

Evolution of Herbivory in Lacertid Lizards: Effects of Insularity and Body Size

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ABSTRACT—I tested the putative correlation between insularity and herbivory in lacertid lizards. Analysis of literature data on 97 populations of 52 species shows that lizard populations on islands more often include plant material in their diet than do mainland populations. To investigate whether this finding reflects adaptation due to recent selection or is merely a product of the phylogenetic history of the populations, I reconstructed the ancestral states for diets and insularity and incorporated them in the analysis. Changes in habitat (island-mainland or mainland-island) often went with changes in diet (herbivore-insectivore or insectivore-omnivore). Insectivorous lizards that find themselves on islands more often turn towards herbivory than do lizards living in mainland situations. Lizards that already have plants in their diet when living on the mainland seem more successful in colonizing islands. Herbivorous populations of lacertids tend to be larger than insectivorous populations, but there is considerable overlap. No difference in mean snout-vent length was found between island and mainland populations.

As expected from their great taxonomic diversity, lizards have evolved a great range of diets; insects and other arthropods, mammals and birds, vertebrate eggs, snails, fish, nectar, and various mixtures of leaves, flowers, and fruits. Although the dietary range of lizards is great, the distribution of foods eaten reveals that complete herbivory is rare compared to a diet of arthropods. Only about 3% of all extant lizard species are known to eat significant quantities of plant food (King, 1996). On the other hand, many species occasionally shift away from a diet only of arthropods, toward an omnivorous or herbivorous diet (e.g., Pough, 1973; Schluter, 1984; Pérez-Mellado and Corti, 1993; King, 1996). Several authors have speculated on the ecological circumstances that could induce insectivorous lizards to expand their diet to include plant material (Pough, 1973; Schluter, 1984; Pérez-Mellado and Corti, 1993; King, 1996). Because plant material is less digestible and may produce substantially slower growth (Pough, 1973; Schluter, 1984), herbivory is often

considered a 'forced move', that lizards will not make unless arthropods are insufficient to meet their energy requirements (but see Johnson and Lillywhite, 1979; Sadek, 1981; Troyer, 1984). Lizards living in habitats where insect abundance is (periodically) low may benefit from (partial) herbivory. Large body size is also considered an incentive for herbivory, because larger lizards putatively have greater energetic needs and are less adept at catching small prey because they must move a greater mass in pursuit (Sokol, 1967; Pough, 1973; Sadek, 1981; but see Greene, 1982). The bulk of exclusively herbivorous lizard species is indeed larger than 300 g (Sokol, 1967; Pough, 1973; but see Greene, 1982).

If the above presumptions are true, insular lizard populations can be expected to feed more often on plant material than mainland populations. Indeed, islands (especially small ones) often have poor arthropod faunas (Janzen, 1973a, b), and at least for some families and genera of lizards, there is a tendency for larger body size in island races (Case, 1978). Although many au-

thors have suggested a relationship between insularity and herbivory (Sadek, 1981; Schluter, 1984; Pérez-Mellado and Corti, 1993), this hypothesis has seldom been tested explicitly. My objective is to provide a test of the presumed correlation between insularity and herbivory, using literature data on the feeding habits of lizards of the family Lacertidae. Since patterns of character correlation among extant species will provide better insight in evolutionary processes if the analyses include phylogenetic information (Brooks and McLennan, 1991), I analysed the data in an explicitly phylogenetic context (Harvey and Pagel, 1991)

