in capture distance derived. Four evenly spaced values of *VMAX* (48.0 to 96.0 ft/s) 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 0.5 probability of success; the remaining 10 simulations are illustrated in Fig. 7. (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 and *VMAX* = 48.0; *K* = 0.3 *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. A generalization seems to apply since

in each case the greater specialization (for either acceleration or speed) has the greater effective variance. Thus excessive specialization seems undesirable owing to increased lion susceptibility. Indeed, it can be seen that the three prey analyzed in fact show a lack of extreme specialization. Whereas the increased susceptibility to capture by the lion due to variance will reduce extreme specialization, other selective pressure (such as other predators or intraspecific social features) will tend to favour one parameter or the other. These two are mutually exclusive and thus favouring one reduces the other so that a prey species cannot achieve the best of both worlds.

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

Case two conditions were usual subsequent to a run stalk. The calculations involved in this iteration are similar to those of case one; however, a new equation for the distance-time relation must be substituted for the predator; specifically:

$$Y(t) = VMAX \times \left( t + \frac{1}{K} - (e^{-K(t+\phi)} - e^{-K\phi}) \right)$$

where,

$$\phi = \frac{-\ln \left( 1 - \frac{VI}{VMAX} \right)}{K}$$

and *VI* represents the initial predator velocity.

Figure 8 illustrates the effect of variation in lion starting velocity upon attack success for an initial predator-prey distance of 75 ft. The relative effect will vary depending upon initial predator-prey distance; however, for normal distance involved, such as 75 ft, the improvement in success is greatest for attacks upon Thomson's gazelle. This expected increase in success suggests a tactical value for the field observation that run stalks are more frequent for gazelle as compared with wildebeest and zebra.

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

Case three conditions were observed although velocities were not measured by filming. Calculations are similar to the previous cases; however, the effect of the slope of the ground requires replacement of the constant *VMAX* which

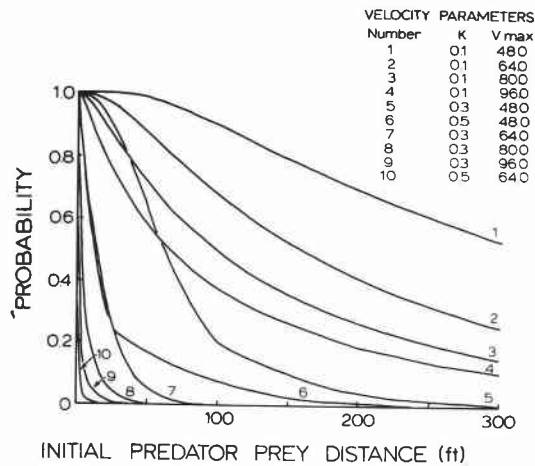


FIG. 7. Simulated prey attack success; initial lion and prey velocities = 0.0; zero slope; direct flight.

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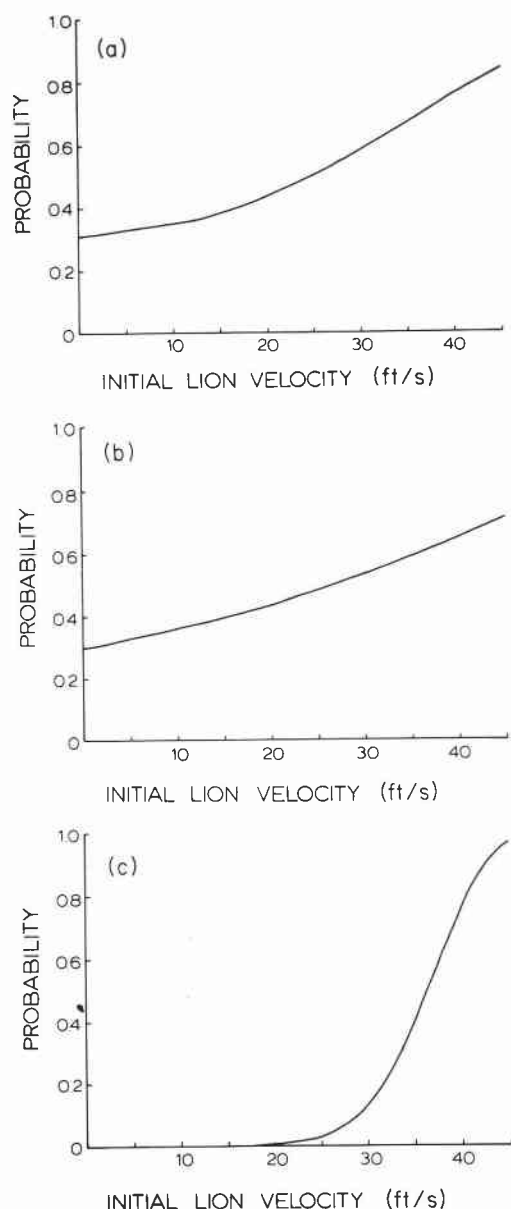


