

ECOLOGICAL CONSEQUENCES OF FORAGING MODE¹

RAYMOND B. HUEY

Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195 USA

AND

ERIC R. PIANKA

Department of Zoology, University of Texas, Austin, Texas 78712 USA

Abstract. Desert lizards are typically either widely foraging or sit-and-wait predators, and these foraging modes are correlated with major differences in ecology. Foraging mode is related to the type of prey eaten by lizards. Widely foraging lizards in the Kalahari desert, the Western Australian desert, and the North American desert generally eat more prey that are sedentary, unpredictably distributed, and clumped (e.g., termites) or that are large and inaccessible (inactive scorpions) than do sit-and-wait lizards. In contrast, sit-and-wait lizards eat more prey that are active. Foraging mode also appears to influence the types of predators that in turn eat the lizards. For example, a sit-and-wait snake eats predominately widely foraging lizards. Crossovers in foraging mode thus exist between trophic levels. Widely foraging lizards may also encounter predators more frequently, as suggested by analyses of relative tail lengths; but tail break frequencies are ambiguous. Daily maintenance energetic expenditures of widely foraging lizards appear to be about 1.3-1.5 times greater than those of sit-and-wait lizards in the same habitats, but gross food gains are about 1.3-2.1 times greater. Widely foraging species also have lower relative clutch volumes, apparently in response to enhanced risks of predation. Foraging mode within one species varies with changes in food availability. Physiology, morphology, and risk of predation might generally restrict the flexibility of foraging mode. Because foraging mode constrains numerous important aspects of ecology, any general model of foraging velocity must be complex.

Key words: *Australian desert; foraging mode; Kalahari desert; lizards; predation; sit-and-wait; termites.*

INTRODUCTION

Like most predators, lizards typically forage in one of two ways. Some are very active, cruising predators ("widely foraging"), whereas others are much more sedentary, ambush predators ("sit-and-wait"). This apparent dichotomy in foraging mode (Pianka 1966, Schoener 1971, Eckhardt 1979) is conspicuous and prompts a variety of significant questions concerning possible ecological correlates of foraging mode: (1) Do types and amounts of prey obtained vary with foraging mode? (2) Is foraging mode related to the types of predators that in turn eat the lizards? Does foraging mode alternate among trophic levels? (3) What are the extra energetic costs of foraging widely? (4) Does foraging mode change with immediate environmental conditions or is it relatively fixed within a species? (5) How does foraging mode constrain reproductive biology?

This paper arose from field observations on seven species of lacertid lizards in the Kalahari semidesert of southern Africa. Five species forage widely and two others sit and wait. The syntopic occurrence of both foraging types in a single, very closely related group offers a convenient "natural experiment" that provides a substantial measure of control over phyloge-

netic and sensory differences and thus an ideal opportunity to determine ecological correlates of foraging mode. To evaluate the generality of our results, we briefly examine data on lizards from independently derived deserts in North America and in Western Australia. These faunas are, however, less suitable for comparative analyses because they involve lizards from different families that may use divergent senses and techniques in locating prey (Stebbins 1948, Stamps 1977, Regal 1978).

We answer Question 1 above by comparing kinds and amounts of prey eaten by widely foraging vs. sit-and-wait lizards. In particular, we contrast the relative utilization of termites, the major prey of Kalahari lacertids (Pianka et al. 1979). Lizards can gain high energy returns from these sedentary and clumped prey. However, because the aboveground activity of some African and Kalahari termites may be spatially and temporally unpredictable (Wilson and Clark 1977, W. Coaton, *personal communication*, R. Huey and E. Pianka, *personal observations*), only widely foraging lizards should routinely encounter and eat termites. Differences in types of predators that eat lizards (Question 2) are determined by examining diets of such sit-and-wait vs. widely foraging predators. Relative energetic expenditures (Question 3) are estimated from time budgets and from empirical equations for lizards that relate metabolism to body mass, body tem-

¹ Manuscript received 28 September 1979; revised 20 October 1980; accepted 24 October 1980.

TABLE 1. Time budget data on foraging mode of Kalahari lacertids. N = number of individuals observed; data given as $\bar{x} \pm 1$ SE. Statistics computed from mean value for each individual. Movement data for *Ichnotropis* are only for juveniles.

Species observed (N , Σ min)	Moves/min	Mean velocity (km/h)	Velocity moving (km/h)	Proportion time moving
<i>Eremias lineoocellata</i> (15, 152.5)	1.54 \pm 0.42	0.074 \pm 0.022	0.477 \pm 0.053	0.143 \pm 0.030
<i>E. lugubris</i> (15, 72.1)	2.97 \pm 0.28	0.315 \pm 0.024	0.561 \pm 0.038	0.574 \pm 0.038
<i>Merole suborbitalis</i> (15, 122.8)	1.83 \pm 0.19	0.061 \pm 0.008	0.461 \pm 0.033	0.135 \pm 0.016
<i>E. namaquensis</i> (25, 131.3)	2.78 \pm 0.31	0.282 \pm 0.031	0.488 \pm 0.025	0.535 \pm 0.052
<i>Ichnotropis squamulosa</i> (5, 20.9)	3.10 \pm 0.14	0.192 \pm 0.011	0.378 \pm 0.059	0.546 \pm 0.079
<i>Nucras tessellata</i> (11, 59.7)	2.90 \pm 0.37	0.378 \pm 0.072	0.719 \pm 0.082	0.502 \pm 0.052

perature, and foraging velocity (Bennett and Dawson 1976, Gleeson 1979). To determine whether foraging mode is sensitive to environmental conditions (Question 4), we examine the response of a normally sit-and-wait lizard to an increase in food abundance. Several foraging models predict that an increase in food availability should result in an increase in foraging velocity (Norberg 1977, T. Moermond, *personal communication*, C. Janson, *personal communication*). Finally, we compare relative clutch volumes (clutch volume divided by body mass) of lizards to ascertain how foraging mode constrains reproductive biology (Vitt and Congdon 1978).