MATERIALS AND METHODS

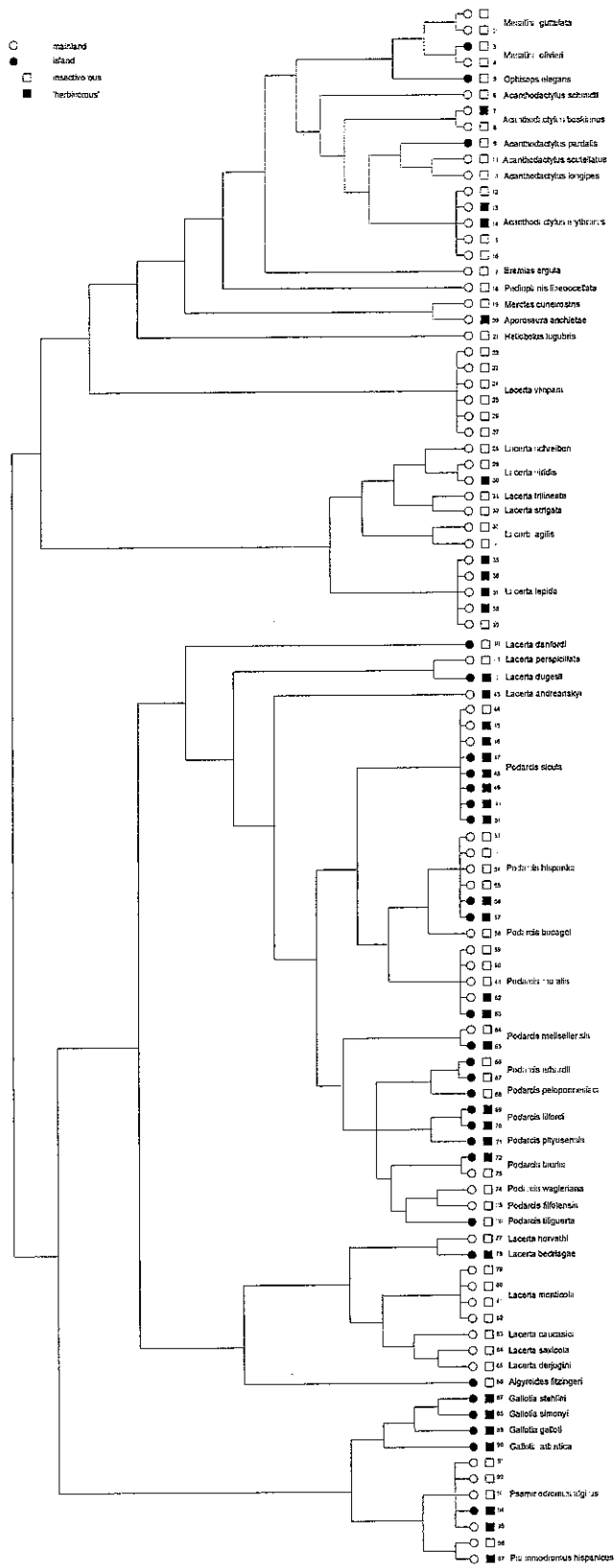
My search of the literature yielded reports on stomach and faeces contents from 97 populations of lacertid lizards, belonging to 52 species (see Appendix). Although lacertid lizards basically feed on arthropods, 15 populations (22.4%) at least occasionally also consume vegetal matter. Probably no lacertid is exclusively herbivorous; even those species that are known to thrive predominantly on plant material in the wild (e.g., *Gallotia galloti*, pers. obs.) are eager to take insects in captivity. For simplicity, I labelled a population 'herbivorous' if its diet includes parts of plants (stalks, leaves, flowers, pollen, nectar, fruits, seeds) during at least part of the activity season. Hence, in this paper, 'herbivorous' refers to the fact that plants are eaten; it does not mean that plants are eaten only. Lizards that eat arthropods or other animal prey, but were never witnessed to consume plants, were labelled 'insectivorous'. Some lizards will take up bits of plant material in the course of swallowing arthropod prey. To distinguish between such 'accidental' herbivory and 'true' herbivory, the label 'herbivorous' was given only to populations for which more than 5% of the individuals examined had at least 5% plant material in their guts or in faeces. Lizards that were seen feeding on plants in nature were also considered 'herbivorous'. In practice, it proved to be easy to classify a lizard population as either 'herbivorous' or 'insectivorous'. The dichotomy is apparent. Also, the consumption of plant material by lacertid lizards is usually considered noteworthy and is therefore well described in

the literature (see references). Still, the data presented here are probably biased towards insectivory. For instance, lizards that consume plants periodically may be misclassified as 'insectivorous' if the population was not sampled during the appropriate periods. However, I will assume that this bias is equivalent in island and mainland habitats.

