

Profitability, encounter rates, and prey choice of African lions

D. Scheel
Department of Ecology,
Evolution and Behavior,
University of Minnesota,
Minneapolis, MN 55455, USA

The prey preferences of African lions (*Panthera leo*) in Serengeti National Park, Tanzania, were examined in three ways. First, lion encounter rates with prey types were measured and compared with a random sample of the prey population. Lions encountered more wart hogs (*Phacochoerus aethiopicus*), Grant's gazelles (*Gazella granti*), wildebeests (*Connochaetes taurinus*), and zebras (*Equus burchelli*) than expected. Second, preferred prey types of lions were identified using conditional logit analysis. Lions preferred to hunt small prey groups, groups that were closer than 200 m, and groups that contained wart hogs, wildebeests, or zebras. Third, a risk-minimization optimal foraging model and a rate-maximization model were used to predict lion preferences. The foraging theory models predict that preferences should change with season and with lion group size. Qualitative support was found for most of these predictions. *Key words*: African lions, diet choice, optimal foraging, predation, preference. [*Behav Ecol* 4:90–97 (1993)]

The encounter rate of predators and prey is one of several variables known to influence predator diet (Pulliam, 1974; Pyke, 1984; Van Orsdol, 1984; Stephens and Krebs, 1986). Optimal diet theory predicts that the inclusion of a prey type in the diet may depend on the encounter rate, profitability, and variance in profitability of more profitable prey (profitability is defined as the quotient of a prey type's net energy value, e , divided by the amount of time, h , required to catch and handle it; Stephens and Charnov, 1982; Stephens and Krebs, 1986).

In this paper, I examine encounter rates and foraging choices of African lions in Serengeti National Park, Tanzania. Lions encountered a higher proportion of some prey species than expected based on random samples of the prey population and also showed a greater tendency to hunt some species. These results are discussed with relation to prey profitability and the variance in profitability (optimal diet theory: Stephens and Charnov, 1982; Stephens and Krebs, 1986) and with respect to lion preferences for prey.

Preferences for prey were identified using conditional logit models (Aldrich and Nelson, 1984; McFadden, 1974; see Labinger et al., 1991 for use of similar models in analyzing predator preference). This method of analysis provides an estimate of lion selectivity of prey that is independent of measures of encounter rates, and it does not assume random associations between prey species. Conditional logit models thus offer advantages over more traditional tests of independence.

I consider two optimal diet models. The predictions for a rate-maximizing forager will depend on encounter rates with prey or patches of prey (Pulliam, 1974; Stephens et al., 1986). Foragers may face a large number of different patches of prey at the same time. Prey types will be found in many patches, but identical patches may not recur often,

if at all. I therefore regarded encounter rates with patches of each prey type as the rate of encounters with patches in which that prey type was the most profitable. I then used the "patches-as-prey" algorithm to predict patch choice for a rate-maximizing forager (Stephens and Krebs, 1986). The forager is predicted to choose the patch containing the most profitable prey item, and, within the chosen patch, it is predicted to forage on the most profitable prey item present. Foraging may involve costs other than handling time, such as the risk of injury. However, for simplicity such costs are ignored in these models.

I also consider an energy-shortfall risk-minimizing model in which predictions are based on a graphical solution for optimal preferences (Stephens and Charnov, 1982). On a plot of energy gain (profitability) versus standard deviation, the prey item that minimizes the risk of an energy shortfall is found by constructing the line with the greatest possible slope from R (energy requirement) on the energy axis to any point contained within the set of prey choices (see Figure 1).

METHODS

I observed lions in a 2000-km² area of Serengeti National Park, Tanzania (latitudes 1°–3°30' S, longitudes 30°50'–36° E), where lions have been studied continuously since 1966. This study population currently comprises about 200 individuals (Packer et al., 1988).

Sampling methods

Lion hunting behavior

I recorded hunting activities of radio-collared female lions and their companions during 96-h watches just before or after each full moon. I located lions at the start of each watch using aerial

D. Scheel is now at the Department of Biology, University of Houston, Houston, TX 77204-5513, USA.

Received 14 November 1991

Revised 4 May 1992

Accepted 4 June 1992

1045-2249/93/\$4.00

© 1993 International Society for Behavioral Ecology

radio-telemetry and followed the lions continuously for 96 h. Night observations were made using light-intensifying goggles and 8×35 binoculars. I measured distances using a Leitz range finder or the vehicle's odometer when possible, or else estimated distances visually. Estimates were accurate to within 10%, based on trials where estimated distances were subsequently measured with the range finder and odometer. During 96-h watches, I recorded 198 hunts during 3500 h of observation between September 1984 and December 1987. An additional 20 hunts were observed opportunistically over the same time period.

I defined hunts broadly as movement by at least one member of a lion group toward potential prey while the lion exhibited a typical stalking stance (for a complete definition and additional methods, see Scheel and Packer, 1991). I define lion group size as the number of adult females in a group (adult females do most of the hunting, Scheel and Packer, 1991).

