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Variation in the effect of profitability on prey size selection by the lacertid lizard *Psammodromus algirus*

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Abstract. Maximizing the average rate of energy intake (profitability) may not always be the optimal foraging strategy for ectotherms with relatively low energy requirements. To test this hypothesis, we studied the feeding behaviour of captive insectivorous lizards *Psammodromus algirus*, and we obtained experimental estimates of prey mass, handling time, profitability, and attack distance for several types of prey. Handling time increased linearly with prey mass and differed significantly among prey types when prey size differences were controlled for, and mean profitabilities differed among prey taxa, but profitability was independent of prey size. The attack distance increased with prey length and with the mobility of prey, but it was unrelated to profitability. Thus, lizards did not seem to take account of the rate of energy intake per second as a proximate cue eliciting predatory behavior. This information was combined with pitfall-trap censuses of prey (in late April, mid-June and late July) that allowed us to compare the mass of the prey captured in the environment with that of the arthropods found in the stomachs of sacrificed free-living lizards. In April, when food abundance was low and lizards were reproducing, profitability had a pronounced effect on size selection and lizards selected prey larger than average from all taxa except the least profitable ones. As the active season progressed, and with a higher availability of food, the number of prey per stomach decreased and their mean size increased. The effect of profitability on size selection decreased (June) and eventually vanished (July–August). This variation is probably related to seasonal changes in the ecology of lizards, e.g. time minimization in the breeding season as a means of saving time for nonforaging activities versus movement minimization by selecting fewer (but larger) prey in the postbreeding season. Thus, the hypothesis that maximizing profitability could be just an optional strategy for a terrestrial ectothermic vertebrate was supported by our data.

Key words: Ectothermy – Foraging currencies – Prey size selection – Profitability – *Psammodromus*

Currency assumptions are of major interest, and must be clearly defined, when analysing foraging behaviour. In predator-prey models, the currency most frequently used is the long-term average rate of energy intake, and profitability (energy obtained per unit of handling time) is usually the key variable (Stephens and Krebs 1986). Much work on feeding behaviour has dealt with small endothermic vertebrates whose high metabolic rates, and hence energy expenditures, force animals to invest a large proportion of their daily time budget in foraging activities, so that they easily become time-constrained. With a few exceptions (e.g. Goss-Custard 1977; Barnard and Brown 1981; Tinbergen 1981; Montgomerie et al. 1984), the results of observational or experimental studies have been in agreement with the prediction that animals maximize their net rate of energy intake while feeding (review by Stephens and Krebs 1986). Nevertheless, in ectothermic terrestrial vertebrates, which have received much less attention from the viewpoint of foraging theory, results are usually contrary to the predictions of the profitability based version of the prey model (e.g. Jaeger and Barnard 1981; Stamps et al. 1981; and discussion by Pough and Andrews 1985). This discrepancy between theoretical predictions and observed behavioral responses could merely reflect the fact that currency and constraint assumptions should be borne in mind when considering differences among organisms with different energy requirements or time constraints. The energetic needs of terrestrial ectotherms such as lizards are well below those of endotherms of a similar body size (Pough 1980; Nagy 1983; Peters 1986). In ectotherms, performance is tightly associated with the thermal environment (Dawson 1975; Bennett 1980; Huey 1982), and only a small proportion of the time budget is devoted to feeding activities (Anderson and Karasov 1981; Huey and Pianka 1981; Paulissen 1987). On the other hand, lizards are easy prey for a wide

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variety of predators, and their activity levels and habitat use may be strongly influenced by predation risk (review by Greene 1988). Therefore, the time they have available for foraging is variable (and in some cases unpredictable) and could influence the currency employed when modelling their optimal foraging tactics.

In spite of the peculiarities of lizards in comparison with endothermic vertebrates, studies on their feeding behaviour have usually emphasized the description of the diet or its relationship with food availability in the foraging environment. In most cases, these studies do not anlayse the currency employed by consumers, their seizing behaviour, or the associated energy balances and time allocation schedules (but see Stamps et al. 1981; Freed 1982; Pough and Andrews 1985; Paulissen 1987; Díaz and Carrascal 1990).

