

## Foraging by the Omnivorous Lizard *Podarcis lilfordi*: Effects of Nectivory in an Ancestrally Insectivorous Active Forager

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**ABSTRACT.**—Foraging modes were described originally for insectivorous lizards, but many species are omnivorous or herbivorous. Because seeking and consuming plants might alter foraging, we studied foraging by the omnivorous *Podarcis lilfordi* at two sites: one where lizards licked nectar from flowers of *Euphorbia paralias* and the other where they sought insects. Movements per minute (MPM) did not differ among groups. Proportion of time spent moving (PTM) was similar in lizards that licked flowers and those that did not. Average speed (AS) was slower, and speed while moving (MS) was faster when foraging for nectar than for insects. Lizards foraging for nectar did not eat insects; those foraging for insects frequently ate them. For lizards foraging for prey, MPM increased as PTM, AS, and capture attempts increased and as PTM decreased. PTM increased as AS and capture attempts increased and decreased as MS increased. AS increased as MS increased. For lizards that licked, proportion of time licking (PTL) was unrelated to MPM, PTM, or AS but increased marginally as MS increased. Lizards foraging for nectar retained the PTM of lizards foraging for prey, but added a large PTL. The ancestral active foraging mode has been retained for hunting insects but modified to search for and lick nectar. While foraging for nectar, lizards greatly reduce attacks on insects, suggesting that, at a given time, an individual forages exclusively for nectar or prey. Reduced predation pressure on islands may have freed lizards to expand the diet by reducing risk during intervals exposed to view while climbing plants and licking nectar.

Two major hunting methods have been studied extensively in insectivorous lizards, active foraging and ambush (= sit-and-wait) foraging (Huey and Pianka, 1981; Perry, 1999; Cooper, 2007; McBrayer et al., 2007). However, approximately 12% of nonophidian lizards are either herbivores or omnivores (Cooper and Vitt, 2002). Search for and consumption of plants may require different sensory abilities and different movements used to search for food, greater time spent consuming food, and different movements between food items within patches than are typical for insectivorous lizards. Therefore, their foraging behavior may not be adequately described by the measures used to characterize foraging modes for prey acquisition by insectivorous species (Cooper and Vitt, 2002; Herrell, 2007). In some previous studies, feeding time has been short relative to search time and has been included in time spent moving (active). Lizards foraging in patches of leaves, fruits, or flowers might devote much more time to feeding and much less to searching for food than is typical of insectivores. These possible differences highlight the importance of separating time spent searching from time spent eating.

Foraging modes are suites of morphological, physiological, ecological, and behavioral correlates (e.g., Huey and Pianka, 1981; Cooper, 1995, 1997; McBrayer et al., 2007). The idea that selection on foraging behavior has molded these various traits has been called the foraging mode paradigm. Selection on foraging behavior has molded these various traits and has been an important driver of major evolutionary trends in lizards (Vitt et al., 2003; Vitt and Pianka, 2005). It is not yet clear how foraging behavior and correlates of foraging modes are affected when plants are added to the diets of lizards formerly limited to prey consumption. Herbivory is associated with large body size (Pough, 1973; Van Damme, 1999; Cooper and Vitt, 2002; Herrell, 2007), and both omnivory and herbivory have evolved frequently on islands where animal food may be limited (hypothesized: Rand, 1978; Pérez-Mellado and Corti, 1993; Van Damme, 1999; Cooper and Vitt, 2002; empirically con-

firmed: Van Damme, 1999; Cooper and Vitt, 2002). Furthermore, morphological and physiological specializations of digestive systems have evolved in herbivorous lizards (Hotton, 1955; Iverson, 1982; Dearing, 1993; Herrel et al., 1998, 2008; Herrel, 2007). These correlates of plant consumption show that consuming and digesting plant matter has important evolutionary consequences for lizards. We hypothesize that plant consumption also molds foraging behavior even in species that consume nectar, pollen, or fruits that are easily assimilated and do not require pronounced morphological modifications. Specifically, when omnivory and herbivory evolve in ancestrally insectivorous lizard lineages, lizards may be expected to adopt foraging behaviors appropriate for locating and consuming plants, altering the ancestral foraging modes.

Because omnivory appears to evolve in many lizards by incorporation of plant consumption levels above those ingested incidentally during prey consumption (Dixon and Medica, 1966; Van Wyk, 2000), foraging behaviors of omnivores are likely to consist of ambush or active foraging coexisting with search for and consumption of plants. To adequately characterize the foraging behavior of such lizards, it may be possible to measure the variables used to study foraging by insectivores and add additional information about search for and consumption of plants. Plant consumption has evolved more frequently in lineages of active than ambush foragers, presumably because lizards usually must move to locate consumable plants, which are stationary (Cooper and Vitt, 2002).

In studies of foraging mode, the most widely used variables are number of movements per minute (MPM) and percent or proportion of time spent moving (PTM) (e.g., Huey and Pianka, 1982; Perry, 1999; Cooper, 2005). Differences among modes also occur in average speed and speed while moving, average speed being faster and speed while moving slower in active foragers (Cooper, 2007). The proportions of attempted captures and successful captures initiated while moving are greater in active than ambush foragers (Cooper and Whiting, 1999; Cooper et al., 1999). In typical studies of insectivores, prey consumption is so rapid and infrequent that time spent consuming prey is ignored or omitted from analyses when lizards occasionally eat large

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prey that requires nontrivial handling time. This omission is unfortunate because comparisons of foraging by insectivores and plant eaters will undoubtedly show greater time spent consuming plants in many cases.

For omnivores, it should be possible to measure the same variables used to study foraging mode in insectivores and to add a measure of time spent handling plant matter. Exclusion of time spent consuming plant products might permit assessment of the effect of plant diet on the ancestral foraging behavior. One likely limitation in comparing foraging behaviors of insectivores and omnivores is that it may be difficult to determine whether time spent moving is motivated by search for prey, plants, or both simultaneously. However, if the same species eats plants in one microhabitat or at one time and animal prey in another, this difficulty might be overcome.