MATERIALS AND METHODS

Foraging modes of lizards were documented by observing several individuals ($\bar{x} = 14.3$, range = 5–25) of six species (Table 1) of lacertids for at least 1 min ($\bar{x} = 5.9$ min/individual) during mid-morning in the summer of 1975–1976. (Data on a seventh Kalahari lacertid, *Nucras intertexta* [see Pianka et al. 1979] are excluded because we have dietary information on only six specimens of this rare species.) For each lizard we recorded distance and duration of each move and duration of each stop. The same observer estimated all distances visually. With the exception of a possible ontogenetic shift in *Ichnotropis squamulosa* (juveniles forage widely [this paper], adults have flexible foraging [Broadley 1979]), our extensive observations of these lizards (> 18 person-months) during all seasons suggest that these species are generally consistent in foraging mode. Some other ectotherms may show greater variability (Robinson 1978, Tollestrup 1979, Toft 1980).

Merole and *Eremias* are very closely related genera (Boulenger 1920, 1921). *Nucras* and *Ichnotropis* are, however, divergent both phylogenetically and ecologically from each other and from the above genera. To maintain tight control over phylogeny, we therefore concentrate on patterns involving species of *Merole* and *Eremias*.

To document diets, prey from preserved stomachs were classified into 46 prey categories, and prey volumes were measured as well (Pianka et al. 1979). For presentation here dietary data are summarized as percentages of termites, the dominant prey of most Kal-

ahari lizards (Pianka 1975), by number and by volume in the diet. To estimate food gained by lizards, we assume equivalent digestion rates among lizards and then divide prey volume by body mass raised to the 0.82 power (Bennett and Dawson 1976), which approximately scales food gain to maintenance metabolic requirements (Avery 1971). Diets of predators on lizards were extracted from the literature (D. G. Broadley 1972 and *personal communication*) and from our own collections.

Metabolic expenditures for each lacertid associated with maintenance and with locomotion were calculated indirectly by modifying Wunder's (1975) method for estimating metabolic rate of active mammals and by using the following parameters (and parameter values): foraging velocity (Table 1), length of activity period (5 h/d, see Table 11 in Pianka et al. 1979), body temperature (T_b) while active (summer \bar{T}_b from Table 1 in Huey et al. 1977: note that T_b is slightly higher in widely foraging lacertids), T_b while inactive (either 30°C or summer \bar{T}_b , which probably bracket actual T_b on inactive lizards), and body mass (6 g for *Eremias lineoocellata*, *E. lugubris*, *Ichnotropis squamulosa*, and *Merole suborbitalis*; 3.5 g for *E. namaquensis*, and 8 g for *Nucras tessellata*). To estimate metabolic rates of inactive lizards, we used equations (Bennett and Dawson 1976) for standard metabolism at 30°C and at 37°C (the latter were corrected to summer \bar{T}_b , assuming a Q_{10} of 2). To estimate metabolic rates of inactive animals, we computed rates at summer \bar{T}_b and multiplied these values by two to compensate for the increment in metabolism associated with nonforaging activity (Bennett and Nagy 1977). The additional cost of transport was estimated using an empirical equation (Gleeson 1979), which was derived from interspecific comparisons, for net cost of transport ($\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{km}^{-1} = 3.77 M^{-0.25}$, where M equals body mass in grams). Oxygen consumption was transformed to energy utilization by assuming a conversion factor of 20.11 J/mL O_2 (Bennett and Gleeson 1979).

We have least confidence in our estimates of the length of the activity periods and of inactive T_b . In the absence of data on activity periods of individual lizards, we have instead approximated these periods from populational activity patterns. (If resulting time estimates are too long [see Simon and Middendorf

TABLE 2. Percentages of termites and of presumed active taxa (dipterans, lepidopterans, coleopterans, orthopterans) in diets of Kalahari lacertids. SW = sit-and-wait, WF = widely foraging, %N = percent termites by number, %A = percent active insects by number, %V = percent termites by volume, n_s = number of stomachs, n_p = number of prey, %S = percent of stomachs containing termites.

Species	Foraging mode	October–April 1969–1970					May–September 1970				T area sample* 1970				Year	
		%N	%V	%A	n_s	n_p	%N	%V	n_s	n_p	%N	%V	n_s	n_p	%S	n_s
<i>Eremias lineoocellata</i>	SW	69.1	39.6	8.7	810	9208	71.9	59.8	325	1967	91.8	64.6	32	522	48.8	1135
<i>E. lugubris</i>	WF	98.4	93.2	0.5	203	11 966	84.7	84.3	35	603	98.7	95.3	40	2270	96.2	238
<i>Meroles suborbitalis</i>	SW	57.9	51.3	6.7	461	6404	73.0	51.9	319	3443	64.2	780
<i>E. namaquensis</i>	WF	75.0	65.3	2.0	181	2396	78.5	74.7	37	302	77.5	218
<i>Ichnotropis squamulosa</i>	WF	98.0	79.1	0.8	112	4574	98.3	77.2	76	3350	94.6	112
<i>Nucras tessellata</i>	WF	21.2	4.6	7.6	79	170	14.1	79

* T study area in Botswana is described in Pianka (1971).