The purpose of this paper is to analyse within the context of optimal foraging theory the feeding behavior of *Psammodromus algirus*, an insectivorous lacertid lizard inhabiting woodland habitats of the western Mediterranean region. In a previous study (Díaz and Carrascal 1990) we considered the selection of prey types by *P. algirus*, and found that prey size (i.e. gross energy content) was the main factor responsible for the selection (consumption vs. availability) of prey types. Our goals here were: (1) to study feeding behaviour in captivity in order to obtain experimental estimates of profitability and attack distance; (2) to analyse the within-prey-type size selectivity under natural conditions; and (3) to follow its temporal variation according to seasonal changes in the activity budget and in prey availability. Because these seasonal changes are expected to influence the time available for foraging (by modulating energy requirements and the time needed for other activities such as thermoregulation or mate searching), they provide a basis for analysing to what extent, and with what temporal constancy, profitability is important for decision making by ectothermic foragers.

Materials and methods

Feeding behaviour and prey profitability

Observations of feeding behaviour in captivity were carried out at the Estación Biogeológica El Ventorrillo (Navacerrada, Central Spain) in July–August 1990. The focal lizards (15 adults and subadults; mean snout-vent length = 68.9 mm, SD = 5.7), captured in the same area where the prey-size selection data were collected, were kept in open terraria with a leaf-litter layer from 1 week before the beginning of trials until these were completed. During their captivity lizards were supplied *ad libitum* with water and food (arthropods captured nearby), and were allowed to thermoregulate by alternatively basking or seeking shade. No food was available for the 2 days prior to a run of trials in order to make initial conditions as homogeneous as possible.

The observations of feeding behaviour took place, always on sunny days, in 100 × 50 × 40 cm cages with transparent metacrylate walls covered with a grid permeable to solar radiation and heat fluxes, but fine-grained enough to avoid the escape of lizards and their prey. A trial started with the introduction of one to three arthropods of randomly selected types (see below) in a cage housing the chosen lizard. If no feeding reaction was observed after 15 min, the trial was repeated with a different lizard. In the experiments, each lizard consumed an average of 6.4 prey items. Not all lizards responded positively to all prey types; on average, eight (range six to ten) different animals preyed upon a given prey type.

Each time a capture was observed, the following data were recorded:

1. Prey type: spiders, orthopterans, coleopterans, insect larvae, dipterans, hemipterans or ants. Although our "prey types" were roughly equivalent to orders, we also took into account the natural history and behavior of the arthropods (e.g. ants or insect larvae).
2. Attack distance (± 1 cm), measured between the lizard's snout and the arthropod location at the moment when the feeding response was elicited.
3. Mobility of the prey item (moving or immobile) when the attack was launched.
4. Handling time (± 0.1 s), defined as the time elapsed between prey capture (lizard took prey with the jaws) and ingestion (lizard finished swallowing the prey and could begin other behaviour).

The dry mass of the arthropods ingested was calculated prior to each trial. For this purpose, we employed the regression equations of Díaz and Díaz (1991) after having measured with callipers (± 0.1 mm) the appriopriate morphological structure(s) (e.g. body or elytron length, head width; see Díaz and Díaz 1991). The energy contents of each prey type (joules per unit dry mass) were obtained from Cummins and Wuycheck (1971). Once we had the data on both energy contents (in joules) and handling times (in seconds), we calculated the profitability of each ingested prey item as the ratio between these two figures, so that each capture could be characterized by a profitability value in joules per second of handling time.