We studied foraging behavior by the Balearic Lizard (*Podarcis lilfordi* Günther, 1874), an omnivorous lacertid lizard (Pérez-Mellado and Corti, 1993). Casual field observations of this species reveal movements similar to those of active foragers, frequent attacks on prey, and often licking of nectar from flowers accessed by climbing the stems of several species of plants, including *Euphorbia paralias*, *Crythmum maritimum*, *Pistacia lentiscus*, *Asphodelus aestivus*, *Carlina corymbosa*, and others. During our study, yellow flowers of *E. paralias* occurred in one area; in a second area, *E. paralias* flowers were absent, and flowers of other plants that lizards lick were absent or rare. We measured aspects of foraging in both the euphorb zone where *E. paralias* occurred and in the other zone (lacking flowers). Our goals were to develop a method of comparing foraging by insectivorous and omnivorous or herbivorous lizards and to examine differences in plant and prey consumption in euphorb and other zones that might reflect differences in motivation of searching movements while foraging.

#### MATERIALS AND METHODS

*Study Site and Observations.*—The study was conducted on Aire, an islet off the coast of Menorca, Balearic Islands, Spain, in late April and early May 2005. Aire has no permanent human habitation but is visited frequently by biologists and boaters. In the euphorb zone, where flowering *E. paralias* plants were abundant, lizards frequently climbed stems of plants bearing yellow flowers, from which they licked nectar. We collected data in both zones on sunny days (1143–1436 h) when lizards were engaged in foraging.

To observe foraging, an investigator walked slowly through the habitat until an adult lizard was detected and then moved very slowly into a position approximately 5 m from the lizard and stood still to observe. After standing for a brief interval to ensure that the lizard was not disturbed, the investigator began verbally recording foraging behaviors using a miniature recorder and a stopwatch. The goal in each trial was to record behavior for 10 min, but some trials were cut short by social interactions or by lizards moving out of sight. Observations lasted  $7.94 \pm 0.81$  min (SE). Ten of 24 trials lasted the full 10 min; the shortest trial duration was 2.92 min. Total time of observations was 190.56 min. After completing a focal observation, the researcher noted the position and direction of movement of the lizard just observed and moved into position to start another focal observation on a different individual. It is possible, but unlikely, that any individuals were observed more than once because 1) only 11 and 13 lizards were observed in the two zones, 2) lizard densities on Aire are exceedingly high

(Barbadillo et al., 1999), and 3) a focal lizard for the next observation was typically visible at the conclusion of a focal observation.

We recorded whether the animal was moving or still continuously throughout each trial, noting each change. We also recorded distances moved (estimated visually) during each movement bout. We practiced estimating distances moved by nonfocal animals by measuring distances moved and comparing them with visual estimates. A lizard that had been moving was considered to have stopped when it remained still for two seconds. Finally, we noted attacks and feeding behaviors, which were classified as feeding attempts on prey, including captures and licking of flowers.

*Variables.*—From these data, we calculated the conventional foraging variables for insectivorous/carnivorous lizards based on movements and feeding behaviors. These were MPM (number of movements per minute), PTM (proportion of time spent moving), and PAM (proportions of attacks initiated while moving). Williams and McBrayer (2011) reported the proportion of attacks initiated when lizards were still (here PAS) as a new variable. This variable is one minus PAM. These variables are equally useful for characterizing foraging modes, with high PAM and low PAS indicating active foraging and low PAM and high PAS indicating ambush foraging. We have reported PAM because it has been used more widely and because *P. lilfordi* is an active forager. Also, we calculated average speed (AS) for the entire observation period and speed while moving (MS). Error inherent in our visual estimates of distances moved affect the accuracy of AS and MS, but speed variables calculated from the data are adequate to reveal any strong correlations with other foraging variables.

In addition to the movement variables and attack variables, we calculated two new variables. The proportion of time spent licking (PTL) was calculated to indicate time devoted to licking nectar. In omnivores and herbivores that consume solid plant matter, proportion of time spent handling plant matter would be substituted for PTL. PTL and PTM were calculated for the entire observation interval. Moving and licking were mutually exclusive.

*Analysis.*—Because some lizards in the euphorb zone licked and others did not, we treated these as two distinct groups to detect any other differences in foraging behavior. We tested differences in foraging behavior among these two groups and the group in the other zone. For MPM, PTM, AS, and MS, we conducted single-factor analyses of variance. For cases in which variances were significantly heterogeneous using Levene's tests, data were transformed logarithmically, and homogeneity of variance was ensured by another Levene's test prior to analysis. When significant main effects were detected, effect size was reported as  $\eta^2$  (Cohen, 1973), and differences among pairs of groups were tested for significance using Tukey's HSD tests.

For variables that had nonnormal distributions because many zero values occurred, we used Kruskal–Wallis tests to assess the main effect and Fisher exact tests of the frequencies of individuals having zero and nonzero values to compare pairs of groups. Some apparently significant *P*-values as shown using unadjusted *P*-values are reported as marginal following sequential Bonferroni adjustment (Wright, 1992). These tests were required for PTL, total captures and attempted captures, and total captures and attempted captures while moving. To examine relationships between variables, we used linear regression or Spearman nonparametric correlations.

TABLE 1. Foraging variables for *Podarcis lilfordi* in two areas, the euphorb zone where *Euphorbia paralias* bearing yellow flowers was abundant and the other zone where these plants were absent. Lizards foraged for insects in the former and nectar in the latter. Data for the euphorb zone are presented separately for lizards that licked flowers and those that did not. MPM = movements per minute; PTM = proportion of time moving; AS = average speed (m/min) during the focal observation; MS = speed while moving (m/min); PTL = proportion time spent licking nectar; FA = number of feeding attempts, including captures, on insect prey per observation; PT(M + L) = proportion of time spent either moving or licking. Data are shown as mean  $\pm$  SE. Sample size were 11 in the Other zone: 9 that licked and 4 that did not in the euphorb zone, and 13 pooled in the euphorb zone.