1976], then our estimates of metabolic rates will be too great, especially for widely foraging lizards.) Actual T_b of inactive lizards are also unavailable, and we have selected two reasonable temperatures in an attempt to bracket actual T_b . Nevertheless, our estimates of metabolic rates for the two sit-and-wait lacertids (143 and 150 $J \cdot g^{-1} \cdot d^{-1}$, assuming inactive $T_b = 30^\circ C$) are reassuringly similar to estimates of metabolism (127–171 $J \cdot g^{-1} \cdot d^{-1}$) for the sit-and-wait iguanid lizard, *Sceloporus occidentalis*, measured using doubly labeled water (Bennett and Nagy 1977).

Reproductive data on relative clutch mass were obtained following procedures of Pianka and Parker (1975) and of Vitt and Congdon (1978).

RESULTS AND DISCUSSION

The foraging velocity of a predator should influence both the rate of encounters with prey and the rate of energy expenditure (Schoener 1971, Gerritsen and Strickler 1977, Norberg 1977, T. Moermond, *personal communication*). Our analysis suggests that foraging velocity influences these as well as numerous other ecologically significant aspects of the ecology of desert lizards.

The ideal data for examining consequences of foraging mode would be based on single individuals (or at least individuals of a single species) that varied foraging mode either spontaneously or in response to known environmental variables. Without such data, we utilize the next best alternative, comparative information on individuals of very closely related species (*Eremias*, *Meroles*). We hope thereby to control possible phylogenetic, sensory, or ecological differences that might otherwise obscure our results.

Foraging mode

Foraging patterns of Kalahari lacertids are summarized in Table 1. Two species (*Meroles suborbitalis* and *Eremias lineoocellata*) move relatively short distances per move and per unit time and also move a small proportion of the time: we classify these as "sit-and-wait" and the remaining, more active species as

"widely foraging." Differences in foraging patterns are quite striking between these two groups.

Lizards from the Australian and North American deserts were classified as "widely foraging" or "sit-and-wait" based on subjective, but extensive, field observations. The former belong to the families Scincidae (Australia) and Teiidae (North America), whereas the latter belong to the Agamidae (Australia) and Iguanidae (North America). A possible exception is *Phrynosoma platyrhinos* (see below).

Prey taxa

Prey that are sedentary and patchily distributed in space and time (e.g., some termites, Wilson and Clark 1977, W. Coaton, *personal communication*) are more likely to be discovered and eaten by actively foraging predators (Gerritsen and Strickler 1977, Krebs 1978, Eckhardt 1979). To determine whether this holds for lizards, we compared termite utilization by lacertid lizards.

Percentages of termites (see Introduction) by number and by volume in the diets of Kalahari lacertids at different seasons are given in Table 2. Pairs of lizard species that typically occur in the same habitats (*E. lineoocellata* and *E. lugubris*, *Meroles*, and *E. namaquensis*; see Pianka et al. 1979) are adjacent in the table. Sit-and-wait species take fewer (G -tests, all $P < .05$) termites than do widely foraging lizards in the same habitat in either season. This result holds even for a "point" sample of three species from the savanna and forest edge habitats on our T study area in Botswana (Pianka 1971) from 20 to 23 February 1970 (Table 2). Percentages of termites by volume and percentages of stomachs containing termites show the same pattern for all comparisons in Table 2. Thus widely foraging lizards (except *Nucras*, see below) eat more termites, prey that are sedentary and clumped but that are temporally and spatially unpredictable (Wilson and Clark 1977).

In contrast, sit-and-wait lizards should encounter and eat more active and mobile prey. Activity levels of most Kalahari insects are largely unknown. Never-

TABLE 3. Percentages of termites in diets of Australian desert lizards. n = number of species with each foraging mode. Arboreal, fossorial, nocturnal, and varanid species excluded. Symbols as in Table 2.

Species habitat (n)	% N	(Range)	% V	(Range)
Non-sandridge				
Sit-and-wait (5)*	29.2 \pm 11.4	(0–52.6)	16.0 \pm 5.59	(0–29.5)
Widely foraging (10)†	79.7 \pm 5.50	(39.0–95.1)	57.4 \pm 4.90	(33.9–82.0)
Sandridge				
Sit-and-wait (4)‡	–0–	(0–0.1)	–0–	(0–0.2)
Widely foraging (4)§	11.9 \pm 5.90	(0–22.7)	3.8 \pm 2.57	(0–11.2)

* *Amphibolurus reticulatus*, *A. inermis*, *A. isolepis*, *A. scutulatus*, *Moloch horridus*.

† *Morethia butleri*, *Menetia greyi*, *Ctenotus ariadne*, *C. atlas*, *C. calurus*, *C. grandis*, *C. helenae*, *C. leonhardii*, *C. pantherinus*, *C. schomburgkii*.

‡ *Amphibolurus clayi*, *A. fordii*, *Diporiphora winneckeii*, *Physignathus longirostris*.

§ *Ctenotus brooksi*, *C. colletti*, *C. dux*, *C. leae*.

theless, mobile taxa such as dipterans and many coleopterans are eaten slightly but significantly more frequently (Table 2, G test, $P < .001$) by sit-and-wait lizards.

Percentages of termites in diets of Australian lizards (Table 3) show a pattern similar to that of the Kalahari data. Widely foraging skink species in non-sandridge habitats eat more termites by number and by volume (Mann-Whitney U tests, P 's $< .001$) than do sit-and-wait agamid species. In fact the percentages by volume do not overlap between foraging groups. This pattern is less pronounced for species on sandridge study areas, where termite nests are inconspicuous.

In areas of the western North American flatland deserts studied by Pianka (1966), only the teiid *Cnemidophorus tigris* routinely forages widely and actively. This lizard eats substantially more termites by number and by volume than any sit-and-wait iguanid (Table 4).