Prey size selection in the field

The data on prey size selection were collected between June 1989 and April 1990 in Soto de Viñuelas, Madrid, Central Spain (40° 35′N, 03° 34′W). The vegetation of the area consists of a holm oak (*Quercus rotundifolia*) forest in which holm-oaks, interspersed with *Cistus ladanifer* and *Halimium viscosum*, are also the major components of the shrub layer, their leaf litter being the main type of substrate. Samples were taken in three distinct time periods: 18–25 April 1990 (hereafter early spring: beginning of the reproductive season), 12–16 June 1989 (hereafter late spring: last weeks of the reproductive season), and 27 July – 1 August 1989 (hereafter midsummer: postbreeding season). In each of these periods we installed a series of regularly spaced pitfall traps ($n = 35$, 54 and 35 in early spring, late spring and midsummer, respectively) whose contents were removed at the end of each sampling period. Each pitfall was a 6.5 cm wide by 10 cm deep plastic pot half-filled with water with $CuSO_4$ in solution. The insects captured were taken to the laboratory, identified to the order (or prey type) level, and measured (± 0.1 mm) with a 40 × dissecting microscope provided with a micrometer, so that their mean dry mass could be estimated as described above (allometric equations in Díaz and Díaz 1991). No method of collecting insects samples the environment exactly the way a foraging lizard does; because the various prey types are expected to differ in their capturabilities, their abundances cannot be compared without bias. Nevertheless, it should be noted that we were not trying to assess the effect of profitability on prey type selection (see Díaz and Carrascal 1990), but its influence on the selection of prey sizes within prey types. Thus, the method employed was useful for estimating the mean dry mass of the prey types available (a key variable for prey selection; Díaz and Carrascal 1990 and Results). Moreover, it provided data about the temporal variation of overall food abundance. However, we did not try to estimate the overall mean mass of all prey available because differences in capturability among differently sized taxa would have biased our estimates in an unknown way. The prey items measured were chosen by random sampling (most common types: ants, spiders and coleopterans) or by stratified random sampling (remaining, less abundant types) from the contents of each pitfall trap.

Data on the size of the prey included in the diet were obtained in the same sampling dates by dissecting a number of individual lizards (24, 25 and 31 in early spring, late spring and midsummer, respectively) whose stomach contents were removed. All prey items were identified to order and their body mass was estimated as described above. Because we only considered the prey types for which we had allometric equations available (Díaz and Díaz 1991), together with data on handling times and thereby profitabilities, we managed to estimate the dry mass of 76% (121 out of 160), 81% (113 out of 139) and 85% (108 out of 127) of the prey consumed in each of the three sampling periods. The mean dry mass of the prey types consumed was averaged over the mean values corresponding to each stomach in order to avoid pseudoreplication, which would have arisen if prey had been captured with clearly clumped distributions (many items in a few stomachs: e.g. larvae in early spring or ants in midsummer).

The selection of prey sizes within a given prey type was quantified by means of a percent size selection index (SSI) relating the difference between the mean dry masses of the prey consumed (W_c) and available (W_a), to the mean dry mass of the prey available:

$$SSI = (W_c - W_a)/W_a \cdot 100$$

All variables were examined and, when necessary, log-transformed to conform with the assumptions of parametric statistics and ANOVA.

Results

In the experimental feeding trials, 112 out of 123 attacks led to the capture and ingestion of a prey item. The time required for handling a given prey increased exponentially with prey length (handling time log-transformed; $r = 0.774$, $df = 110$, $P < 0.001$) and linearly with prey mass ($r = 0.888$, $df = 110$, $P < 0.001$). The percentage of variance explained by the regression line with untransformed axes (79%; $F = 411.8$, $df = 1$, 110) was substantially higher than using either log-transformed handling time (52%; $F = 119.2$) or both handling time and prey mass (53%; $F = 122.8$). Handling time differed significantly among prey types when controlling for prey size differences