Prey populations

To estimate the frequency of each species in herds in the general study area, I designated five fixed transects varying from 11 to 21 km in length and recorded herbivores along each transect approximately once a month. Herbivores within 500 m of the transect were recorded unless visibility was limited by brush or terrain, in which case the sampling area was reduced accordingly. Two transects were located in woodland habitat, two in plains habitat, and one in riverine habitat spanning the woodland/plains border (see Scheel and Packer, in press, for exact locations). Transects were located haphazardly with respect to lion habitat use and, except for the riverine habitat transect, did not continuously follow roads or drainage lines.

The frequency of each species in areas used by lions was recorded two ways: (1) on the day each transect was sampled, lions in the vicinity were located by radio-telemetry and all herbivore groups within 1000 m of the lions were censused; and (2) during 96-h watches, all herbivore groups within 1000 m of lions were censused hourly. Herds within 1000 m were usually visible to an observer and lions were observed to react to animals at least that distant. At night, moonlight was generally sufficient to allow censusing using light-amplification goggles. However, I did not record censuses when it was too dark to see herbivore groups clearly.

I considered all herbivore groups included in any hourly census to be available to lions should the lions decide to hunt. However, a lion that does not hunt may be occupied with other activities, may not be hungry, or may find no suitable prey in its vicinity. Thus, I restricted the analysis of observed lion preferences to only those prey available at the start of a hunt. This includes in the analysis only those sets of prey from which foraging lions actually made a choice.

The set of available herbivore groups from which lions decide to hunt is referred to as the "choice set" and includes all prey stalked by lions during the hunt and all herbivore groups present in the most recent hourly census before the hunt started. Herbivores recorded in censuses more than 1 hr before the hunt may be considered part of the choice set when hunts occurred on dark nights,

provided that the lions had not moved outside of the area of the most recent census before beginning to hunt ($N = 10$, less than 5% of 215 hunts in which prey was identified; it was not possible to tell if previously censused prey had moved out of an area in such cases). I included hunts recorded opportunistically outside of 96-h watches only if prey were censused at the time of the hunt.

For all of the above samples of prey populations, mixed-species herds were recorded once for each species they contained. The foraging model parameters λ , representing encounter rates with patch types, were calculated differently as required by the assumptions of the models (see below).

Analysis of choice behavior

Conditional logit analysis (McFadden, 1974) was developed for consumer research into human choice behavior and assumes that all consumers (lions) are identical (or are held constant) with respect to the process of choosing. Differences among the product sets (herds present at the start of a hunt) are examined for their influence on choice behavior (Aldrich and Nelson, 1984). Because all lions are assumed to be identical, I combined data from all prides sampled (however, see Results with respect to pride size). Conditional logit analysis offers advantages over more traditional tests of independence because there is no need to assume that prey types are encountered independently of one another. However, choice sets (prey available at the start of a hunt) differ significantly in the alternatives they offer to different pride sizes (see Results). It was therefore not possible to examine the effects on lion preferences of lion-related variation (such as lion group size or time since last meal) because that would require examining the choices made by different groups of lions from identical choice sets. Where appropriate, I also used goodness-of-fit tests (G test and chi square) in comparing sampled prey.

The herbivore group, rather than a particular individual or species, is recorded as the unit that lions stalk. Each hunt is considered a decision to stalk each of the prey species present in the group. This method of structuring the data is appropriate because lions may not necessarily all hunt the same individual in a herd, but in no case in this study did two lions of the same group simultaneously choose to hunt two different herds.

The characteristics of each herbivore group that were entered into the conditional logit analysis were (1) the log of the total number of individuals in each herbivore group (log was used because group size varied from 1 to >3000), (2) group composition as measured by the presence or absence of each of 10 species (Table 1) and by the frequency of individuals of each species (expressed as a proportion of the total group size), and (3) the distance from the prey group to the lions. I assumed that herds were identical except for variation as described by these variables. Both presence/absence and proportion of total herd for a given species could not be entered into the same model because of their colinearity. Models were therefore run twice, once using presence/absence and once using proportion. I estimated models in a reverse, step-wise fashion. Hunts that began when the choice set contained only a single herbivore group do not

Table 1
Prey recorded on fixed transects differed significantly from prey found near lions

Common name	Proportion of herds containing each species ^a		
	All herds Transect (N = 2188)	Within 1000 m of lions	
		Tran- sect ^b (N = 700)	Focal- animal ^c (N = 2703)
Thomson's gazelle	0.36	0.34	0.33
Grant's gazelle	0.14	0.16	0.25
Zebra	0.12	0.13	0.20
Wildebeest	0.07	0.09	0.19
Topi	0.14	0.13	0.11
Kongoni	0.14	0.14	0.09
Wart hog	0.05	0.06	0.07
Ostrich	0.004	0	0.02
Impala	0.10	0.08	0.02
Buffalo	0.03	0.05	0.02

^a Total proportions do not equal 1.0 because some herds contained two or more species.

^b There were 176 lion groups near transects.

^c Recorded during 96-h follows of lions.

contain information about lion choices among prey alternatives and thus are not included in conditional logit models. I ran conditional logit analyses using the CLOGIT module of the SYSTAT statistics package (Wilkinson, 1988).