Populations and species cannot be considered independent data points because they share some of their evolutionary history. More closely related species may share characteristics because they inherited them from their common ancestor, not because they have each independently evolved them. Also, because related species tend to occupy similar environments, they may be similar because they share many features in their current environments (and not just the one considered in the analysis, in this case insularity). For these reasons, the assumption of independency is not met and traditional statistics, such as the chi-square test, may not reveal true association. In an attempt to circumvent this problem, I reconstructed the phylogenetical relationships among the species in the analysis from various sources in the literature (Fig. 1). The degree of phylogenetical relatedness between populations within a single species was assumed to be proportional to the physical distance separating them. For each species for which I had data on more than two populations, I performed a cluster analysis with the latitudinal and longitudinal co-ordinates of the respective population sites as input. I calculated geometric (Euclidean) distances between all possible pairs and used the single linkage (nearest neighbour) rule to form clusters (Everitt, 1980). The shape of the resulting hierarchical plot was considered as a representation of the phylogeny of the populations. I used the MIX (Mixed method parsimony) module of PHYLIP V3.57 (Phylogeny Inference Package, Felsenstein, 1995) to reconstruct the ancestral states for diet (herbivore/insectivore) and insularity (island/mainland), assuming parsimony.

Differences in body size between herbivorous and insectivorous species and between island and mainland species were examined with analysis of variance. Conventional analysis of variance also requires independent data points. In-

FIG. 1 Hypothesized phylogenetic relationships for the lacertid species used in the analyses. The branching patterns are not always well known; some information in the literature is conflicting. The present tree is a "best current compromise" cladogram based on the studies of Arnold, 1973, 1983, 1989, 1991; Lutz and Mayer, 1985; Arnold, 1989; Mayer and Lutz, 1989, 1990; Mayer and Benyr, 1994; and Bauwens et al., 1995. Depicted branch lengths are not realistic. The symbols at the tips refer to the environment (circles; open = mainland, filled = island) and diet (squares; open = insectivore; filled = herbivore) of the respective populations. The numbers refer to the appendix



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TABLE 1. Number of habitat and diet transitions that occurred between ancestral and descendant populations during the hypothesized phylogenetical history of the species considered (ancestral → descendant state)

	insectivore→insectivore	insectivore→herbivore	herbivore→insectivore	herbivore→herbivore
mainland→mainland	111	9	6	28
mainland→island	6	6	1	13
island→mainland	0	0	1	0
island→island	2	0	0	11

dependency of data points may inflate the degrees of freedom and therefore significance levels obtained from customary F-tables cannot be trusted. As an alternative, Garland et al. (1993) proposed using empirically scaled computer simulation models of traits evolving along a given phylogenetic tree to obtain null distributions of F statistics for comparative data sets. These null distributions allow to test hypotheses, accounting for the nonindependency due to phylogenetic topology, branch lengths and model of character change. I used the PDSIMUL-programme (Garland et al., 1993) to generate 1000 simulations of the evolution of body size in the lacertid lizard phylogeny. As little information is available on divergence times in lacertid phylogeny, all branch lengths were set to unit length. This complies to a speciation model of evolution, with all changes occurring in association with speciation events (Rohlf et al., 1990; Garland et al., 1993). For each of the 1000 sets of simulated tip values, I calculated within- and between-group sums of squares, means squares, and corresponding F-ratio, using the convenient PDANOVA-programme (Garland et al., 1993). I then computed the 95th percentile of the distribution of these 1000 F ratios and compared it to the F ratio for the real data set.

RESULTS

Of the 67 mainland populations for which I found data, 52 (77.6%) were insectivorous; 15 (22.4%) also consumed plant material. Of the 30 island populations, 8 (27.7%) were insectivorous and 22 (73.3%) were herbivorous. These proportions differ significantly ($\chi^2 = 22.8$, $P < 0.0001$). Lacertids living on islands seem to show a greater tendency towards herbivory than those on the mainland.

Because the independency of data points may hamper the interpretation of the above statistics, I introduced the phylogenetical relationships among the species considered into their analysis. The constructed tree suggests 27 changes in