The relationship between foraging mode and diet is complex in the North American ant specialist, *Phrynosoma*. Horned lizards were originally believed to be sit-and-wait foragers because of their slow gait and camouflaged morphology (Pianka 1966). However, recent evidence demonstrates that *Phrynosoma* do in fact move frequently, albeit extremely slowly (Whitford and Bryant 1979): indeed, a moving *Phrynosoma cornutum* covers less ground in an entire day than a *Nucras* does in 10 min (Whitford and Bryant 1979, Table 1)! These slow foraging movements of *Phrynosoma* appear directed, and some species actually trapline from ant nest to ant nest (K. Tollestrup, *personal communication*). Defensive behaviors of ants and termites (aggression, cessation of activity, shift of nest sites, Whitford and Bryant 1979, S. Rissing, *personal communication*) may prevent *Phrynosoma* and other lizards from sitting for extended periods beside a nest disk or foraging trail (Whitford and Bryant 1979). For such species the dichotomy of foraging widely vs. sitting and waiting, which adequately characterizes the majority of lizard species, may be of limited utility.

Nucras tessellata is an exception in being the only

widely foraging lizard in our samples that rarely eats termites (Table 2). However, this species' diet is specialized and most unusual: scorpions constitute 53% of its diet by volume (Pianka et al. 1979)! Scorpions, which are active at night and spend the day in burrows, are distributed unpredictably since probably not all scorpion burrows are occupied; movement patterns of *Nucras* seem to reflect a search for burrows with scorpions. Other lizards that might be exceptions to the association of foraging widely and termite eating should include very large lizards such as monitor lizards (*Varanus*) that eat only larger prey (Pianka 1968, 1970).

Despite such exceptions and considerations, the association between foraging widely and termite eating is exceedingly tight for small, ground-dwelling desert lizards. This pattern, which holds for unrelated lizards in North America, western Australia, and southern Africa, has considerable generality.

A coupling between foraging mode and type of prey (see Toft 1980) is relevant to models of optimal foraging (Schoener 1971). Widely foraging predators will not only encounter prey more frequently (Norberg 1977, T. Moermond, *personal communication*), but also contact different types of prey (Gerritsen and Strickler 1977, Eckhardt 1979). Thus the prey world of a predator appears to be partly a function of its foraging mode.

TABLE 4. Percentages of termites in diets of United States desert lizards. Data summarized from Pianka (1965). *Phrynosoma* is an ant specialist. Symbols as in Table 2.

Species	Foraging mode	Termites in diet		Samples	
		% N	% V	n_s	n_p
<i>Cnemidophorus tigris</i>	WF	86.6	27.9	1918	73 030
<i>Uta stansburiana</i>	SW	37.0	16.9	681	8280
<i>Gambelia wislizenii</i>	SW	0.0	0.0	167	940
<i>Phrynosoma platyrhinos</i>	SW	0.4	1.0	171	13 507
<i>Callisaurus draconoides</i>	SW	18.2	4.4	289	2835
<i>Uma scoparia</i>	SW	2.7	0.7	42	2139

TABLE 5. Food gain of Kalahari lacertids. Index of food gain = volume of food divided by body mass^{0.82}.

Species	Foraging mode	October–April		May–September	
		$\bar{x} \pm SE$	(n)	$\bar{x} \pm SE$	(n)
<i>Eremias lineoocellata</i>	SW	0.038 ± 0.001	573	0.044 ± 0.002	327
<i>E. lugubris</i>	WF	0.079 ± 0.005	180	0.040 ± 0.006	38
<i>Meroles suborbitalis</i>	SW	0.045 ± 0.002	348	0.039 ± 0.039	319
<i>E. namaquensis</i>	WF	0.058 ± 0.004	127	0.055 ± 0.055	37
<i>Ichnotropis squamulosa</i>	WF	0.070 ± 0.004	107
<i>Nucras tessellata</i>	WF	0.043 ± 0.007	68

This association may also be important to models of interspecific competition because foraging velocity, via its effects on prey taxa, should influence dietary overlap among syntopic predators (Hespenheide 1975, Gerritsen and Strickler 1977, C. Janson, *personal communication*). Species with different foraging modes coexist in the same habitats in the Kalahari. Interestingly, widely foraging lacertids actually overlap more in diet (prey taxa by volume) with other widely foraging lacertids in a different habitat than they do with sit-and-wait lacertids in the same habitat (see Table 13 in Pianka et al. 1979; *Nucras* excluded). A foraging model (C. Janson, *personal communication*) predicts that both types of foragers can coexist if both mobile and nonmobile prey are sufficiently abundant.

Food intake and energetic expenditures

To correlate food intake with foraging mode, one would ideally like to know the total volume of prey consumed by a lizard at the end of its daily activity period. These data are unavailable, but we have determined the volume of prey (scaled approximately to maintenance metabolic rate) from lizards that had been captured at various times before the end of their activity periods. This approach will underestimate food intake both for lizards that capture a single large prey item and then retreat to cover and for lizards that might be active later than the lizard collectors.

Widely foraging lacertids generally capture significantly more food relative to their maintenance requirements than do the sit-and-wait lacertids (Table 5) dur-

ing warm months of the year. Indeed, *E. lugubris* captures 2.1 times more food “per day” than does *E. lineoocellata* between October and April; though the differential is not as pronounced, *E. namaquensis* captures 1.3 times more food “per day” than does *Meroles*. This pattern is less clear during winter (Table 5), but widely foraging lizards are rarely active in this season (Pianka et al. 1979). Unfortunately, we cannot determine whether this differential restriction in seasonal activity reflects higher thermal preferences of widely foraging lacertids (Huey et al. 1977), a limited aerobic scope of lizards active at low T_b in winter (Moberly 1968), or an interaction with predators or seasonal food levels. Termites are certainly available in winter, although their relative densities are unknown; in any case, termites constitute more than half the volume of the winter diet of *E. lineoocellata*.