Estimating foraging model parameters

I used the gross energy value of a prey type (estimated as the average amount of meat available per pride from prey killed during this study) as an approximation of the net energy value of each prey species (e). I calculated the amount of available meat on carcasses from published data on carcass weights and compositions for each age–sex class of prey (Blumenschine and Caro, 1986; Ledger, 1968; Sachs, 1967).

Handling time (h) is the sum of time spent hunting per kill (including stalking, capturing, and killing) and time spent feeding per carcass. I calculated the time lions spent hunting per kill using data from two sources. I calculated the number of hunts per kill using data combined from this study and Schaller (1972) for topis (*Damaliscus korrigum*), Thomson's gazelles (*Gazella thomsoni*), wart hogs, wildebeests, and zebras and using data from this study alone for buffaloes, kongonis (*Alcelaphus buselaphus*), and Grant's gazelles. The time lions spent stalking per hunt (including time spent catching and killing the prey) was calculated using data from this study only. When hunting mixed herds, the time lions spent hunting was tabulated once for each species present. For all calculations, only those hunts meeting Schaller's (1972) definition (lions must approach prey to within 60 m) were used. I then calculated the time spent stalking per kill from these two measures.

I calculated consumption times per kill based on the number of lions present, the size of the carcass, and the rate at which lions feed. Consumption times

for buffaloes are based on an assumption that an average of five lions feed on each carcass (since buffaloes were captured only by large prides). I calculated consumption times for all other species once for large prides (five lions per carcass) and once for small prides, assuming an average of 2.5 lions per carcass (Figure 1 and Table 1: For small prides of one to four adult females, most lions were found in groups of two or three; Packer et al., 1990). Schaller (1972) reports that lions feed at an average rate of about 20 min/kg of meat per lion. I calculated consumption times for carcasses using these figures and the amount of available meat per carcass.

Data were not sufficient to partition profitabilities both by prey species and pride size, although hunting success and foraging success are known to vary with pride size (Packer and Ruttan, 1988; Packer et al., 1990). However, with the exception of buffalo, the frequencies of prey types in choice sets are not correlated with pride size (see Table 3). The differences in energetic costs of capturing each prey type are likely to be small relative to both the gross energy value of the prey and to other costs (such as the risk of injury), which are not directly measurable in terms of energy.

For each prey type, I estimated the standard deviation of the profitability from all hunts of that species, where profitability of each hunt was calculated as energy gained (zero if the hunt failed) divided by handling time (stalking, capture, killing, and estimated feeding times). Only data from this study were used in calculating standard deviations and standard errors.

For the rate-maximization optimal diet model, I identified patches (herds) and ranked them by the most profitable prey item (species) present within each one, as required by the "patches-as-prey" algorithm (Stephens and Krebs, 1986). The encounter rate of the predator with prey patches (λ) was calculated for each of these patch types (i.e., λ could be calculated for the rate of encounters with the patch type defined as "herds in which wildebeest is the most profitable species present"). The rate λ pertains only to the most profitable prey in such patches (e.g., wildebeests) and hence should not be regarded as the rate of encounters between lions and each species of prey.

Values of λ were estimated using data from hourly censuses recorded during 96-h focal animal watches of lion behavior and are expressed for each herd type as the number of herds present within 1000 m of lions per hour. I considered all lions to be foraging at all times (Packer et al., 1990). Lions are extremely opportunistic hunters and, without actively searching, may capture prey that inadvertently wander close to them (Schaller, 1972). For this reason, it is not generally possible to be certain a lion is not foraging. Thus, λ is calculated as encounters per hour total time.

Prey density in the study area fluctuated seasonally, so values of λ were calculated for seasons when migrants were common and when migrants were scarce. I based calculations on 10 96-h watches when migrants were clearly abundant for the duration of the sample (herds of more than 100 wildebeests or zebras present or of more than 1000 Thomson's or Grant's gazelles) and on 10 96-h watches when migrants were clearly scarce for the

duration of the sample (no herds larger than 100 wildebeests or zebras and none larger than 150 Thomson's or Grant's gazelles). For each season, I included three watches in woodland habitat (12 days) and seven (28 days) in plains habitat.

Wart hogs were the only species for which encounter rates fluctuated diurnally. Wart hogs are active only during the day, and they spend the night in burrows. Thus, wart hogs were not recorded in prey censuses and were not available to lions after dark (see Scheel, in press). Rather than use the average λ over both night and day for wart hogs (as was done for other species), I calculated λ as encounters per daylight hour.

For the risk-minimizing model, I based estimates of energy requirements on published daily intake rates for Serengeti lions (Packer et al., 1990). Requirements are calculated as the necessary intake per pride per hour spent hunting and handling food, assuming lions require an average of 5–8 kg of meat per day, spend 20 min/kg per lion consuming food (see above) and hunt 35 min per day (the average time spent actively hunting during 96-h watches). Each lion thus requires between 2.2 and 2.5 kg of meat per hour spent hunting and eating. Small prides therefore require 2.5 times this amount; large prides, five times this amount.