Variable	Foraging zone			
	Other	Euphorb		
		Licked	Did not lick	Pooled
MPM	2.09 $\pm$ 0.37	1.65 $\pm$ 0.24	1.72 $\pm$ 0.07	1.67 $\pm$ 0.16
PTM	0.32 $\pm$ 0.05	0.30 $\pm$ 0.04	0.52 $\pm$ 0.06	0.36 $\pm$ 0.04
AS	0.4 $\pm$ 0.1	1.2 $\pm$ 0.2	1.2 $\pm$ 0.1	1.2 $\pm$ 0.1
MS	1.3 $\pm$ 0.1	3.5 $\pm$ 0.6	2.4 $\pm$ 0.2	3.1 $\pm$ 0.4
PTL	0.0 $\pm$ 0.0	0.36 $\pm$ 0.05	0.0 $\pm$ 0.0	0.25 $\pm$ 0.06
FA	4.6 $\pm$ 1.6	0.0 $\pm$ 0.0	0.2 $\pm$ 0.2	0.1 $\pm$ 0.1
PT(M + L)	0.32 $\pm$ 0.05	0.65 $\pm$ 0.04	0.52 $\pm$ 0.06	0.61 $\pm$ 0.04

## RESULTS

**Movement Variables.**—MPM did not differ significantly in analyses of three groups (other zone, euphorb zone for lizards that licked flowers, and euphorb zone for lizards that did not lick [ $F_{2,21} = 0.58$ ,  $P = 0.57$ ; Table 1]). PTM differed significantly among lizards in the other zone, lizards in the euphorb zone that licked, and lizards in the euphorb zone that did not lick ( $F_{2,21} = 3.80$ ,  $P = 0.039$ ; Table 1). The effect size was  $\eta^2 = 0.27$ . PTM was significantly greater for lizards in the euphorb zone that did not lick than for those in the same zone that licked (Tukey's HSD test,  $P = 0.038$ ) and marginally greater than for those in the other zone ( $P = 0.06$ ). In an analysis in which the two groups of lizards in the euphorb zone were pooled, PTM did not differ between lizards in the euphorb and other zones ( $F_{1,22} = 0.47$ ,  $P = 0.50$ ; PTM for pooled euphorb zone was  $0.36 \pm 0.04$ ,  $N = 13$ ).

Among the three groups of lizards, AS differed significantly ( $F_{2,21} = 14.38$ ,  $P \ll 0.001$  using log-transformed data; Table 1). The effect size was substantial ( $\eta^2 = 0.58$ ). AS was significantly faster for lizards in the other zone than for those in the euphorb zone that licked (Tukey's HSD test,  $P \ll 0.001$ ) or did not lick ( $P = 0.001$ , but did not differ significantly between the two groups in the euphorb zone ( $P = 0.82$ )). MS differed significantly among the three groups of lizards ( $F_{2,21} = 16.12$ ,  $P \ll 0.001$  using log-transformed data; Table 1). The effect size was large ( $\eta^2 = 0.61$ ). MS was significantly slower for lizards in the other zone than for those in the euphorb zone that licked (Tukey's HSD test,  $P \ll 0.001$ ). The other differences among pairs of the three groups were not significant ( $P > 0.20$  each). In analysis pooling lickers and nonlickers in the euphorb zone, the pooled lizards had significantly greater MS using log-transformed data ( $F_{1,22} = 30.10$ ,  $P \ll 0.001$ ; MS was  $3.14 \pm 0.41$  m/min for pooled lizards in the euphorb zone,  $N = 13$ ).

**Feeding Variables.**—All lizards in the euphorb zone (including those that licked and those that did not lick) had significantly higher PTL than those in the other zone ( $\chi^2 = 12.18$ ;  $P \ll 0.001$ ; PTL was  $0.25 \pm 0.06$  for lizards in the euphorb zone,  $N = 13$ ). The total number of prey captures and attempted captures initiated while moving differed significantly among groups (Kruskal-Wallis test,  $\chi^2 = 14.18$ ,  $P \ll 0.0018$ ). The proportion of lizards that made at least one capture or attempted capture while moving was significantly greater for lizards in the other zone (8 of 11) than in lizards in the euphorb zone that licked (0

of 9; Fisher  $P = 0.001$ ) and was marginal between lizards in the other zone and those that did not lick in the euphorb zone (0 of 3;  $P = 0.026$ ) but was not significant between the two groups in the euphorb zone ( $P > 0.10$ ). For all attempts and captures, whether moving or still, the difference among groups was significant ( $\chi^2 = 11.49$ ,  $P = 0.003$ ). The proportion of lizards that made at least one capture or attempted capture was significantly greater for lizards in the other zone (8 of 11) than in lizards in the euphorb zone that licked (0 of 9, Fisher  $P = 0.001$ ) but did not differ significantly between lizards in the other zone and those that did not lick in the euphorb zone ( $P = 0.24$ ) or between the two groups in the euphorb zone (1 of 4 for those that did not lick,  $P = 0.31$ ). Only 2 of 50 feeding attempts and captures were initiated while lizards were still, giving PAM = 0.96.

**Relationships among Variables.**—MPM was unrelated to PTM ( $F_{1,22} = 1.92$ ,  $P = 0.17$ ), AS ( $F_{1,22} = 0.75$ ,  $P = 0.75$ ), or MS ( $F_{1,22} = 1.61$ ,  $P = 0.22$ ) for all lizards. These relationships were significant or marginal in the other zone where lizards foraged for prey (PTM:  $\rho = 0.66$ ,  $t_9 = 2.60$ ,  $P = 0.029$ ; AS:  $\rho = 0.82$ ,  $t_9 = 4.23$ ,  $P = 0.002$ ; MS:  $\rho = -0.54$ ,  $t_9 = -1.94$ ,  $P = 0.084$ ; Fig. 1) but were not significant in the euphorb zone where no feeding attempts on prey occurred, with the exception of a marginally negative relationship between MPM and MS (PTM:  $\rho = 0.36$ ,  $t_{13} = 1.28$ ,  $P = 0.23$ ; AS:  $\rho = -0.11$ ,  $t_{11} = 0.36$ ,  $P = 0.73$ ; MS:  $\rho = -0.59$ ,  $t_{11} = -2.43$ ,  $P = 0.033$ ). MPM was correlated with total captures and attempts ( $\rho = 0.47$ ,  $t_{22} = 2.47$ ,  $P = 0.022$ ) and captures and attempts while moving ( $\rho = 0.47$ ,  $t_{22} = 2.50$ ,  $P = 0.020$ ).