Nucras tessellata, a widely foraging lizard that has a low food intake (Table 5), is again an exception. Both of the above-mentioned biases may be involved. *Nucras* eats unusually large prey items (mean size of prey is nearly 10 times larger than the mean size of prey of other lacertids, Pianka et al. 1979). Also, these lizards are active somewhat later in the morning than other lacertids (Pianka et al. 1979); and we admit that high ambient temperatures in the desert at this time sometimes inspired us to cease our collecting and to seek shade and liquid before these lizards had retreated.

Estimates of daily energetic expenditures of lacertids (Table 6; Materials and Methods) suggest that the energetic cost of foraging widely is substantial. *Ere-*

TABLE 6. Estimated energy expenditures of Kalahari lacertids. Values for species may differ slightly because of differences in mass, T_b , or foraging velocity; see Materials and Methods. \dot{E}_{sit} = metabolic rate ($J \cdot g^{-1} \cdot d^{-1}$) while active but not moving, \dot{E}_{move} = net cost of movement, \dot{E}_{30° = metabolic expenditure while inactive assuming $T_b = 30^\circ C$, $(\dot{E}_{summer})T_b$ = expenditure while inactive assuming $T_b =$ summer T_b , $\Sigma \dot{E}_{30^\circ}$ and $(\Sigma \dot{E}_{summer})T_b$ = total metabolism ($J \cdot g^{-1} \cdot d^{-1}$) assuming inactive T_b of 30° and of summer T_b , respectively.

Species	Foraging mode	\dot{E}_{sit}	\dot{E}_{move}	\dot{E}_{30°	$(\dot{E}_{summer})T_b$	$\Sigma \dot{E}_{30^\circ}$	$(\Sigma \dot{E}_{summer})T_b$
<i>Eremias lineoocellata</i>	SW	64.3	17.9	67.6	123.0	149.8	205.2
<i>E. lugubris</i>	WF	67.2	76.3	67.6	127.6	211.1	271.1
<i>Meroles suborbitalis</i>	SW	60.9	14.9	67.7	115.8	143.5	191.6
<i>E. namaquensis</i>	WF	70.0	78.3	74.2	133.0	222.5	281.3
<i>Ichnotropis squamulosa</i>	WF	58.7	46.5	67.6	111.6	172.7	216.8
<i>N. tessellata</i>	WF	69.8	85.1	64.3	132.6	219.2	287.5

mias lugubris expend approximately 1.41–1.32 times more energy than do *E. lineoocellata* (these estimates assume that inactive $T_b = 30^\circ\text{C}$ or = summer \bar{T}_b , respectively); and *E. namaquensis* use approximately 1.55–1.47 times more energy than do *Meroles*). Note: these increments are only slightly affected by estimates of length of activity. For example, if the length of the activity period were doubled to 10 h/d, then *E. lugubris* would use 1.56 or 1.47 times more energy than do *E. lineoocellata*.

Predation on Kalahari lizards

To determine whether foraging mode might influence predation on the lizards themselves, we summarize limited data on diets of horned adders (*Bitis caudalis*, $N = 51$) collected in the Kalahari (Broadley 1972 and our own collection). (Whether *Bitis* is the dominant predator on these lizards is unknown). These snakes, which lie almost completely covered with sand, are archetypal sit-and-wait predators on lizards during the day. Thus they should capture widely foraging lacertids relatively more frequently than sit-and-wait lacertids (Gerritsen and Strickler 1977). Indeed, of the 14 lacertids removed from the stomachs of horned adders, 10 were widely foraging (71.4%). Yet only 25.4% of lacertids in our collection ($N = 2563$) are widely foraging. Such collections are rough indices of relative abundance (see Turner 1977: 160). Thus a sit-and-wait predator captures widely foraging lizards greatly in excess of their apparent relative abundance (G -test, $P < .0001$).

Very limited data are available on a widely foraging predator. Stomachs of two Secretary Birds (*Sagittarius serpentarius*) contained six sit-and-wait and five widely foraging lacertids (D. G. Broadley, *personal communication*).

Movement patterns of lizards affect the types of predators that eat them. For example, sit-and-wait horned adders capture widely foraging lizards disproportionately to their abundance. Crossovers in foraging mode between trophic levels are thus demonstrable in the Kalahari: widely foraging lizards, which eat sedentary prey, are in turn eaten by sit-and-wait predators.

An increase in foraging velocity should increase encounters with predators (Salt 1967) and therefore enhance overall risk of predation (Andrews 1979). Without a detailed capture-recapture study (Schoener 1979, Schoener and Schoener 1980), we cannot directly establish an association between foraging mode and incidence of predator attack. However, if risk of predation is high to a long-lived species, selection might favor the evolution of a relatively long tail (Vitt and Congdon 1978), which would decrease the probability that a given attack would be successful (see Congdon et al. 1974). In contrast, short-lived species might have relatively short tails, which would increase energy and nutrients for growth and reproduction (see Maiorana

1977). This pattern does not hold in *Anolis* (Moermond 1979a, b), which are, however, arboreal and can have prehensile tails (T. Moermond, *personal communication*). Interestingly, widely foraging lacertids generally have proportionately longer tails (ANOVA, $P < .001$) than do sit-and-wait lacertids (*E. lugubris* tail: snout-vent length = 2.47 ± 0.05 , *E. namaquensis* = 2.38 ± 0.04 , *Nucras* = 2.36 ± 0.03 , *Ichnotropis* = 2.09 ± 0.10 vs. *E. lineoocellata* = 2.15 ± 0.03 , *Meroles* = 2.10 ± 0.11 ; random samples of 20 adults with complete tails). The short tail of adult *Ichnotropis* might reflect either an ontogenetic shift in foraging mode (Broadley 1979) or a short life-span (Maiorana 1977).