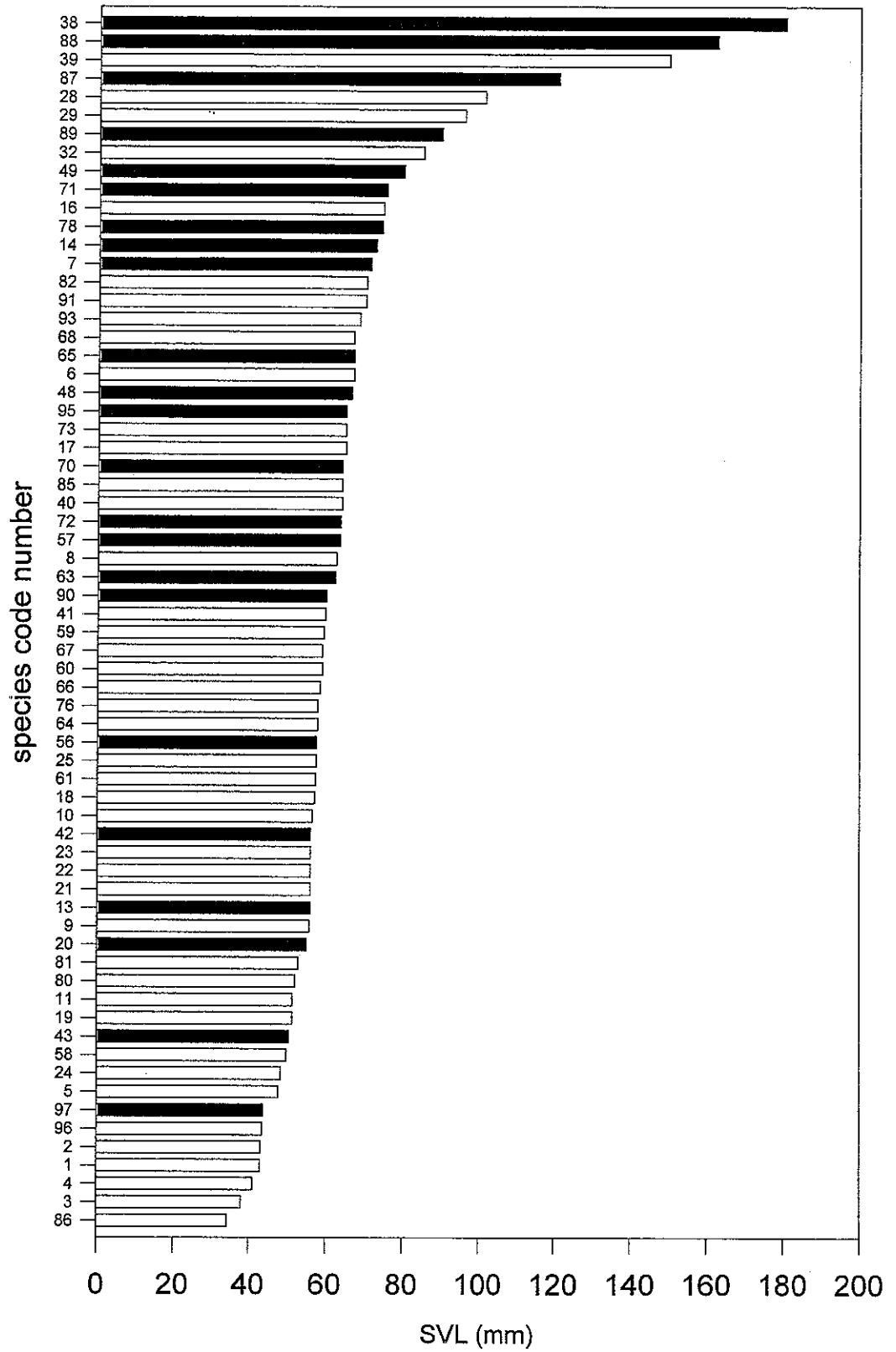
habitat (from mainland to island or vice versa) between ancestral and descendant nodes (Table 1). In eight of these cases (29.6%) such transition is attended by a change in diet (insectivore to herbivore or vice versa). In 167 events, the habitats of ancestors and descendants are the same. In 15 of these 167 cases (9.0%), ancestors and descendants have different diets. Thus, populations that live in a different type of environment than their direct ancestors are more likely to differ in dietary habits than populations that share the same type of environment with their ancestors ($\chi^2 = 9.38$, $P = 0.0022$).

The tree includes 12 instances in which insectivorous ancestors, living on the mainland, have a descendant living on an island. In six of these cases (50%), the descendant population has a diet that includes plant material. There are 120 occasions of insectivorous, mainland ancestral populations having descendants on the mainland. Only 9 (7.5%) of these descendants are 'herbivorous'. These proportions differ significantly (Fisher's exact test, $F = 13.49$, $P < 0.001$), suggesting that lizards more often switch to herbivory when they find themselves in islands than when on the continent.