FIG. 8. (a) Wildebeest: Effect of initial lion velocity upon attack success; initial lion-prey distance = 75 ft; initial prey velocity = 0.0; zero slope; direct flight. (b) Zebra: Effect of initial lion velocity upon attack success; initial prey velocity = 0.0; zero slope; direct flight. (c) Thomson's gazelle: Effect of initial lion velocity upon attack success; initial lion-prey distance = 75 ft; initial prey velocity = 0.0; zero slope; direct flight.

necessitates reference to the complete form of the constant ( $K$ ),

$$K = FR/(VMAX \times M).$$

(This form also allows the calculation of the

force which the lion is capable of directing rearwards when its initial velocity is zero, which is found to be 10255 poundals (1 poundal  $\approx$  0.138 N) or 145 hg (319 lb). This magnitude is about what would be expected (Ikai 1968).

Since, as noted, the resistance to motion ( $RES(V)$ ) increases in approximately direct proportion to the velocity ( $V$ ):

$$RES(V) = FR/VMAX \times V.$$

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:

$$DF = MASS \times SIN(OMEGA) \times g$$

where  $g$  is the gravitational constant.

The constant ( $VMAX$ ) of the velocity equation can now be replaced by newly defined downslope ( $VD$ ) and upslope ( $VU$ ) maximum velocity constants. Consider firstly downslope running. Maximum downslope velocity still occurs when  $RES(VD)$  equals the total propelling force ( $FR + DF$ ); thus,

$$DF + FR = FR/VMAX \times VD,$$

which yields, with rearrangement:

$$VD = VMAX + [SIN(OMEGA) \times g/K].$$

The maximum upslope velocity is derived similarly yielding

$$VU = VMAX - [SIN(OMEGA) \times g/K]$$

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.

Figure 9 illustrates one downslope and one upslope example of the effect of slope upon attack success for wildebeest. Slopes to  $60^\circ$  are shown, but those beyond about  $10^\circ$  are of more

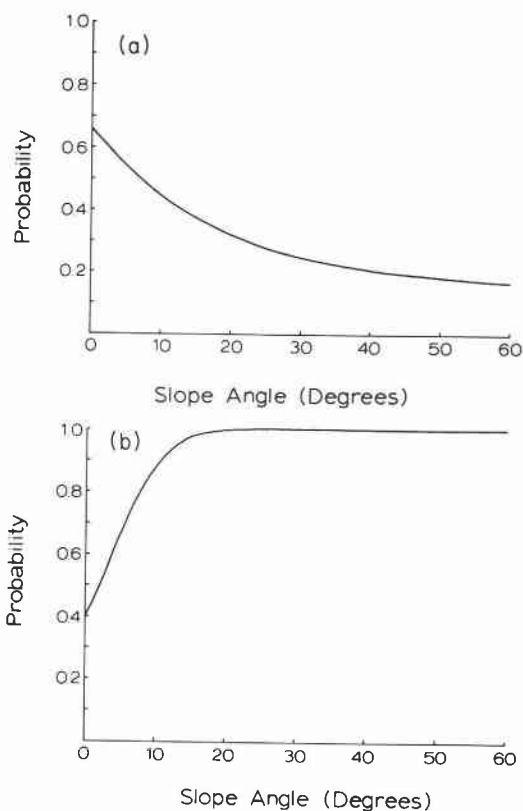


FIG. 9. (a) Effect of slope angle upon wildebeest attack success; initial lion-prey distance = 75 ft; direct flight; downslope movement; initial prey and lion velocities = 0.0. (b) Effect of slope angle upon wildebeest attack success; initial lion-prey distance = 75 ft; direct flight; upslope movement; initial prey and lion velocities = 0.0.

theoretical then 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. An analogous situation presented by Best and Partridge (1928) does however provide some support. They applied a constant external resistive force to human runners by winding a light cord around a metal drum. They found that external resistances of varying magnitude slowed the runners by an amount predicted from equations equivalent to the above.

The effect of slope might be of some significance in the design of artificial waterholes if it were desired to increase or decrease attack success.

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

Case four conditions frequently occurred in

conjunction with attacks after diurnal run stalks, although in these cases an initial predator velocity would also exist. Analysis of the effect of a restricted escape route requires two simplifying assumptions. Firstly the prey is assumed to follow a nonmaneuvering straight-line course at some angle ( $\theta$ ) to the initial predator-prey axis. Secondly, the predator velocity is assumed to be directed towards the location of the prey at each moment (specifically at the end of each integrating interval).