For all data, PTM was not significantly related to either AS ( $F_{1,22} = 2.30$ ,  $P = 0.14$ ) or MS ( $F_{1,22} = 1.23$ ,  $P = 0.28$ ). In the other zone, PTM increased as AS increased ( $\rho = 0.77$ ,  $t_9 = 3.62$ ,  $P = 0.006$ ; Fig. 2A) and decreased marginally as MS increased ( $\rho = -0.54$ ,  $t_9 = -1.94$ ,  $P = 0.085$ ; Fig. 2B). In the euphorb zone, PTM was unrelated to AS ( $\rho = 0.35$ ,  $t_{11} = 1.23$ ,  $P = 0.24$ ), and decreased marginally as MS increased ( $\rho = -0.53$ ,  $t_{11} = -2.06$ ,  $P = 0.064$ ). PTM was marginally correlated with total captures and attempts while moving ( $\rho = 0.47$ ,  $t_{22} = 2.47$ ,  $P = 0.022$ ). This relationship did not pertain to lizards that licked in the euphorb zone, where attempts or captures were rare but was stronger in the other zone ( $\rho = 0.75$ ,  $t_9 = 3.49$ ,  $P = 0.007$ ; Fig. 3). AS and MS were significantly related ( $F_{1,22} = 25.42$ ,  $P \ll 0.001$ ,  $R^2 = 0.54$ ; Fig. 4) according to the equation  $AS = 0.73MS + 0.15$  m/min. The intercept did not differ significantly from zero ( $t_{22} = 1.00$ ,  $P = 0.33$ ).

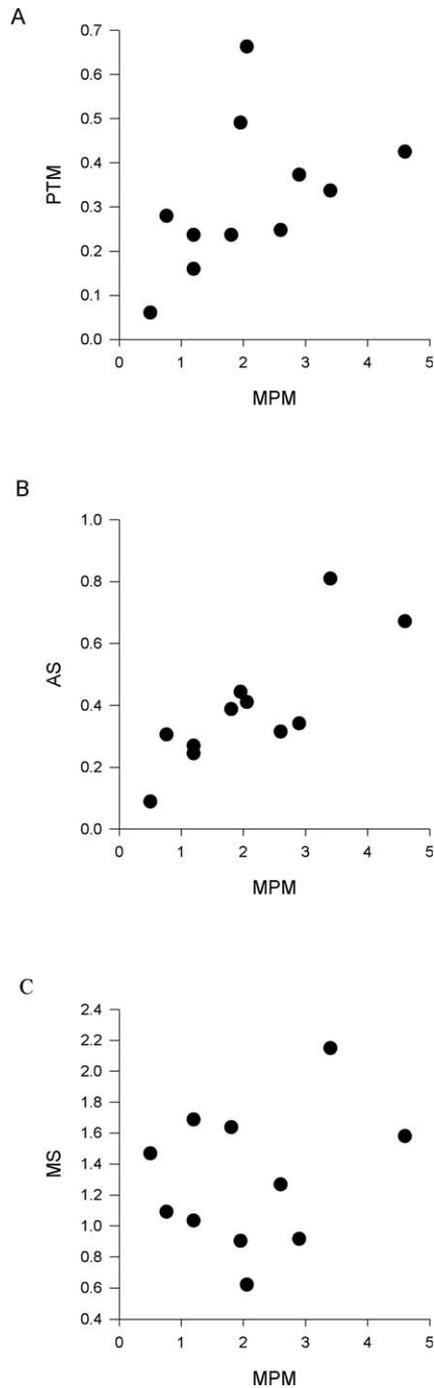


FIG. 1. Relationships in the other zone where *Podarcis lilfordi* foraged for insects between number of movements per minute (MPM) and A) proportion of time spent moving (PTM), B) average speed (AS in m/min), and C) speed while moving (MS in m/min).

For lizards that licked in the euphorb zone, PTL ( $F_{1,7} = 1.02$ ,  $P = 0.35$ ) was not significantly related to MPM or PTM ( $F_{1,7} = 3.63$ ,  $P = 0.10$ ). In the same group, PTL was not significantly related to AS ( $F_{1,7} = 0.45$ ,  $P = 0.17$ ) but increased marginally as MS increased ( $F_{1,7} = 5.15$ ,  $P = 0.058$ ).

Only one feeding attempt on animal prey occurred in the euphorb zone: an individual that never licked and was on the ground caught and ate an insect. Total captures and feeding attempts were significantly related to MPM ( $\rho = 0.75$ ,  $t_9 = 3.44$ ,  $P = 0.007$ ; Fig. 5A) and marginally to PTM ( $\rho = 0.55$ ,  $t_9 = 1.97$ ,  $P = 0.081$ ; Fig. 5B) in the other zone. Total captures and feeding attempts in the other zone were unrelated to AS ( $\rho = 0.52$ ,  $t_9 = 1.85$ ,  $P = 0.10$ ) or MS ( $\rho = -0.14$ ,  $t_9 = -0.42$ ,  $P = 0.69$ ).