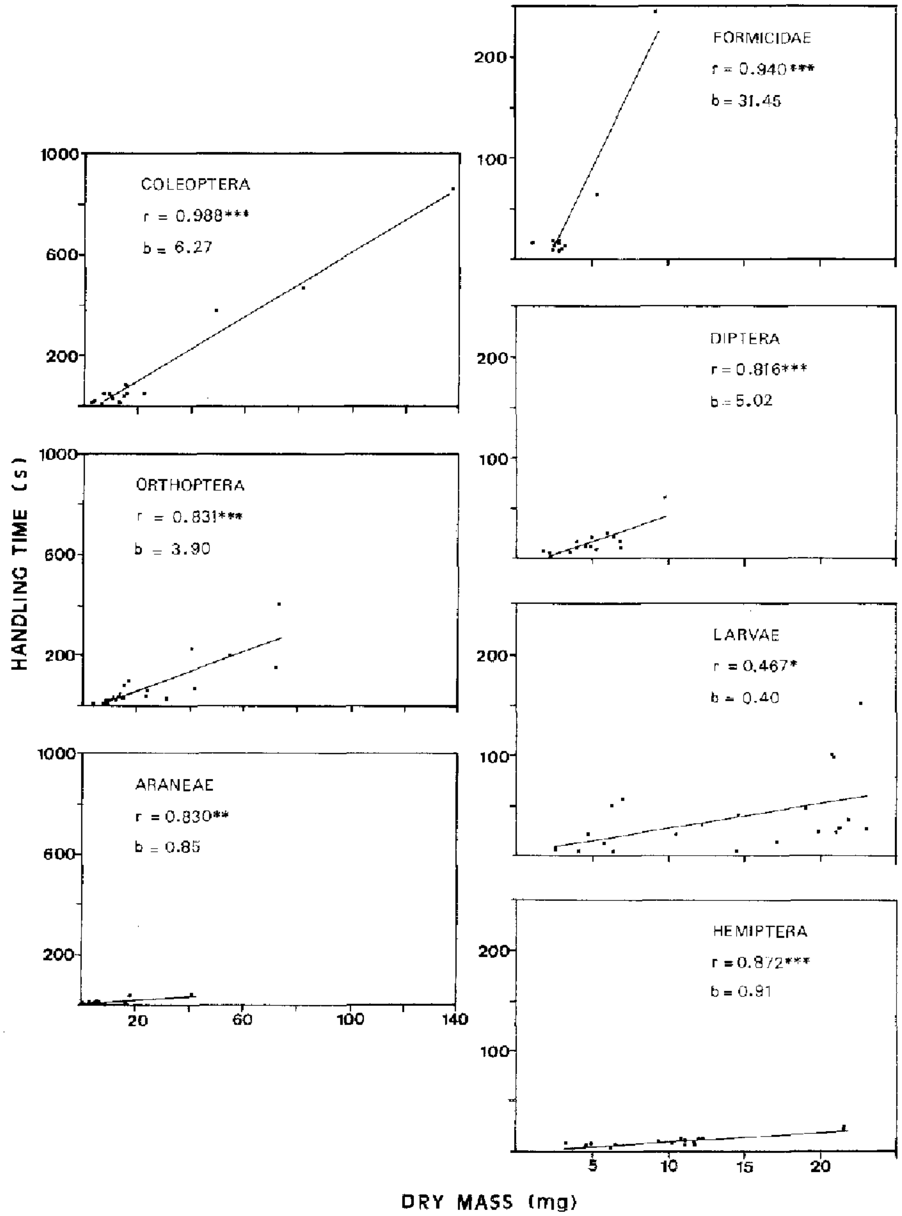

Fig. 1. Linear regressions, with correlation coefficients (r) and regression slopes (b), between handling time (s) and dry mass (mg) for each of the prey types fed to lizards in experimental trials. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

(ANOVA on the residuals of handling time vs. body mass: $F = 5.18$, $df = 6, 105$, $P < 0.001$). Controlling for the effects of prey mass, ants and coleopterans were the items with longer handling times, and spiders and hemipterans those with faster handling (see regression slopes in Fig. 1).