The calculations proceed similarly to those of case one and the results can be seen in Fig. 10 for wildebeest and Thomson's gazelle as prey and an initial predator-prey distance of 23 m (75 ft). It can be noted that the effect is minimal for small angles but highly significant for larger angles. Furthermore, 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. This expected increase in success further explains the tactic of

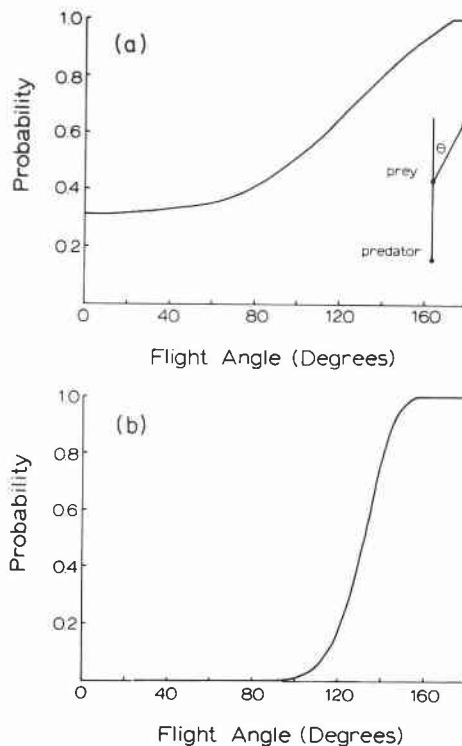


FIG. 10. (a) Wildebeest: Effect of prey flight angle upon attack success; initial lion-prey distance = 75 ft; initial prey and predator velocities = 0.0; zero slope. (b) Thomson's gazelle: Effect of prey flight angle upon attack success; initial lion-prey and predator velocities = 0.0; zero slope.

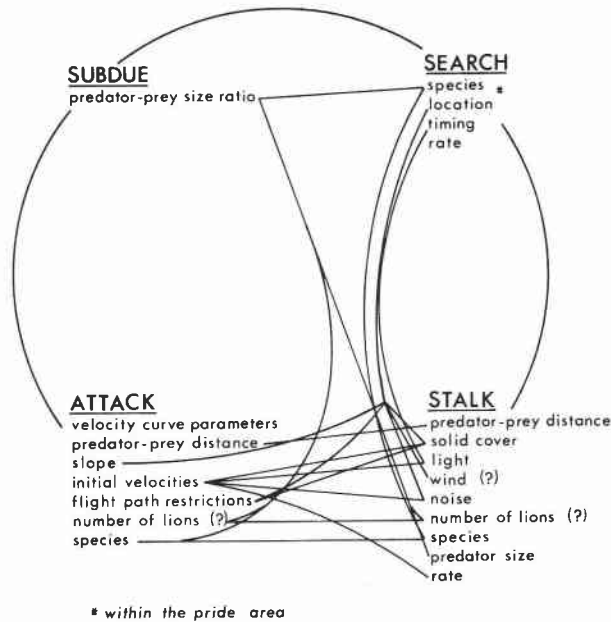


FIG. 11. The strategic and tactical variables affecting the success of prey capture events. Internal lines join related or identical variables in different events.

relatively high use of run stalks combined with restricted escape routes by the lion diurnally for gazelle as compared with wildebeest and zebra (Table 5).

Restricted escape routes is another feature which could be considered in designing water-holes and so forth.

#### *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 (Bouliere and Verschuren 1960)) are rarely captured except for young individuals. 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.

Field observations suggest that subduing prey is (1) unimportant for prey the size of wildebeest or smaller in size; (2) yields 28.6% failure for otherwise successfully attacked prey of zebra size; and (3) 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.

#### *The Lion as a Strategist and Tactician*

We have found that within the circumstances encountered in this study, 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 11 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 Fig. 11) 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 in Fig. 11, predator size and the velocity curve parameters, 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. First, prey is only captured within a specific size range with the upper limit defined by the ability to subdue prey (although cooperation among individuals can allow some raising of this limit). The lower limit is defined by energetic efficiency. Second, most prey capture involves the lion using its high acceleration to overtake more slowly accelerating prey. For a given prey capture situation, specific tactics based upon adjusting the values of the remaining variables are used to achieve maximum or at least 'satisfactory' success 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 others have been identified. The lion, in pursuing very young or enfeebled prey, uses its greater stamina to overtake a fatiguing prey. A second type, not specifically identified for the lion but common for the cheetah (unpublished data) involves a greater *V<sub>MAX</sub>* 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 fissioned 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 possible anti-search features). The velocity curve parameters of the prey define the bounds within which a variety of tactics are used to keep beyond the range or to avoid situations where the interaction of its velocity curve with that of the predator would result in its being overtaken. 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 nonfeeding activities.

The analysis presented here has been specific to adult female 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 fissioned.

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