The tree includes 48 herbivorous populations that live(d) on the mainland. Fourteen (29.2%) of them have descendants on islands. This is a higher proportion compared to the 132 insectivorous mainland populations, 12 (9.1%) of whom gave rise to descendant populations on islands ($\chi^2 = 11.48$, $P = 0.0007$). This finding seems to suggest that herbivory is a trait that helps lizards to settle successfully on islands.

Of the 197 diet studies, 66 reported the average adult body size (snout-vent length) of the lizard population sampled. Herbivorous populations are on average larger than insectivorous populations (Fig. 2, mean \pm sd for herbivorous populations: 70.8 ± 1.41 mm; for insectivorous populations: 58.9 ± 1.29 mm; two-way analysis of variance on log 10-transformed SVLs, $F = 7.75$, $df = 1, 64$, $P = 0.007$). There is no size dif-

FIG. 2. Mean adult snout-vent lengths (in mm) of herbivorous (filled) and insectivorous (open) lacertid lizards. The numbers refer to the appendix.



ference between island and mainland populations ($F = 0.0041$, $df = 1.64$, $P = 0.61$), and the diet* environment effect is not significant either ($F = 0.043$, $df = 1.64$, $P = 0.10$).

To account for the independency of data-points, I also tested the F-values against empirically obtained null-distributions (see materials and methods). The difference between herbivorous populations and insectivorous populations remained significant (one way analysis of variance on log 10-transformed SVLs, $F = 6.58$; while more than 95% of the 1000 simulations yielded F-values smaller than 6.23, so $P < 0.05$). No difference in SVL was found between island and mainland populations (actual $F = 0.31$, 95%-boundary of simulations was 12.61, so $P > 0.05$).

To further investigate correlations between dietary changes and body size evolution, I estimated the SVL for each ancestral node in the phylogenetic tree by averaging the SVLs of its two daughters. The mean difference in SVL between an insectivorous ancestor and its herbivorous daughters is 0.24 ± 5.50 mm ($N = 6$). Three lizards grew bigger while changing from an insectivorous to a herbivorous diet, three grew smaller. The reverse transition, from herbivorous to insectivorous, is accompanied with a mean change of -4.31 ± 7.00 mm ($N = 5$) in SVL. Here, four lizards grew smaller and one grew larger. If both the ancestral population and the daughter population are insectivorous, the mean change in SVL was 0.20 ± 4.77 mm ($N = 60$). In 28 of these 60 'transitions', SVL was reduced; in the remaining 32, SVL increased. Finally, in situations where both the ancestral and the descendant population are herbivorous, mean SVL increased with 1.19 ± 13.73 mm ($N = 24$). In 10 cases, descendants were smaller than their ancestor, while in 14 cases they were larger. An ANOVA on these mean differences in SVL reveals no significant differences between the four different types of transitions ($F = 0.63$, $df = 3.91$, $P = 0.60$). This suggests that a dietary transition is not immediately followed by a change in SVL.

The estimated ancestral SVLs can also be used to test the hypothesis that large insectivorous lizards are more likely to switch toward herbivory than small insectivorous lizards. Insectivorous ancestors with herbivorous daughters had an average SVL of 65.48 ± 6.70 mm ($N = 60$), while insectivorous ancestors with insectivorous descendants had an average SVL of 59.46 ± 12.14 mm ($N = 6$). This difference is not significant ($t = 1.19$, $df = 64$, $P = 0.24$).

DISCUSSION

Herbivory and Insularity.—My analyses confirm earlier suggestions (Pérez-Mellado and

Corti, 1993) that herbivory in lacertid lizards is associated with insularity. Although the supplementation of the arthropod-based diet with plant matter is certainly not confined to island situations, insular lizards tend to be more catholic in this respect than mainland lizards.