The profitability of the arthropods ingested was unrelated to prey mass, either for the total sample ($r = -0.060$, $df = 110$, $P > 0.5$) or each of the seven prey types (Table 1). Therefore, the energy obtained per time invested was largely independent of prey size. Mean profitabilities differed significantly among prey types (ANOVA: $F = 20.26$, $df = 6, 105$, $P < 0.001$). Hemipterans were the most profitable prey type followed by larvae, spiders, orthopterans, flies, coleopterans and ants (Table 1). Mean profitability values were inversely correlated with the slopes of the regression lines relating handling time to the mass of the captured items (see Fig. 1 and Table 1; $r = -0.945$, $df = 5$, $P < 0.002$), suggesting that the average profitability of a prey type was determined by the costs in handling time incurred by size increase within that type. These costs, in turn, were roughly related to the percentage of chitin in the arthropod taxa according to the data of Zach and Falls (1978). No association was found between the mean profitabilities of the prey types and the average distance at which they elicited attack ($r = -0.308$, $df = 5$, $P > 0.5$). Instead, the distance at which the attack was launched was weakly correlated with prey length (probably an easier visual cue than prey mass: $r = 0.201$, $df = 117$, $P < 0.05$). Length being equal, the attack distance was larger for arthropods detected while moving than for prey detected while immobile (ANOVA with the residuals of the regression relating attack distance to prey length: $F = 12.19$, $df = 1, 116$, $P < 0.001$). The size of the prey offered appeared to influence both handling time and the distance at which the attacks took place, but it did not affect their gross profitability: the increase in energy content was compensated by a similar increase in handling time.

In our field data, the mean dry mass of the prey ingested by lizards increased (Fig. 2: $f = 12.28$, $df = 2, 74$, $P < 0.001$), and their mean number decreased ($F = 4.58$, $df = 2, 77$, $P < 0.02$), as the active season progressed. Overall food abundance also appeared to vary through time ($F = 33.03$, $df = 2, 121$, $P < 0.001$), increasing markedly after the early spring. Despite the lack of association between profitability and prey size, lizards tended to

Table 1. Pearson's product-moment correlations, with associated probabilities, between profitability and mass within each prey type; and mean profitabilities (in J/s), with standard deviations, of the prey types tested in the experimental feeding trials

	r	P	Profitability (J/s)		
			$\bar{x}$	SD	n
Araneae	0.385	0.272	$18.88^{a,b}$	10.57	10
Coleoptera	−0.364	0.201	7.14^{c}	4.21	14
Diptera	−0.217	0.372	8.57^{c}	2.82	19
Formicidae	−0.461	0.154	3.55^{d}	1.88	11
Hemiptera	0.166	0.509	29.60^{a}	11.00	18
Larvae	0.032	0.890	21.85^{b}	25.06	21
Orthoptera	−0.190	0.436	$9.47^{b,c}$	4.28	19

Means followed by the same superscript letter are not significantly different: Tukey's test on log-transformed data

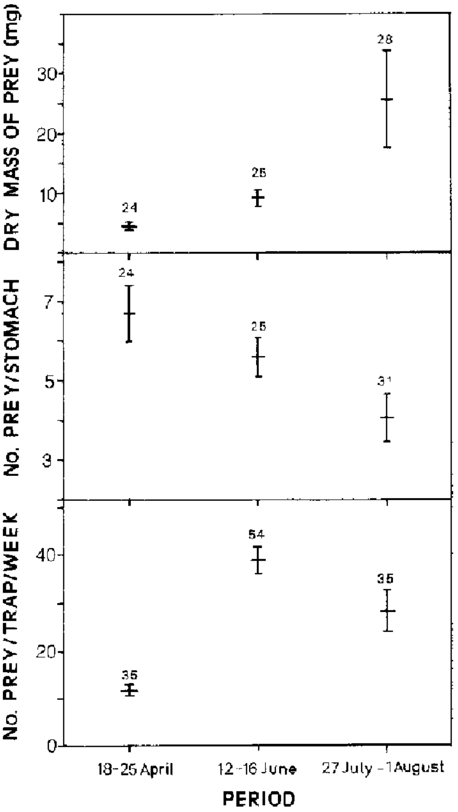

Fig. 2. Seasonal variation (mean ± 1 SE and sample size) of the mean dry mass of the prey consumed, the mean number of prey per stomach, and the overall abundance of available prey