Frequency of broken tails has also been used as an index of risk of predation (Rand 1954, Tinkle and Ballinger 1972, Schall and Pianka 1980), but the basis of this index has recently been questioned (Schoener 1979, Jaksic and Fuentes 1980). In any case, any association between foraging mode and frequency of broken tails is not apparent for Kalahari lacertids (*E. lugubris* = 17.7%, $N = 226$; *E. namaquensis* = 39.8%, $N = 191$; *Nucras* = 31.1%, $N = 87$; *Ichnotropis* = 24.2%, $N = 120$; *E. lineoocellata* = 24.6%, $N = 943$; *Meroles* = 42.6%, $N = 772$).

Sit-and-wait tropical frogs rely on camouflage or jumping to avoid or to escape predators. Interestingly, widely foraging anurans (Dendrobatidae, Bufonidae) are generally very poisonous (Toft 1980, 1981).

Shifts in foraging mode

Our analysis has largely treated foraging mode as fixed within a species. Some foraging models predict, however, that individuals will shift foraging mode in response to food availability (Norberg 1977, T. Moermond, *personal communication*, C. Janson, *personal communication*); and short-term intraspecific variation has been documented in several reptiles and amphibians (Tollestrup 1979, Toft 1980).

Several foraging models predict that both sit-and-wait and widely foraging predators should increase foraging velocity in response to increased abundance of food (Norberg 1977, T. Moermond, *personal communication*, C. Janson, *personal communication*). To determine whether a Kalahari lizard might alter foraging mode, we consider changes in the behavior and diet of *Ptenopus garrulus* during swarms of termites. *Ptenopus* is a crepuscular and nocturnal gecko that usually sits and waits partially exposed in its burrow and makes short chases (determined from tracks) after prey. However, these geckos forage widely away from their burrows during termite swarms. The average percentage of termites in the diet of *Ptenopus* from our T study area in Botswana (Pianka 1971) is strongly correlated with the percentage of geckos that were outside their burrows on a given night or visit ($r_s = .99$, $N = 6$).

These observations are consistent with the above

TABLE 7. Relative clutch volume (= clutch volume divided by total body mass) of Kalahari lacertid lizards. Data from females with oviducal eggs only.

Species (N)	Foraging mode	$\bar{x} \pm SE$
<i>Eremias lineocellata</i> (42)	SW	18.7 \pm 0.83
<i>E. lugubris</i> (22)	WF	14.6 \pm 0.65
<i>Meroles suborbitalis</i> (23)	SW	21.9 \pm 1.04
<i>E. namaquensis</i> (5)	WF	16.5 \pm 2.74
<i>Ichnotropis squamulosa</i> (1)	WF	15.0
<i>Nucras tessellata</i> (1)	WF	15.8

models that predict an increase in foraging velocity with an increase in food abundance. A second example of flexible foraging modes is on a lacertid (*Aporosaura anchietae*), which lives on vegetationless dunes in the Namib Desert. When the wind is blowing, *Aporosaura* sits and waits for wind-blown seeds and invertebrates; but when winds are calm, *Aporosaura* forages widely for prey (Robinson 1978, Robinson and Cunningham 1978). C. Janson's (*personal communication*) model predicts that sitting and waiting is favored energetically when movement rates of prey are high.

Relative clutch mass

Vitt and Congdon (1978) observed that sit-and-wait lizards typically have higher relative clutch masses (clutch volume or mass divided by body mass) than do widely foraging lizards and speculated that relative clutch mass, body shape, and foraging mode are co-evolved characters. For example, a widely foraging lizard with a large clutch mass and associated squat body form might experience substantial risk of predation or

low foraging efficiency or both. The pattern observed by Vitt and Congdon (1978) holds neatly among Kalahari lacertids: widely foraging species have significantly lower relative clutch masses (Table 7, ANOVA, $P < .001$) and longer tails (see above) than do sit-and-wait species.

Other constraints on foraging mode

Although temporary shifts in foraging mode are observable within species, some constraints must exist on the flexibility of foraging mode. Widely foraging and sit-and-wait predators may differ strikingly (Table 8) in morphological (Vitt and Congdon 1978, Moermond 1979a, Toft 1980) and physiological adaptations (e.g., endurance, Bennett and Licht 1973, Ruben 1976a, b, Toft 1980) as well as in sensory mode and in learning ability (Goodman 1971, Regal 1978). Foraging mode within a species may not, therefore, be as flexible as is assumed in some ecological models of foraging. Interestingly, for physiological reasons associated with endurance capacity, constraints on shifting foraging mode are probably not symmetrical: a sustained reduction in foraging velocity (widely foraging to sit-and-wait) is more likely than a sustained increase in foraging velocity (sit-and-wait to widely foraging).

Moreover, an animal that switches from its normal foraging mode and associated defensive behaviors may usually experience substantially increased risks of predation. For example, *Ptenopus* sometimes temporarily forage widely outside their burrows in pursuit of swarming termites on rainy or overcast afternoons in summer (as mentioned above, these geckos are normally nocturnal). At such times, we saw many geckos

TABLE 8. Postulated correlates of foraging mode.