Effects of lion hunting-group size

Lion group size appears to be constrained by factors other than foraging considerations (Packer et al., 1990). Small groups of lions in the Serengeti appear unable to capture buffaloes (Packer et al., 1990), yet buffaloes are an important prey item for large Serengeti prides (Scheel and Packer, 1991). The preference of lions for buffaloes is therefore expected to depend on the group size of the hunting lions (see Results). As conditional logit analysis is not appropriate to examine the effects of lion-dependent variables on choice, I examined choice sets present when lions of different group sizes began hunting to see if choice sets varied with lion hunting-group size. This comparison was done using a G^2 test for sparse contingency tables (Koehler, 1986).

RESULTS

Prey populations

I recorded 17 species of herbivores on the transects in more than 2000 herds, 700 of which were near lions. More than 2000 herds were also recorded near lions during hourly censuses, of which 432 are included in choice sets (present at the start of hunts). More than 90% of all herbivores recorded were 1 of 10 prey species (Tables 1 and 2). This is true for herbivores in all sample sets, whether prey are censused by individuals or groups and whether hunts are counted individually or by time, distance, or percentage of meat obtained by predation. Only these 10 species are included in these analyses.

Frequencies of each species in herbivore groups sampled on fixed transects differed significantly from those recorded in the vicinity of lions. This was true for both samples of prey near lions (chi-square goodness-of-fit test, prey within 1000 m of lions near transects: $\chi^2 = 20.9$, $df = 9$, $p < .025$;

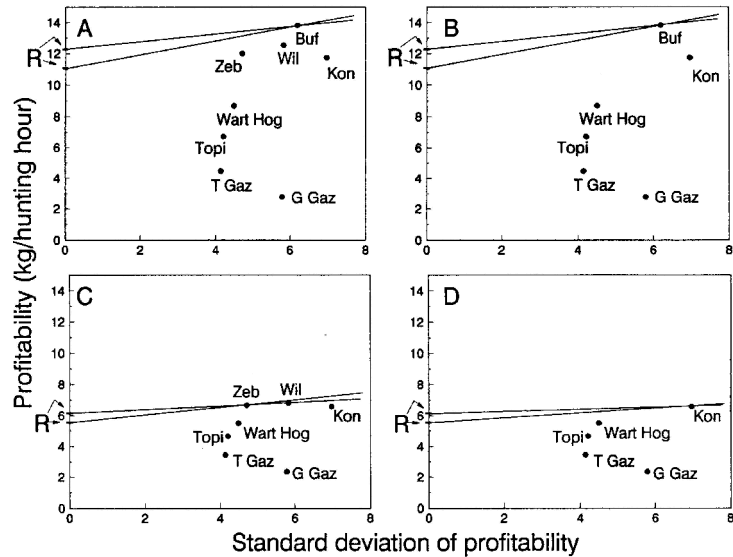


Figure 1 Energy value and standard deviation for lions hunting in Serengeti National Park. The figure shows prey available to (A, B) large (greater than five adult females) and (C, D) small (less than five adult females) groups of lions when migrants are abundant (A, C) and migrants are scarce (B, D). Low and high estimates of energy requirement (R) are calculated as kilograms of meat required by each pride per hour spent hunting and eating (see Methods); large prides have higher requirements because more lions are present. The risk-minimizing choice is indicated by the line of greatest possible slope from R to any point within the set of available prey. Profitabilities are expressed as kilograms of meat per pride (not per lion), and change with pride size because the prey is consumed more quickly when many lions are present. Profitabilities do not change with season. Availability of prey changes both with pride size (buffaloes are not available to small prides) and with season (wildebeests and zebras are not available when migrants are scarce).

available prey recorded during focal animal samples of lion behavior: $\chi^2 = 1297$, $df = 9$, $p < .001$). In both these samples of prey near lions (Table 1), wart hogs, wildebeests, zebras, and Grant's gazelles were present with greater than expected frequency relative to their frequencies in herds on fixed transects. Thomson's gazelles, impalas, topis, and kongonis were present near lions with less than expected frequency in each sample. Both buffaloes and ostriches were present near lions more often than expected in one sample and less often than expected in the other.

Frequencies of species in herbivore groups near lions (available herds recorded during focal animal samples) differed significantly from those present at the start of hunts (Table 2, choice sets; chi-square goodness-of-fit test, $\chi^2 = 74.45$, $df = 9$, $p < .001$). This was due primarily to the presence of wart hogs at the start of hunts much more frequently, and

Table 2 Frequencies of herbivore species recorded on 96-h follows near lions and at the start of hunts

Common name	Proportion of herds containing each species ^a		
	Available herds ^b ($N = 2703$)	Choice sets ($N = 432$)	Herds hunted ($N = 215$)
Thomson's gazelle	0.33	0.25	0.13
Grant's gazelle	0.25	0.19	0.12
Zebra	0.20	0.14	0.18
Wildebeest	0.19	0.17	0.18
Topi	0.11	0.07	0.07
Kongoni	0.09	0.07	0.05
Wart hog	0.07	0.16	0.24
Ostrich	0.02	0.03	0.005
Impala	0.02	0.02	0.005
Buffalo	0.02	0.04	0.05

^a Total proportions do not equal 1.0 because some herds contained two or more species.