Table 2. Mean dry mass (mg), with standard deviations and sample sizes, of the prey types available and consumed in each study period

	Early spring						Late spring						Midsummer					
	Available			Consumed			Available			Consumed			Available			Consumed		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Araneae	4.84	7.17	25	7.73	4.06	10	7.10	7.60	46	7.09	7.70	9	7.23	7.20	18	6.48	3.96	14
Coleoptera	13.98	15.32	16	7.11	3.76	6	10.15	22.63	40	9.79	14.29	19	10.14	22.60	15	12.91	4.36	15
Diptera	0.25	0.28	17	2.08	1.23	10	0.19	0.21	4	2.44	2.34	4	–	–	–	–		–
Formicidae	1.90	2.56	29	1.61	1.97	3	2.07	3.44	53	2.49	0.84	3	1.05	0.99	34	3.18	3.17	4
Hemiptera	1.11	0.45	7	5.72	5.69	12	1.47	1.37	30	11.59	14.00	13	2.58	1.55	9	7.13	3.43	7
Larvae	2.28	2.67	14	5.99	3.80	16	9.38	5.66	6	11.32	5.28	10	–	–	–	–	–	–
Orthoptera	–	–	–	–	–	–	27.36	23.86	4	15.30	11.56	6	56.87	66.62	2	96.03	196.3	15

Table 3. Prey size selection comparing the dry mass of the prey consumed (C) and available in the environment (A)

	Early spring		Late spring		Midsummer	
	Trend	*P*	Trend	*P*	Trend	*P*
Araneae	C > A	0.014	C ≈ A	0.759	C ≈ A	0.718
Coleoptera	C ≈ A	0.912	C ≈ A	0.129	C > A	0.051
Diptera	C > A	0.000	C > A	0.061	–	–
Formicidae	C ≈ A	0.897	C ≈ A	0.109	C > A	0.023
Hemiptera	C > A	0.057	C > A	0.000	C > A	0.020
Larvae	C > A	0.001	C ≈ A	0.356	–	–
Orthoptera	–	–	C ≈ A	0.455	C ≈ A	1.000

Probability values refer to the results of Mann-Whitney U-tests. Mean dry mass values and sample sizes are given in Table 3.

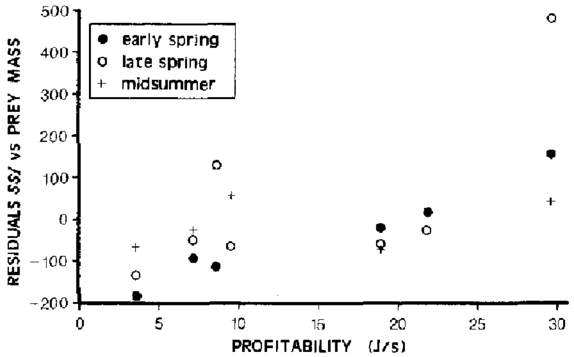

Fig. 3. Effect of profitability on prey size selection in each study period: Relationship between the size selection index (SSI) controlling for the effects of prey mass (residuals of SSI vs. prey mass; see text for details) and the mean profitability of the prey types