	Sit-and-wait	Widely foraging
Prey type	Eat mobile prey	Eat sedentary and unpredictable (but clumped or large) prey
Volume prey captured per day	Generally low	Generally high
Daily metabolic expense	Low	High (Bennett and Gorman 1979)
Types of predators	Vulnerable primarily to widely foraging predators	Vulnerable to both sit-and-wait and to widely foraging predators
Rate of encounters with predators	Probably low	Probably high (Salt 1967)
Mode of escape from predators	Camouflage, speed, saltation	Camouflage, speed, aposematism (poisonous) (Toft 1980)
Morphology	Stocky (short tails)	Streamlined (generally long tails) (Vitt and Congdon 1978)
Probable physiological correlates	Limited endurance	High endurance capacity (Bennett and Licht 1973, Ruben 1976a, b)
Relative clutch mass	High	Low (Vitt and Congdon 1978)
Sensory mode	Visual primarily	Visual or chemoreceptory (Enders 1975, Regal 1978)
Learning ability	Limited*	Enhanced learning and memory, larger brains (Regal 1978)

* Unless use trapline (T. L. Poulson, *personal communication*).



FIG. 1. The Kalahari gecko *Ptenopus garrulus* normally sits and waits for prey at night from the entrance of its burrow. If, however, termites swarm on a rainy afternoon in summer, *Ptenopus* forage widely away from the security of their burrows. Shrikes frequently take advantage of these shifts in foraging mode and time of activity, with grim consequences for the geckos.

impaled on thorn bushes by shrikes (Fig. 1). Obviously, shifts in foraging mode and in time of activity can greatly increase risks of predation and nullify associated energetic gains!

CONCLUSION

Foraging mode appears to influence numerous aspects (Table 8) of the lives of desert lizards and may be intimately related to the evolution of body shape, physiological capacity, and neurobehavioral phenomena. Ecological correlates of foraging mode are obviously diverse and complex. Models of optimal foraging that include foraging mode as a variable could be made increasingly realistic by incorporating some of these intricacies, for example, by studying interactions among three rather than only two trophic levels.

ACKNOWLEDGMENTS

We thank A. F. Bennett, D. G. Broadley, W. G. H. Coaton, S. Fretwell, C. Janson, W. G. Whitford, S. Rissing, T. W. Schoener, K. Tollestrup, T. C. Moermond, C. A. Toft, D. S. Wilson, an anonymous reviewer, and especially T. L. Poulson for encouraging and constructive comments on the manuscript or for discussion. We are particularly indebted to C. M. Cavalier for assistance in obtaining the time budget data and for our Christmas event in the Kalahari. We also thank C. K. Brain, L. W. Coons, D. Christie, W. D. Haacke, M. G. L. and M. Mills, T. Papenfuss, and C. and E. Le Riche for assistance in the field and the directors of Wildlife and National Parks (Botswana), National Parks Board (South Africa), and Nature Conservation (Cape Province) for permission to work

and to collect specimens in their respective areas. Research was supported by the National Geographic Society, National Science Foundation grants (GB-8727, GB-31006, and DEB 78-12024), Los Angeles County Museum of Natural History, the Miller Institute for Basic Research in Science, and the Museum of Vertebrate Zoology (University of California, Berkeley).

LITERATURE CITED

- Andrews, R. M. 1979. The lizard *Corythophanes cristatus*: an extreme "sit-and-wait" predator. *Biotropica* 11:136-139.
- Avery, R. A. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology* 40:351-365.
- Bennett, A. F., and W. R. Dawson. 1976. Metabolism. Pages 127-223 in C. Gans and W. R. Dawson, editors. *Biology of the Reptilia. Volume 5 (Physiology A)*. Academic Press, New York, New York, USA.
- Bennett, A. F., and T. T. Gleeson. 1979. Metabolic expenditure and the cost of foraging in the lizard *Cnemidophorus murinus*. *Copeia* 1979:573-577.
- Bennett, A. F., and G. C. Gorman. 1979. Population density, thermal relations, and energetics of a tropical insular lizard community. *Oecologia* 42:339-358.
- Bennett, A. F., and P. Licht. 1973. Relative contributions of anaerobic and aerobic energy production during activity in amphibia. *Journal of Comparative Physiology* 81:277-288.
- Bennett, A. F., and K. A. Nagy. 1977. Energy expenditure in free-ranging lizards. *Ecology* 58:697-700.
- Boulenger, G. A. 1920. *Monograph of the Lacertidae. Volume I*. British Museum of Natural History Publication, London, England.
- . 1921. *Monograph of the Lacertidae. Volume II*. British Museum of Natural History Publication, London, England.
- Broadley, D. G. 1972. The horned viper *Bitis caudalis* (A. Smith) in the central Kalahari. *Botswana Notes and Records* 4:263-264.
- . 1979. A field study of two sympatric 'annual' lizards (genus *Ichnotropis*) in Rhodesia. *South African Journal of Zoology* 14:133-138.
- Congdon, J. D., L. J. Vitt, and W. W. King. 1974. Geckos: adaptive significance and energetics of tail autotomy. *Science* 184:1379-1380.
- Eckhardt, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecological Monographs* 49:129-149.
- Enders, F. 1975. The influence of prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, and Salticidae). *American Naturalist* 109:737-763.
- Gerritsen, J., and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of the Fisheries Research Board of Canada* 34:73-82.
- Gleeson, T. T. 1979. Foraging and transport costs in the Galapagos marine iguana, *Amblyrhynchus cristatus*. *Physiological Zoology* 52:549-557.
- Goodman, D. 1971. Differential selection of immobile prey among terrestrial and riparian lizards. *American Midland Naturalist* 86:217-219.
- Hespenheide, H. A. 1975. Prey characteristics and predator niche width. Pages 158-180 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- Huey, R. B. 1981, *in press*. Temperature, physiology, and the ecology of reptiles. In C. Gans and F. H. Pough, editors. *Biology of the Reptilia. Volume 12 (Physiology B)*. Academic Press, New York, New York, USA.