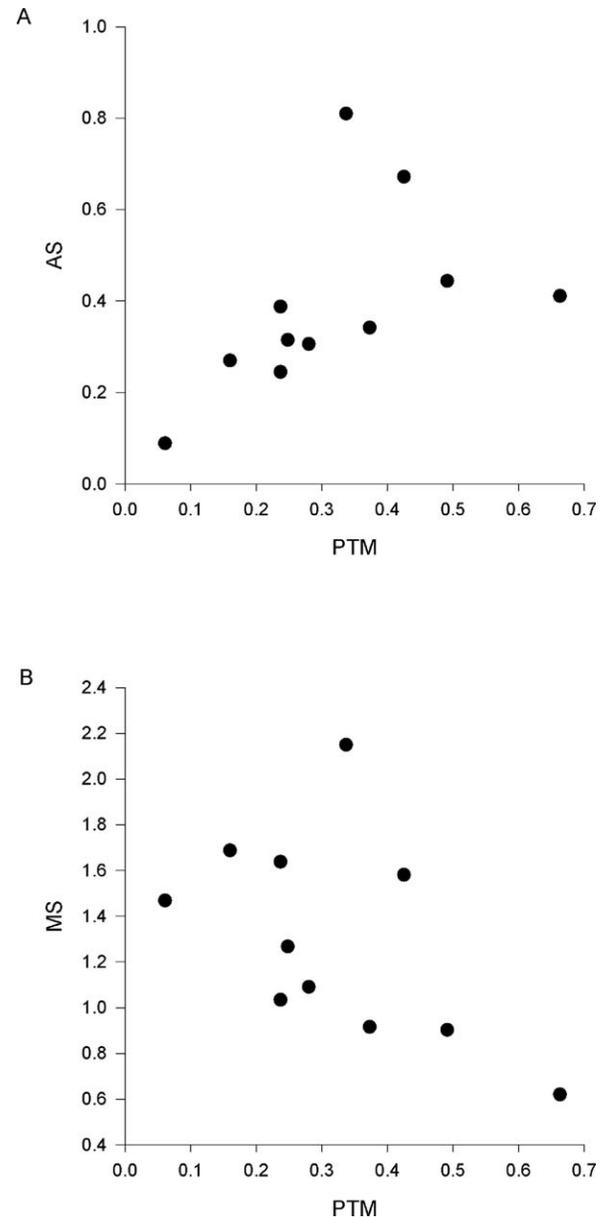


FIG. 2. Relationships in the other zone where *Podarcis lilfordi* foraged for insects between proportion of time spent moving (PTM) and A) average speed (AS in m/min) and B) speed while moving (MS in m/min).

#### DISCUSSION

Lizards foraging for nectar appeared to add a large proportion of the time feeding to their activity budget while retaining a proportion of time moving similar to that of lizards foraging for animal prey. In addition, movement and feeding variables and relationships between the variables revealed a pattern of similarities and differences related to foraging for plants and animal prey. In summary, MPM was similar among groups, whereas PTM was lower, AS slower, MS faster, PTL greater, and prey capture attempts were less frequent for lizards that licked nectar than foraged for insects.

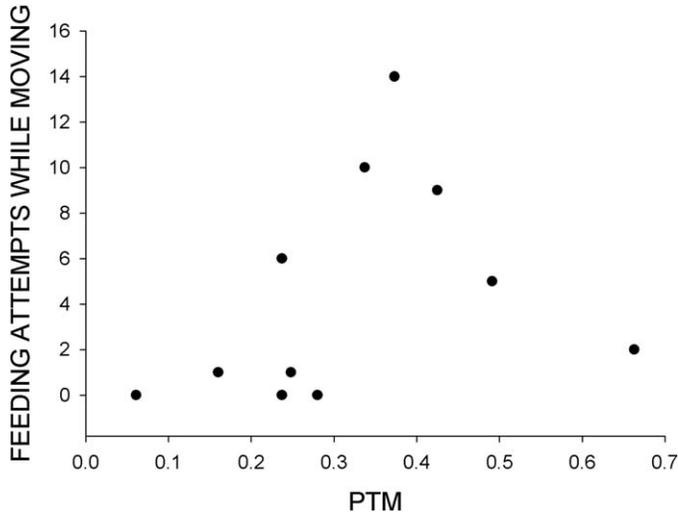


FIG. 3. Relationships in the other zone where *Podarcis lilfordi* foraged for insects between proportion of time spent moving (PTM) and number of feeding attempts (including captures) initiated while moving.

*Foraging Variables.*—The number of movements per minute did not differ among groups, but reasons for some movements did. Lizards that licked flowers often moved directly from one inflorescence to another, whereas lizards foraging for insects in the other zone sometimes terminated movements to attempt to or actually capture prey.

The higher PTM by lizards that did not lick than did lick in the euphorb zone reflects greater search time or time moving between patches of plants by lizards on the ground than by those that climbed plants and licked flowers, often moving very short distances between flowers. The marginally greater PTM for lizards in the euphorb zone that did not lick than for those in the other zone might indicate that some movements by lizards that did not lick in the euphorb zone were driven by motives other than foraging.

Alternatively, the overall similarity of PTM between zones might indicate that time allocated to search is similar for foraging on insects and nectar. This seems unlikely because plants bearing flowers are abundant and easily detected visually (Nicoletto, 1985; Kaufman et al., 1996) and perhaps

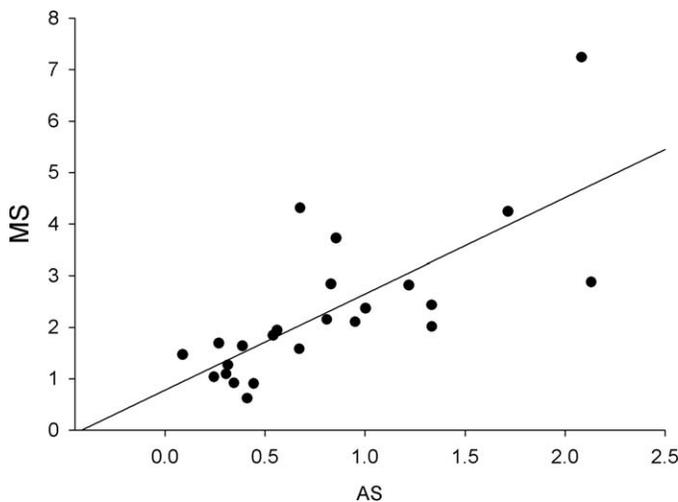


FIG. 4. Relationships for all *Podarcis lilfordi* between average speed (AS in m/min) and speed while moving (MS in m/min).