select large prey, though this tendency varied among prey types and study periods (Tables 2 and 3). In the early spring lizards selected prey larger than average from all taxa except the least profitable ones (ants and coleopterans). Hemipterans were the only taxon that was positively size-selected in all time periods (Table 3). These findings suggest that, other things being equal, and assuming that lizards maximize the energy returns of their foraging effort, stronger size selectivity would be expected within the more profitable taxa. The SSI, however, was unrelated to the mean profitabilities of the prey types ($r = 0.153$, $P > 0.5$, $n = 18$ taxa in three time periods). This lack of association could be due to the confounding effect of size differences among prey types. In fact, the SSI was primarily a negative nonlinear function of mean prey size ($r = -0.899$, $df = 16$, $P < 0.001$): selectivity for large prey items decreased with increasing average mass of the prey taxa. When the effects of size differences among taxa were controlled for by considering the residuals of this latter model, selectivity increased with prey profitability (Fig. 3: $r = 0.635$, $df = 16$, $P < 0.005$). Nevertheless, this association was variable through time. Thus, in the early spring profitability did affect size selection ($r^2 = 0.953$, $df = 4$, $P < 0.001$). In this period, food abundance was relatively low, and lizards included in their diet a high number of relatively small prey despite the selection of the larger items from all but the least profitable taxa (Table 3). In late spring, food availability reached its peak, the number of prey per stomach decreased, their man size increased, and profitability had a marginal effect on size selection ($r^2 = 0.484$, $df = 5$, $P = 0.08$). Finally, in mid summer lizards consumed small numbers of large-sized prey and the association between profitability and size selection did not reach significance ($r^2 = 0.142$, $df = 3$, $P > 0.1$).

Discussion

Perhaps the most striking aspect of our results is that lizards did not seem to care too much about the rate of energy intake per second when making their foraging choices. Profitability itself was strongly dependent on time constraints (slopes of handling times on prey mass). Our experimental feeding trials showed that the relationship between handling time and prey mass was best fitted by a linear model. This is in contrast to the results obtained by other authors who modelled the handling time of their avian (Sherry and McDade 1982) or reptilian (Pough and Andrews 1985) predators as a power function of arthropod mass. This discrepancy implies that the rate at which handling time increased with prey size was relatively lower in *P. algirus* than in the other insectivores examined. Handling costs were specific to prey taxa in a way that could be predicted by certain prey characteristics such as chitin contents (Zach and Falls 1978; Jaeger and Barnard 1981) or body shape (Loop 1974; Sherry and McDade 1982). When controlling for size effects, soft and round arthropods (hemipterans, spiders) were easier to handle, and hence more profitable, than hard, elongated ones (coleopterans, ants). Moreover, heavily chitinized exoskeletons negatively affect the gut passage time of food (Skoczylas 1978), and this would also lower the long-term rate of enery assimilation from the more chitinous prey (Jaeger and Barnard 1981).

The effect of the encounter distance on the decision to attack used in the predator-prey model (Schoener 1979) has usually been analysed assuming complete information about prey types (Stephen and Krebs 1986). This implies that the forager knows the effective profitabilities (energy/time) of its potential prey, and that such information is used for deciding when to attack and at what distance. Under these assumptions, the more profitable items should be attacked at a greater distance. Moreover, as long as greater distances cost more time and energy (i.e. longer pursuit runs), they should require higher profitabilities to counteract travel costs. These predictions, however, were not supported by our data, since mean attack distances were not positively correlated with profitabilities over the range of prey types examined. Furthermore, the selectivity (use vs. availability) for the four prey types most frequently consumed in summer (Formicidae, Araneae, Hemiptera and Orthoptera; Díaz and Carrascal 1990) was not significantly correlated with their mean profitability ($r_s = 0.400$, $P = 0.488$). The absence of significant relationships with prey profitability might be due to the existence of perceptual constraints when the precise energy value of poten-