^b Herds near lions.

Table 3

The occurrence of each species in herds ($N = 425$) present at the start of hunts ($N = 212$) varied with the size of the pride (adult females)

Common name	No. of lions							Total
	1	2	3	4	5	6	7	
Thomson's gazelle	17 (14) ^a	12 (21)	30 (29)	27 (33)	1 (14)	1 (8)	0 (0)	88
Grant's gazelle	15 (12)	9 (16)	37* (36)	6 (7)	1 (14)	0 (0)	0 (0)	68
Zebra	22 (18)	10 (18)	6 (6)	11 (14)	0 (0)	1 (8)	0 (0)	50
Wildebeest	32 (26)	12 (21)	9 (9)	6 (7)	0 (0)	0 (0)	2 (40)	61
Topi	3 (2)	2 (4)	3 (3)	12 (15)	0 (0)	3 (25)	1 (20)	24
Kongoni	6 (5)	7 (12)	3 (3)	5 (6)	0 (0)	1 (8)	2 (40)	24
Wart hog	24 (20)	4 (7)	14 (14)	13 (16)	1 (14)	1 (8)	0 (0)	57
Buffalo	2 (1)	0 (0)	1 (1)	1 (1)	4* (57)	5* (42)	0 (0)	13
Total herds	121	56	103	81	7	12	5	

Some herds contain more than one species. Not all species present were stalked in each hunt.

^a Numbers in parentheses indicate percentage of total herds present for each group size that contained each species.

* Large contribution to the G^2 value (buffalo, 5 lions: $G^2 = 14.8$, 6 lions: $G^2 = 18.2$; Grant's gazelle, 3 lions: $G^2 = 13.1$. All other individual cell contributions were $G^2 < 6.0$).

buffalo somewhat more frequently, than expected based on their occurrences near lions. The presence of these species more often at the start of hunts suggests that they either are actively sought out or that their presence influences the decision to hunt. Thomson's gazelles, Grant's gazelles, and zebras were all present at the start of hunts somewhat less frequently than expected. Thus the herbivore groups present when lions began to hunt were not a representative sample of all herbivore groups available to lions, nor were prey available to lions a representative sample of prey recorded in the absence of lions.

Differences in choice sets by lion group size

Lion hunting-group size varied from one to seven adult females (cases where males were observed hunting in the absence of females are not included). The composition of choice sets differed significantly across lion group sizes. This effect was primarily due to the presence of buffaloes in choice sets for groups of five and six lions considerably more often than expected (Table 3; $G^2 = 139.7$, $Z = 19.8$, $p < .001$, after Koehler, 1986). Aside from Grant's gazelles, which were present more often than expected for groups of three lions, the occurrence of other species in choice sets did not vary significantly with lion group size. Ostriches and impalas were not considered in this analysis due to small sample sizes when broken down by lion group size.

Lion choice of prey groups

The analysis of lion choice of prey groups used conditional logit models to compare characteristics of herds stalked by lions with those of all herds present in the choice set. As hunts by all pride sizes are included, differences in preferences across pride sizes (if they exist) are obscured.

Whether recorded as proportion of total herd size or by the presence or absence of a species, lions preferred herds containing wart hogs (proportion: $T = 2.875$, $p < .05$; presence: $T = 3.186$, $p < .05$), wildebeests (proportion: $T = 2.378$, $p <$

$.05$; presence: $T = 2.365$, $p < .05$), or zebras (proportion: $T = 2.247$, $p < .05$; presence: $T = 2.409$, $p < .05$). There was no significant trend to prefer or avoid any of the seven other common prey species, using either measure of herd composition. Lions preferred to stalk prey that were closer over prey that were farther away (proportion, distance of 0–50 m: $T = 3.444$; 51–200 m: $T = 2.614$; >200 m: $T = -6.058$; presence, 0–50 m: $T = 3.633$; 51–200 m: $T = 3.250$; >200 m: $T = -6.883$, all $p < .05$). Herds that were smaller were preferred over larger herds [log(herd size) in proportion model: $T = -2.952$, $p < .05$; presence model: $T = -2.491$, $p < .05$]. The overall fit of either model containing the five significant variables was significant (proportion model: $\chi^2 = 87.61$, $df = 6$, $p < .001$; presence: $\chi^2 = 92.50$, $df = 6$, $p < .001$).

Foraging model predictions

Foraging model parameters for prey types are given in Table 4. For each species except Grant's gazelles, at least 25% of kills were calves or juveniles. The weights (kg of meat) and times spent stalking per kill for these species incorporate the small size and ease of capturing young individuals in the observed proportions. No estimates were available for impalas (*Aepyceros malampus*) or ostriches (*Struthio camelus*) because no successful hunt of these species was observed.