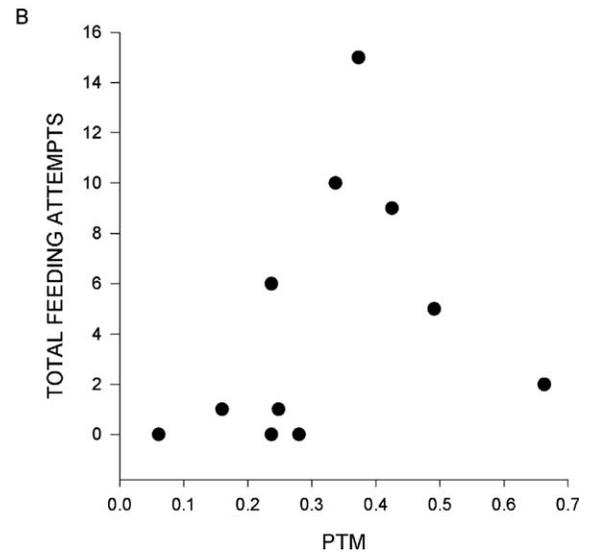
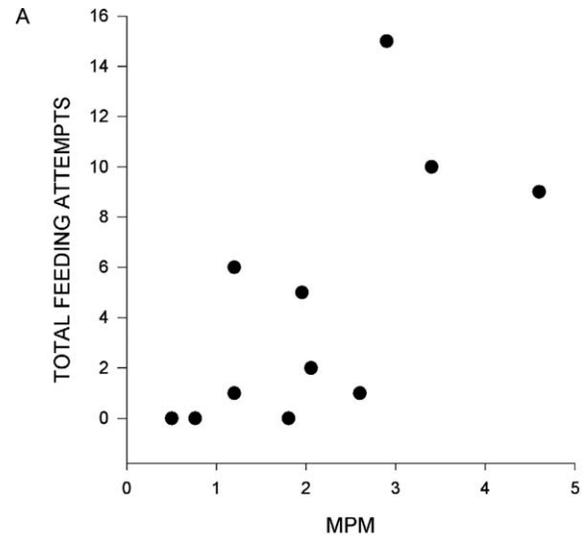


FIG. 5. Relationships in the other zone where adult *Podarcis lilfordi* foraged for insects between total number of feeding attempts (including captures) and A) number of movements per minute (MPM) and B) proportion of time spent moving (PTM).

by aroma (Cooper and Pérez-Mellado, 2001), suggesting that all time spent moving may not be motivated by foraging or that lizards eating nectar continue to search for animal prey. Search for insects seems unlikely to occupy much time while foraging for nectar because only one feeding attempt was observed in the euphorb zone despite the presence on insects on the ground and on plants.

Faster AS by lizards in the other zone is consistent with more intensive, prolonged search while foraging for insects than for plants, which can be seen from a distance, allowing faster, more direct movements between plants and flowers. That MS was greater for lizards in the euphorb zone than in the other zone also suggests more rapid movement while foraging primarily for plants than for insects.

Differences between foraging for nectar and insects were greater in feeding variables than movement variables. PTL accounted for one fourth of the time for all lizards in the

euphorb zone and for more than a third of the time for those that licked flowers, whereas no lizard in the other zone licked or consumed plant matter. Lizards in the other zone frequently attacked or caught insects, but only one attack on an insect was observed in the euphorb zone despite the presence of insects there. Therefore, lizards in the euphorb zone foraged almost exclusively for nectar and those in the other zone for insects. This difference in large measure reflects differences in availability of plant and animal food in the zones. It further suggests that, where abundant nectar is available, lizards shift foraging to focus on nectar and may reduce foraging for insects, whereas abundant energy is available from nectar. Differences in movement variables between zones suggest that dietary differences are accompanied by changes in searching behavior.

*Relationships between Variables.*—MPM and PTM were unrelated for the entire data set. This contrasts with interspecific correlations of  $r = 0.70$  for 80 species including few herbivores or omnivores (Cooper, 2005) and  $r = 0.86$  in 14 lacertid species (Verwajen and Van Damme, 2008). Intraspecific correlations between foraging variables have been largely ignored because most studies have focused on differences between foraging modes, but MPM and PTM were positively correlated in all four lacertid species studied by Perry et al. (1990), with  $r$ -values of 0.68–0.82. Therefore, the lack of correlation between MPM and PTM in *P. lilfordi* suggests a change in movement patterns associated with nectar consumption. PTM increased significantly as MPM increased in the other zone where lizards foraged only for prey but not in the zone where some lizards foraged almost exclusively for plants. This relationship was nonsignificantly positive in the euphorb zone and may not have differed meaningfully between zones.

For the entire data set, neither MPM nor PTM was correlated with either of the speed variables. This agrees with the lack of relationship between MPM and MS in a comparative study of 58 insectivorous lizard species (Cooper, 2007). However, the lack of relationship holds only in the area where lizards foraged for prey. In the euphorb zone, AS decreased as MPM increased, suggesting that AS is slower there when movements are more frequent, which was the observed (marginal) relationship in the euphorb zone. Short movements between flowers within plants may account for this relationship.

When searching for animal prey, *P. lilfordi* retains active foraging typical of insectivores. Results for the whole data set conflict with the increase of AS as MPM and PTM increased and decrease in MS as PTM increased in a comparative study (Cooper, 2007). Differences in relationships between variables when foraging for prey and plants obscured typical relationships for insectivores. For lizards foraging for prey in the other zone, AS increased as MPM and PTM increased, and MS decreased as PTM increased. Also, PTM values, and the high PAM, are typical for actively foraging insectivores.