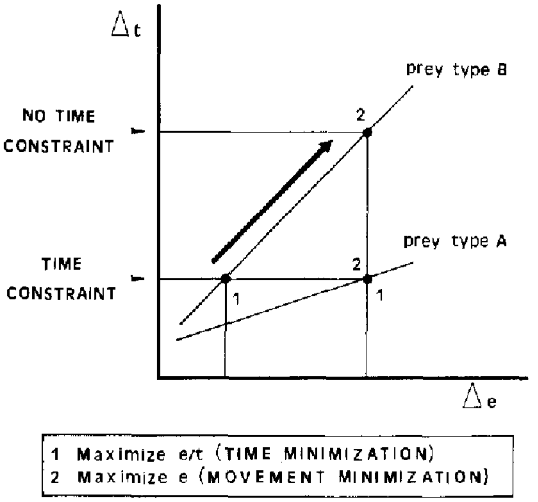

Fig. 4. Model describing the observed change of the foraging currency that explains the behaviour of *Psammodromus algirus (direction of the arrow)*. Under time constraints (e.g. in the breeding season), only the more profitable prey types (*A*) should be positively size selected as a means of saving time for nonforaging activities. This time minimization strategy (strategy *1*) leads profitability to play an important role in prey size selection. With no time constraints and with the forager itself probably subject to a heavy predation pressure, all prey types (*A* and *B*) should be positively size selected no matter what their mean profitability. This movement minimization strategy (strategy *2*) causes prey size (and hence energy content) to be the overriding parameter for prey selection in order to minimize the number of captures that would reveal the presence of lizards to their own predators

tial prey needs to be assessed from a distance, so that the particular profitability of a prey item would only be known while it was being handled. The assumption of the model, that the forager has complete information on the profitability of prey, might not be valid for this lizard species.

On the other hand, the attack distance was positively related to prey size, an index of gross energy intake that does not account for benefits in terms of energy per second of feeding time. Prey size was also the best predictor of lizard selectivity for different prey types in the postbreeding season (Díaz and Carrascal 1990). The importance of prey size as a key variable determining prey type selection and attack distance in *P. algirus* (Díaz and Carrascal 1990; this study) suggests that the policy for prey selection in this ectothermic forager in not to maximize the rate of net energy intake, but to maximize the gross energy intake per captured item, thus minimizing number of captures.

However, prey profitability had a pronounced effect on size selectivity within prey types during the breeding season (Fig. 3). Seasonal variation in this effect was seemingly due to the availability of potential prey and by temporal changes in both energy (*e*) and time (*t*) requirements. Under time constraints, it would be better for a foraging lizard to be more size-selective only when choosing from the more profitable prey types, as a means of reducing foraging time. The selection of the larger items within the more profitable types (strategy 1 in Fig. 4) would allow lizards to convert part of their foraging time into time devoted to other activities. This would be of adaptive value if the time budget was skewed towards non-foraging activities (Díaz 1991) or under conditions of low density or small size of available arthropods. All these circumstances are typical of the early spring, when average profitability accounted for 95% of the variation in size selection within prey types. In early spring, the abundance of prey was relatively lower (Fig. 2), and there were no orthopterans that could increase the mean mass of the prey consumed (personal observation). Thus, the relevance of profitability determining prey size selection within prey types (maximization of e/t in Fig. 4) should be related to time constraints (*t*). Conversely, in midsummer reproduction was over so that energy requirements were lower and activity was considerably reduced (Rose 1981; Díaz 1991). With no apparent time constraints, the importance of profitability as a foraging currency diminished. With an increased abundance of larger arthropods (mainly grasshoopers), lizards consumed small numbers of large sized prey (Fig. 2), thus shifting their foraging strategy towards the selection of large prey no matter their mean profitability (Díaz and Carrascal 1990). The prevalence of the gross energy intake per capture unit as a foraging currency (strategy 2, maximization of *e* in Fig. 4) is consistent with the "movement minimization" strategy suggested by Pough and Andrews (1985). Gross energy intake (*e*) may be more important than profitability (e/t) if there is a trade-off between energy gains and predation risk (Sih 1980; Werner et al. 1983). Eating large prey implies making fewer captures, which would be adaptive if the probability of lizards being detected by their own predators was more directly related to the number of sudden capture movements than to the time invested in handling the captured prey (Pough and Andrews 1985). Such movement minimization strategy induced by predation risk would be consistent with previous results that showed an effect of prey availability on the relative abundance of *P. algirus* – habitats with high arthropod densities would allow lizards to minimize number of movements that would reveal their presence to their potential predators (Díaz and Carrascal 1991). Similarly, thermoregulating animals have been shown to select the compass directions around shrub patches that minimize the distance between basking sites and protective shrub cover (Díaz 1992).

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