- Huey, R. B., E. R. Pianka, and J. A. Hoffman. 1977. Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology* **58**:1066-1075.
- Krebs, J. R. 1978. Optimal foraging: decision rules for predators. Pages 23-63 in J. R. Krebs and N. B. Davies, editors. *Behavioural ecology: an evolutionary approach*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Jaksić, F. M., and E. R. Fuentes. 1980. Correlates of tail losses in twelve species of *Liolaemus* lizards. *Journal of Herpetology* **14**:137-141.
- Maiorana, V. C. 1977. Tail autotomy, functional conflicts and their resolution by a salamander. *Nature* **265**:533-535.
- Moberly, W. R. 1968. The metabolic response of the common iguana, *Iguana iguana*, to activity under restraint. *Comparative Biochemistry and Physiology* **27**:1-20.
- Moermond, T. C. 1979a. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology* **60**:152-164.
- . 1979b. The influence of habitat structure on *Anolis* foraging behavior. *Behaviour* **70**:147-167.
- Norberg, R. A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. *Journal of Animal Ecology* **46**:511-529.
- Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* **47**:1055-1059.
- . 1968. Notes on the biology of *Varanus eremius*. *Western Australian Naturalist* **11**:39-44.
- . 1970. Notes on the biology of *Varanus gouldi flavirufus*. *Western Australian Naturalist* **11**:141-144.
- . 1971. Lizard species density in the Kalahari desert. *Ecology* **52**:1024-1029.
- . 1975. Niche relations of desert lizards. Pages 292-314 in M. Cody and J. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- Pianka, E. R., R. B. Huey, and L. R. Lawlor. 1979. Niche segregation in desert lizards. Pages 67-115 in D. J. Horn, G. R. Stairs, and R. D. Mitchell. *Analysis of ecological systems*. Ohio State University Press, Columbus, Ohio, USA.
- Pianka, E. R., and W. S. Parker. 1975. Age-specific reproductive tactics. *American Naturalist* **109**:453-464.
- Rand, A. S. 1954. Variation and predator pressure in an island and mainland population of lizards. *Copeia* **1954**:260-262.
- Regal, P. J. 1978. Behavioral differences between reptiles and mammals: an analysis of activity and mental capabilities. Pages 183-202 in N. Greenberg and P. D. MacLean, editors. *Behavior and neurology of lizards*. Publication (ADM) 77-491, Department of Health, Education, and Welfare, Washington, D.C., USA.
- Robinson, M. D. 1978. Nutritional ecology of a Namib Desert sand dune lizard, *Aporosaura anchietae*. Abstract. Second International Congress of Ecology (INTECOL), Jerusalem, Israel.
- Robinson, M. D., and A. B. Cunningham. 1978. Comparative diet of two Namib Desert sand lizards (Lacertidae). *Madoqua* **11**:41-53.
- Ruben, J. A. 1976a. Aerobic and anaerobic metabolism during activity in snakes. *Journal of Comparative Physiology* **109**:147-157.
- . 1976b. Correlation of enzymatic activity, muscle myoglobin concentration and lung morphology with activity metabolism in snakes. *Journal of Experimental Zoology* **197**:313-319.
- Salt, G. W. 1967. Predation in an experimental protozoan population (*Woodruffia-Paramecium*). *Ecological Monographs* **37**:113-144.
- Schall, J. J., and E. R. Pianka. 1980. Evolution of escape behavior diversity. *American Naturalist* **115**:551-556.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**:369-404.
- . 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* **60**:1110-1115.
- Schoener, T. W., and A. Schoener. 1980. Ecological and demographic correlates of injury rates in some Bahamian *Anolis* lizards. *Copeia* **1980**:839-850.
- Simon, C. A., and G. A. Middendorf. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. *Ecology* **57**:1317-1320.
- Stamps, J. A. 1967. Social behavior and spacing patterns in lizards. Pages 265-334 in C. Gans and D. W. Tinkle, editors. *Biology of the Reptilia*. Volume 7 (Ecology and Behaviour A). Academic Press, New York, New York, USA.
- Stebbins, R. C. 1948. Nasal structure in lizards with reference to olfaction and conditioning of the inspired air. *American Journal of Anatomy* **83**:183-222.
- Tinkle, D. W., and R. E. Ballinger. 1972. *Sceloporus undulatus*: a study of the intraspecific competitive demography of a lizard. *Ecology* **53**:570-584.
- Toft, C. A. 1980. Feeding ecology of thirteen syntopic species of anurans. *Oecologia* **45**:131-141.
- . 1981. *in press*. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *Journal of Herpetology*.
- Tollestrup, K. 1979. The ecology, social structure, and foraging behavior of two closely related species of leopard lizards, *Gambelia silus* and *Gambelia wislizenii*. Dissertation. University of California, Berkeley, California, USA.
- Turner, F. B. 1977. The dynamics of populations of squamates, crocodylians and rhynchocephalians. Pages 157-264 in C. Gans and D. W. Tinkle, editors. *Biology of the Reptilia*. Volume 7 (Ecology and Behaviour A). Academic Press, New York, New York, USA.
- Vitt, L. J., and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *American Naturalist* **112**:595-608.
- Whitford, W. G., and M. Bryant. 1979. Behavior of a predator and its prey: the horned lizard (*Phrynosoma cornutum*) and the harvester ants (*Pogonomyrmex* spp.). *Ecology* **60**:686-694.
- Wilson, D. S., and A. B. Clark. 1977. Above ground predator defence in the harvester termite, *Hodotermes mossambicus* (Hagen). *Journal of the Entomological Society of South Africa* **40**:271-282.
- Wunder, B. A. 1975. A model for estimating metabolic rate of active or resting mammals. *Journal of Theoretical Biology* **49**:345-354.