When lizards foraged for plants, AS was unrelated to MPM or PTM, but MS was negatively related to MPM and PTM. This suggests that foraging for plants alters relationships between movement variables used to measure foraging. Larger sample sizes are needed to assess the effects on MPM and PTM of licking, moving between clusters of flowers, and searching for plants versus animal prey.

*Foraging Modes for Prey and Nectar and Implications for Evolution of Omnivory.*—Differences in foraging variables while foraging for insects and plants and relationships between the foraging variables indicate that *P. lilfordi* retains the ancestral active foraging mode of European lacertids (Arnold, 1990;

Cooper, 1994, 1995) when foraging for insects. When foraging for nectar, some of movement variables are altered and time spent feeding increases greatly. Although lizards ate only insects or nectar, not both, individual lizards at times eat both (VP-M, pers. obs.). *Podarcis lilfordi* consumes various plants and invertebrates and single stomachs sometimes contain both plant and animal foods (Pérez-Mellado and Corti, 1983). This strengthens the argument that individuals behave as active foragers when hunting animals exclusively and alter their foraging behavior as indicated above to incorporate plants into the diet.

Our observations characterize a transition from active foraging to omnivory with nectar consumption. Different alterations of ancestral foraging modes might occur in lizards that consume different types of plant materials (e.g., fruits and leaves) that require different searching and handling techniques. Transition from ancestral ambush foraging might have somewhat different effects than transition from active foraging to omnivory. We predict that in such cases, lizards continue to ambush prey. Their movements between plant patches may be relatively rapid, as is MS of ambushers (Cooper, 2007), but movements between flowers or fruits within plant patches may be shorter and more frequent than in ambush foragers. The latter effect occurs in *Platysaurus broadleyi* feeding on figs (Greeff and Whiting, 2000).

The proportion of time spent moving and eating was much greater for lizards foraging for nectar than for lizards foraging for insects. This was so because PTM, an index of search time, was similar in the other zone and for lizards that licked flowers in the euphorb zone but was greater for lizards in the euphorb zone that did not lick. The addition of substantial PTL in the euphorb zone made the total of feeding and moving times greater there than in the other zone. Although we did not measure time spent attempting to capture or consuming small prey, both were very short in this study because only very small prey were attacked, and no chases were observed. Longer time licking nectar than eating prey suggests that small volume may require longer consumption time than is needed for insect prey. If insects are sufficiently abundant for lizards to obtain adequate nutrition, lizards could increase the time available for other activities and/or reduce exposure to predation by limiting time exposed on stems of flowering plants. This may in part explain why a much greater proportion of lizards are insectivorous than omnivorous or herbivorous (approximately 88%, Cooper and Vitt, 2002). Alternatively, lizards may spend a long time licking because nectar-bearing flowers are abundant.

Reduced predation risk might help explain why omnivory is more frequent on islands than mainland in lizards (Cooper and Vitt, 2002), including lacertids (Van Damme, 1999). A common explanation has been that prey availability is reduced on islands, forcing lizards to broaden their diets, but insular lizards often achieve high density that might be a consequence of competitive release (Van Damme, 1999). However, predator suites are often depauperate and predation is often reduced on islands, accounting for evolution of island tameness (e.g., Darwin, 1839; Lack, 1947; Blumstein and Daniel, 2005; *P. lilfordi*: Cooper et al., 2009; Cooper and Pérez-Mellado, 2010, 2012). Relaxed predation might allow lizards to spend more time feeding in exposed sites, permitting expansion of the diet to include nectar and other plant matter. This was suggested by Janzen (1973), who hypothesized that long basking time required to digest plants efficiently places herbivores at greater risk than insectivores when predation is intense. Arguing that active foraging by insectivores may increase risk by increasing

the probability of being detected by predators while moving, Pianka (1973) proposed that herbivory may lower predation risk. *Podarcis lilfordi* are exposed to view and are likely most vulnerable to avian predators such as kestrels (*Falco tinnunculus*) when they climb plants to feed on nectar. Studies of risk while foraging on ground versus plants above ground and while basking during digestion of plants could clarify these issues.