The rate-maximization model parameters, λ (Table 5), indicate the seasonal shift in prey density and the habitat choice of lions. In calculating values of λ , each herd was characterized by the most profitable species it contained. Herds characterized by a migratory species were the most frequently encountered patch types when migrants were abundant (Table 5). When migrants were scarce, however, herds characterized by a migratory species were among the least frequently encountered patch types. All semi- and nonmigratory species more frequently characterized herds encountered by lions when migrants were scarce than when migrants were common (G test, $G = 96.0$, $df = 4$, $p < .001$). Regardless of whether a species was the most profitable one within a herd, all semi- and nonmigratory

Table 4
Estimates of profitability for lions hunting common Serengeti herbivores

Common name	Meat (kg)	h/hunt	Hunts/kill	h/kill	h to eat ^a	h_i (h)	e_i/h_i (kg/h)	
							Mean	SE ^b
Buffalo	240 (2) ^c	0.55 (5)	2.5 (5)	1.37	16.02	17.40	14	2.8
Wildebeest	85.2 (4)	0.32 (20)	3.4 (78) ^a	1.10 ^a	11.35	12.47 ^a	6.8 ^a	0.67
Zebra	82.2 (4)	0.35 (16)	3.8 (73) ^a	1.35 ^a	10.95	12.32 ^a	6.7 ^a	0.63
Kongoni	37.4 (1)	0.22 (3)	3.0 (3)	0.68	4.15	4.83	6.6	2.03
Wart hog	37.2 (9)	0.57 (36)	3.2 (54) ^a	1.8 ^a	4.13	5.93 ^a	5.5 ^a	0.41
Topi	37.3 (2)	0.45 (10)	6.7 (27) ^a	3.07 ^a	4.97	8.03 ^a	4.6 ^a	0.69
Grant's gazelle	27.4 (1)	0.47 (9)	9.0 (9)	4.30	3.65	7.95	3.4	0.73
Thomson's gazelle	3.6 (6)	0.27 (18)	3.8 (435) ^a	1.03 ^a	0.47	1.52 ^a	2.3 ^a	0.73

^a Values estimated with combined data from this study and Schaller (1972).

^b Standard errors for profitabilities were calculated using data from this study only.

^c Sample sizes (kills or hunts) are indicated in parentheses.

species were encountered by lions more frequently when migrants were scarce than when migrants were abundant (G test, $G = 67.0$, $df = 4$, $p < .001$). However, this was not true of the same species when recorded on transects (G test, $G = 9.23$, $df = 4$, $p > .05$), suggesting that lions actively seek out semi- and nonmigratory species when prey is scarce.

Predicted preferences of a rate-maximizing forager

In general, the diet was predicted to contain the five most profitable species when migrants were scarce (profitabilities, Table 4; predictions, Table 5). When migrants were present, only the four most profitable species remained in the predicted diet. However, profitability changes with pride size for two reasons: larger prides have lower handling times because there are more lions to consume the prey, and small groups of one to four lions appeared to be unable to capture buffaloes in this study. Thus, for groups of five or more lions, buffaloes were predicted to be the most preferred prey in both seasons, whereas for smaller groups, buffaloes had an effective profitability of zero and were expected to be least preferred. For small lion groups, wildebeests and zebras were predicted to be most preferred when they were available.

When migrants were scarce, kongonis were predicted to be the most preferred prey for small groups of rate-maximizing lions (because wildebeests and zebras are migrants). Wart hogs were predicted to be the second most preferred prey for small lion groups in the absence of migrants.

Predicted preferences of a risk-minimizing forager

Figure 1 shows the set of prey types most commonly available to lion prides. For large lion prides in either season (Figure 1A,B), the choice of buffaloes results in the lowest risk of an energy shortfall, followed by zebras and wildebeests if they are available, and kongonis when migrants are scarce.

For small prides of lions (Figure 1C,D), zebras and wildebeests are the risk-minimizing choices when they are available; kongonis and wart hogs are risk-minimizing when migrants are scarce. When migrants are abundant, small lion groups should prefer zebras and wildebeests to wart hogs.

Predictions of the two models were nearly identical. The only difference was that the rate-maximization model predicts a preference for wildebeests over zebras, and the risk-minimization model predicts the reverse for small prides in the presence of migrants. However, differences between the profitability of wildebeests and zebras were slight.

Table 5
Estimates of λ for a diet choice model of rate-maximizing Serengeti lions during seasons of prey scarcity and abundance

Common name ^a	λ (herds/h) ^b		Include in diet?		Migratory behavior	Reference ^c
	Scarce ($N = 570$)	Abundant ($N = 953$)	Scarce	Abundant		
Buffalo	0.035	0.011	Yes	Yes	Semimigratory	3,4,7
Wildebeest	0.004	0.382	Yes	Yes	Migratory	3,4,6,7
Zebra	0.008	0.246	Yes	Yes	Migratory	4,6,7
Kongoni	0.119	0.031	Yes	Yes	Semimigratory	1,2,3,6
Wart hog	0.116	0.056	Yes	No	Nonmigratory	1,5,6,7
Topi	0.104	0.101	No	No	Semimigratory	2,3,4,6
Grant's gazelle	0.181	0.100	No	No	Semimigratory	4,6,7
Thomson's gazelle	0.094	0.175	No	No	Migratory	3,4,6,7

^a Species are listed in order of decreasing profitability (see Table 4).

^b N indicates number of herds included.

^c References for migratory behavior: 1, Bertram, 1979; 2, Grimsdell, 1979; 3, Jarman, 1974; 4, Jarman and Sinclair, 1979; 5, Rodgers, 1984; 6, Schaller, 1972; 7, Sinclair, 1977.

DISCUSSION

I have used three overlapping but distinct models to examine lion foraging behavior. In the first model, the frequencies of lion encounters with prey are used to infer lion preferences. In the second model, lion choice of which prey groups to hunt is modeled under the assumption that all lions are equal and that diet is only influenced by variation in qualities of the prey. In the third model, optimal foraging theory is used to predict lion diet with the assumption that prey individuals belong to one of only a few different types and that lions may be rate maximizers or risk minimizers. Although differences preclude statistical comparison between models, it is useful to consider all three models because each can illuminate shortcomings of the others.

Encountering prey

In this study, lions encountered and chose to stalk a distinct subset of the prey present in the study area. Over both samples of prey near lions (lions on transects and 96-h focal individual samples; all lion group sizes) wart hogs, wildebeests, and zebras (the three species preferred by lions, as measured by the conditional logit models) were more abundant in the prey populations, whereas Thomson's gazelles, topis, ostriches, and impalas (four of the seven species not preferred) were less abundant. Of the remaining three species that were not preferred (Grant's gazelles, kongonis, and buffaloes), only Grant's gazelles were present at higher than expected frequencies near lions.

Furthermore, prey present when lions began to hunt (the choice sets) was richer in wart hogs (the most preferred prey species) and in buffaloes than was the population of all prey near lions not hunting. The foraging theory models predict that buffaloes should be preferred prey for large prides, but not for small. Buffaloes only occurred more frequently than expected in choice sets for large lion groups and not in choice sets for small lion groups.

Choice of prey groups to hunt

Across all pride sizes, lions preferred to hunt only prey groups containing wart hogs, wildebeests, and zebras. Combined with the result that lions also appear to encounter these three species preferentially, this suggests that lions actively seek to include these species in their diet in preference to other available prey. Buffaloes, although preferentially encountered by large prides of lions, were not statistically preferred by all lions over other prey types. This may be readily accounted for if preference for buffaloes is lion group-size specific. The lack of interest on the part of small prides of lions may thus obscure any preference by large prides of lions in conditional logit models where all pride sizes were grouped. This accords well with the foraging theory assumption that lion prey choice is based on the profitability of prey types—buffaloes are unique among prey types considered here in that their profitability changes dramatically with pride size. This is because small groups of lions appear to be unable to attack buffaloes successfully.

Foraging theory considerations of prey choice

It has long been recognized that lions hunt opportunistically (Packer et al., 1990; Schaller, 1972). The predictions of the foraging models are based on the assumption that species are the correct prey types for which to calculate profitability and variance in profitabilities. However, the fact that lions prefer close prey over distant prey, frequently hunt young individuals, and adjust their foraging behaviors according to their own group size (see above and Scheel and Packer, 1991) suggests that lions do not consider all members of a species to be equally profitable under all circumstances.

The predictions of foraging theory are useful to consider despite these limitations because they suggest unique ways to examine the other models. Foraging theory considerations clearly predict that preference for buffaloes should be lion group-size specific. This prediction held when tested. Both models also predict seasonal variation in the lions' foraging behavior: when migrants are abundant, wart hogs are not predicted to be part of the lions' diet (rate maximization; Table 5) or else are predicted to be lower on the preference list (risk minimization; Figure 1). Predation of wart hogs was considerably higher when migrants were scarce than when they were abundant (Scheel, in press). Encounters with wart hogs were also higher when migrants were rare (Table 5), suggesting that lions were actively seeking prey when migrant species were not available. Additionally, the predictions of the foraging models accord reasonably well with the observed behavior of the lions: the preferred prey (wart hogs, wildebeests, and zebras) were also the most profitable. The only exception to this is kongonis, which appear to be more profitable than lion preferences would suggest (however, the data for kongonis are limited to only three hunts).

Buffaloes, wildebeests, zebras, and wart hogs provide Serengeti lions with almost 90% of the food they obtain from predation (Scheel and Packer, 1991) and thus are the most important prey species in the diet of these lions. Although my results are not a conclusive, quantitative test of either the rate-maximization or risk-minimization foraging models, they suggest that large, long-lived predators may be sensitive to variation in prey profitability. Note, however, that the expected profitabilities of particular prey items appear to fluctuate with many factors, including the age of the prey, the distance of the prey from the lions, the prey group size, and the lions' group size. The effect of variation in the expected profitability of prey was apparent in the tendencies of lions to prefer prey in small herds and in nearby herds. Such herds are likely to have higher profitabilities (or lower variances) under the circumstances than the same animals in a larger, more distant herd.

These results also suggest that mobile predators may structure their behavior to maximize encounters with prey types that have high profitability or low variance, and thus that optimal foraging behavior may include not only decisions of which prey to consume but also of which prey to encounter. This is possible when the location of specific prey is predictable.