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## LITERATURE CITED

- ARNOLD, E. N. 1990. Why do morphological phylogenies vary in quality? An investigation based on the comparative history of lizard clades. Proceedings of the Royal Society of London, Series B 240:135–172.
- BARBADILLO, L. J., L. J. LACOMBA, V. PÉREZ-MELLADO, V. SANCHO, AND L. F. LÓPEZ-JURADO. 1999. Anfíbios y reptiles de la Península Ibérica, Baleares, y Canarias. GeoPlaneta, Barcelona, Spain.
- BLUMSTEIN, D. T., AND J. C. DANIEL. 2005. The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society of London, Series B, Biological Sciences 272:1663–1668.
- COOPER, W. E., JR. 1994. Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. Journal of Chemical Ecology 20:439–487.
- . 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. Animal Behavior 50:973–985.
- . 1997. Correlated evolution of prey chemical discrimination with foraging, lingual morphology, and vomeronasal chemoreceptor abundance in lizards. Behavioral Ecology and Sociobiology 41:257–265.
- . 2005. The foraging mode controversy: both continuous variation and clustering of foraging movements occur. Journal of Zoology 267:179–190.
- . 2007. Foraging modes as suites of coadapted movement traits. Journal of Zoology 272:45–56.
- COOPER, W. E., JR., AND V. PÉREZ-MELLADO. 2001. Food chemicals elicit general and population-specific effects on lingual and biting behaviors in the lacertid lizard *Podarcis lilfordi*. Journal of Experimental Zoology 290:207–217.
- . 2010. Island tameness and predation in lizards. In V. Perez-Mellado and C. Ramon (eds.), Islands and Evolution, pp. 231–253. Institut Menorquí d'Estudis, Mao, Menorca, Spain.
- . 2012. Historical influence of predation pressure on escape behavior by *Podarcis* lizards in the Balearic Islands. Biological Journal of the Linnean Society (doi: 10.1111/j.1095.8312.01933.x).
- COOPER, W. E., JR., AND L. J. VITT. 2002. Distribution, extent, and evolution of plant consumption by lizards. Journal of Zoology 257:487–517.
- COOPER, W. E., JR., AND M. J. WHITING. 1999. Foraging modes in lacertid lizards from southern Africa. Amphibia-Reptilia 20:299–311.
- COOPER, W. E., JR., M. J. WHITING, J. H. VAN WYK, AND P. L. F. N. MOUTON. 1999. Movement- and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa. Amphibia-Reptilia 20:391–399.
- COOPER, W. E., JR., D. HAWLENA, AND V. PÉREZ-MELLADO. 2009. Islet tameness: escape behavior and refuge use in populations of the Balearic lizard (*Podarcis lilfordi*) exposed to differing predation pressure. Canadian Journal of Zoology 87:912–919.
- DARWIN, C. 1839. Journal of Researches into the Geology and Natural History of the Various Countries Visited by H. M. S. Beagle, under the Command of Captain Fitzroy, R. N. from 1832–1836. Henry Colburn, London, U.K.
- DEARING, M. D. 1993. An alimentary specialization for herbivory in the tropical whiptail lizard *Cnemidophorus murinus*. Journal of Herpetology 27:111–114.
- DIXON, J. R., AND P. A. MEDICA. 1966. Summer food of four species of lizards from the vicinity of White Sands, New Mexico. Contributions in Science Natural History Museum of Los Angeles County 121:1–6.
- GREEFF, J. M., AND M. J. WHITING. 2000. Foraging-mode plasticity in the lizard *Platysaurus broadleyi*. Herpetologica 56:402–407.
- GÜNTHER, A. 1874. Description of a new European species of *Zootoca*. Annals and Magazine of Natural History 14:158–159.
- HERREL, A. 2007. Herbivory and foraging mode in lizards. In S. M. Reilly, L. B. McBrayer, and D. B. Miles (eds.), Lizard Ecology: The Evolutionary Consequences of Foraging Mode, pp. 209–236. Cambridge University Press, Cambridge.
- HERREL, A., P. AERTS, AND F. DE VREE. 1998. Ecomorphology of the lizard feeding apparatus: a modelling approach. Netherlands Journal of Zoology 48:1–25.
- HERREL, A., K. HUYGHE, B. VANHOODYONCK, T. BACKELJAU, K. BREUGELMANS, I. GRBAC, R. VAN DAMME, AND D. J. IRSCHICK. 2008. Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. Proceedings of the National Academy of Science, USA 105:4792–4795.
- HOTTON, N., III. 1955. A survey of adaptive relationships of dentition and diet in the North American Iguanidae. American Midland Naturalist 53:88–114.
- HUEY, R. B., AND E. R. PIANKA. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.
- IVERSON, J. B. 1982. Adaptations to herbivory in iguanine lizards. In G. M. Burghardt and A. S. Rand (eds.), Iguanas of the World, pp. 60–76. Noyes Publications, Park Ridge, NJ.
- JANZEN, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687–708.
- KAUFMAN, J. D., G. M. BURGHARDT, AND J. A. PHILLIPS. 1996. Sensory cues and foraging decisions in a large carnivorous lizard, *Varanus albigularis*. Animal Behaviour 52:727–736.
- LACK, D. 1947. Darwin's Finches. Cambridge University Press, Cambridge.
- MCBRAYER, L. D., D. B. MILES, AND S. M. REILLY. 2007. The evolution of the foraging mode paradigm in lizard ecology. In S. M. Reilly, L. D. McBrayer, and D. B. Miles (eds.), Lizard Ecology: The Evolutionary Consequences of Foraging Mode, pp. 508–521. Cambridge University Press, New York.
- NICOLETTI, P. F. 1985. The roles of vision and the chemical senses in predatory behavior of the skink, *Scincella lateralis*. Journal of Herpetology 19:487–491.
- PÉREZ-MELLADO, V., AND C. CORTI. 1993. Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). Bonner Zoologisches Beilage 44:193–220.
- PERRY, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. American Naturalist 153:99–109.
- PERRY, G., I. LAMPL, A. LERNER, D. ROTHENSTEIN, E. SHANI, N. SIVAN, AND Y. L. WERNER. 1990. Foraging mode in lacertid lizards: variation and correlates. Amphibia-Reptilia 11:373–384.
- PIANKA, E. R. 1973. The structure of lizard communities. Annual Reviews of Ecology and Systematics 4:53–74.
- POUGH, F. H. 1973. Lizard energetics and diet. Ecology 54:837–844.
- RAND, A. S. 1978. Reptilian arboreal folivores. In G. G. Montgomery (ed.), The Ecology of Arboreal Folivores, pp. 115–122. Smithsonian Institution Press, Washington, DC.
- VAN DAMME, R. 1999. Evolution of herbivory in lacertid lizards: effects of insularity and body size. Journal of Herpetology 33:663–674.
- VAN WYK, J. H. 2000. Seasonal variation in stomach contents and diet composition in the large girdled lizard, *Cordylus giganteus* (Reptilia: Cordylidae) in the Highveld grasslands of the northeastern Free State, South Africa. African Zoology 35:9–27.
- VERWAJEN, D., AND R. VAN DAMME. 2008. Foraging mode and its flexibility in lacertid lizards from Europe. Journal of Herpetology 42:124–133.
- VITT, L. J., AND E. R. PIANKA. 2005. Deep history impacts present-day ecology and biodiversity. Proceedings of the National Academy of Science 102:7877–7881.
- VITT, L. J., E. R. PIANKA, W. E. COOPER JR., AND K. SCHWENK. 2003. History and the global ecology of squamate reptiles. American Naturalist 162:44–60.
- WILLIAMS, S. C., AND L. D. MCBRAYER. 2011. Attack-based indices, not movement pattern, reveal intraspecific variation in foraging behavior. Behavioral Ecology 22:993–1002.
- WRIGHT, S. P. 1992. Adjusted *P*-values for simultaneous inference. Biometrics 48:1005–1013.