I thank George John for introducing me to conditional logit analysis; Craig Packer and Gary Oehlert for advice;

Craig Packer and two anonymous reviewers for helpful comments on earlier versions of the manuscript; David S. Babu, Director of Tanzania National Parks, Karim Hirji, Coordinator of the Serengeti Wildlife Research Institute, and the Tanzanian National Scientific Research Council for permission and facilities; and Craig Packer, Steve Scheel, Jon Grinnell, Barbie Allen, Marcus Borner, Anne Pusey, John Fanshawe, Larry Herbst, Bruce Davidson, Richard Mathews, Samantha Purdy, Alan Root, Charlie Trout, and Ken Scheel for assistance with field work. This work was supported by National Science Foundation grants BSR 8406935 and 8507087 to Craig Packer and Anne Pusey and by the Dayton Natural History Fund of the Bell Museum of Natural History fellowships and a University of Minnesota Doctoral Dissertation fellowship to D.S.

REFERENCES

- Aldrich JH, Nelson FD, 1984. Linear probability, logit and probit models. Sage University Paper Series on Quantitative Applications in the Social Sciences, Series No. 45. Beverly Hills, California: Sage Publications.
- Bertram BCR, 1979. Serengeti predators and their social systems. In: Serengeti: dynamics of an ecosystem (Sinclair ARE, Norton-Griffiths M, eds). Chicago: University of Chicago Press; 221–248.
- Blumenschine RJ, Caro TM, 1986. Unit flesh weights of some East African bovids. *Afr J Ecol* 24:273–286.
- Grimsdell JJR, 1979. Changes in populations of resident ungulates. In: Serengeti: dynamics of an ecosystem (Sinclair ARE, Norton-Griffiths M, eds). Chicago: University of Chicago Press; 353–359.
- Jarman PJ, 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215–267.
- Jarman PJ, Sinclair ARE, 1979. Feeding strategy and the pattern of resource partitioning in ungulates. In: Serengeti: dynamics of an ecosystem (Sinclair ARE, Norton-Griffiths M, eds). Chicago: University of Chicago Press; 130–163.
- Koehler K, 1986. Goodness of fit tests for log-likelihood models in sparse contingency tables. *J Am Stat Assoc* 81:483–493.
- Labinger Z, Katzir G, Benjamin Y, 1991. Prey size choice by captive pied kingfishers, *Ceryle rudis* L. *Anim Behav* 42:969–975.
- Ledger HP, 1968. Body composition as a basis for comparative study of some East African mammals. *Symp Zool Soc Lond* 21:289–310.
- McFadden D, 1974. Conditional logit analysis of qualitative choice behavior. In: *Frontiers in econometrics* (Zeremba P, ed). New York: Academic Press; 105–142.
- Packer C, Herbst L, Pusey AE, Bygott D, Hanby JP, Cairns SJ, Borgerhoff Mulder M, 1988. Reproductive success of lions. In: *Reproductive success: studies of individual variation in contrasting breeding systems* (Clutton-Brock TH, ed). Chicago: University of Chicago Press; 363–383.
- Packer C, Ruttan L, 1988. The evolution of cooperative hunting. *Am Nat* 132(2):159–198.
- Packer C, Scheel D, Pusey AE, 1990. Why lions form groups: food is not enough. *Am Nat* 136:1–19.
- Pulliam HR, 1974. On the theory of optimal diets. *Am Nat* 108:59–74.
- Pyke GH, 1984. Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523–579.
- Rodgers WA, 1984. Warthog ecology in south east Tanzania. *Mammalia* 48(3):327–350.
- Sachs R, 1967. Liveweights and measurements of Serengeti game animals. *East Afr Wildl J* 5:24–36.
- Schaller GB, 1972. *The Serengeti lion: a study of predator-prey relations*. Chicago: University of Chicago Press.
- Scheel D, in press. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. *Anim Behav*.
- Scheel D, Packer C, 1991. Group hunting behaviour of lions: a search for cooperation. *Anim Behav* 41(4):697–709.
- Scheel D, Packer C, in press. Variation in lion diet: tracking a moveable feast. In: *Serengeti II: research, management and conservation of an ecosystem* (Sinclair ARE, Arcese P, eds). Chicago: University of Chicago Press.
- Sinclair ARE, 1977. *The African buffalo: a study of resource limitation of populations*. Chicago: University of Chicago Press.
- Stephens DW, Charnov EL, 1982. Optimal foraging: some simple stochastic models. *Behav Ecol Sociobiol* 10:251–263.
- Stephens DW, Krebs JR, 1986. *Foraging theory. Monographs in behavior and ecology* (Krebs JR, Clutton-Brock T, eds). Princeton, New Jersey: Princeton University Press.
- Stephens DW, Lynch JF, Sorensen AE, Gordon C, 1986. Preference and profitability: theory and experiment. *Am Nat* 127(4):533–553.
- Van Orsdol KG, 1984. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *Afr J Ecol* 22:79–99.
- Wilkinson L, 1988. *SYSTAT: the system for statistics*. Evanston, Illinois: SYSTAT.