Which circumstances that are typical for island situations could induce lizards to broaden their host list in this way? Insufficient numbers of arthropod prey seems an obvious motive. Most of the papers from which I drew the diet profiles do not report the abundance of potential prey items, so I cannot test the hypothesis directly with the present data. However, oceanic islands, especially small and remote ones, are known to harbor fewer species of arthropods than mainland sections of similar size (e.g., Gressitt, 1965, 1970; Baroni-Urbani, 1971; Janzen, 1973a, b; Carlquist, 1974; Weissman and Rentz, 1976). The one study I know of that compared densities (besides species richness) of arthropods between island and mainland sites also found a dramatic decrease in densities for beetles and bugs, though not for Homoptera (Janzen, 1973b). Whether the results from this study on neotropical foliage insects also apply to the islands in this study, remains to be tested, but it seems likely that islands, on average, will contain less arthropods. This finding seems in contradiction with the fact that many populations of lizards, including lacertid lizards, achieve remarkably high densities on islands (e.g., *Podarcis sicula salpini* on Vivaro di Nerano: Ouboter, 1981; *P. lilfordi* on the Balearic Islands: Pérez-Mellado, 1989; *P. hispanica atrata* on the Columbretes Archipelago: Castilla and Bauwens, 1991). This phenomenon has often been attributed to competitive release, the lack of competitors resulting in higher resource densities per capita (e.g., MacArthur et al., 1972; Case, 1975; Case et al., 1979; Stamps and Buechner, 1985). Clearly, detailed data on both lizard and arthropod prey densities will be required to clarify the relationship between prey availability and diet preferences (Sadek, 1981).

Janzen (1973b) questioned whether low arthropod density alone is sufficient to explain the prevalence of herbivory in island populations of lizards. He argued that a second factor, low predation pressure, is necessary to allow evolution towards a herbivorous life style. His line of reasoning was as follows: Efficient processing of plant material requires long periods of high body temperatures (e.g., Throckmorton, 1973; Troyer, 1987; van Marken Lichtenbelt, 1992, 1997), a condition which, in most ectotherms, can only be achieved by prolonged basking. Basking involves exposition to diurnal predators; prolonged basking sessions may be too risky in situations with many predators about. On islands,

where predation pressure is often relaxed, lizards can safely bask for long periods of time and thus can digest plant matter. Two assumptions are vital to this hypothesis. Firstly, lizards trying to achieve high body temperatures should be more vulnerable to predation. This seems reasonable at first glance, since thermoregulation in heliothermic lizards (most lacertids) involves basking sessions on relatively exposed sites and shuttling between sun and shade, two activities that may render the animals more conspicuous to predators. However, although endorsed by many authors (e.g., Pianka and Pianka, 1970; Huey and Slatkin, 1976; Shine, 1980), this assertion has, to my knowledge, never been tested explicitly. Moreover, even if longer digesting periods make herbivorous lizards more vulnerable after a meal, insectivorous lizards may actually run higher risks while foraging. Hunting and subduing arthropod prey is probably a more conspicuous way of foraging than is eating plants. Accordingly, Pianka (1973) has speculated that herbivory may be ecologically advantageous in that it permits a smaller foraging range and better predator avoidance. A thorough study of both costs and benefits (in terms of predation risk) of herbivory is needed to solve this matter. Secondly, predation pressure should be low on islands compared to mainlands. Truly, the numbers and densities of predatory species are often reduced on islands (Stamps and Buechner, 1985; Van Damme et al., 1997), but whether this actually translates in lower predation risk is a continuing debate (Wright, 1981; Wright et al., 1984; Adolph and Roughgarden, 1983; Waide and Reagan, 1983; McLaughlin and Roughgarden, 1989). Even a small colony of a single predator species may exert high predation pressure on an island population of lizards. For instance, lack of alternative resources could induce an island predator to specialize on lizards. In conclusion, my results support the assumption of a link between insularity and a tendency toward herbivory, but much remains to be learned about the mechanisms underlying this link.

Herbivory and Body Size—Even though the initial assertion that herbivorous lizards tend to be over 300 g (Pough, 1973) has later been lowered by the discovery of herbivory in many lizard species well below that weight, it remains that herbivory in lizards is associated with large body size (Schluter, 1984; King, 1996). My results show that this also applies to lacertid lizards. The reasons for the correlation between body size and herbivory remain unclear. Earlier ideas, as would body size constrain the ability to masticate or digest plant food (Szarski, 1962; Sokol, 1967) have been rejected (Johnson and Lillywhite, 1979; King, 1996); there seems to be

no physiological or structural reason for a herbivorous lizard to be large (King, 1996). However, there may be ecological reasons. Mautz and Nagy (1987) argued that in a situation with large seasonal variation in food availability, small individuals, because of their relatively high energy requirements to body mass, would be outcompeted by larger individuals. Such a situation would also select for herbivory. Another possibility is that a herbivore lifestyle facilitates the evolution of large body sizes. For instance, capturing sufficient amounts of arthropods may require a degree of agility that cannot be attained by large lizards. In this scenario, large body size would be selected for by other forces (competition, predation) and herbivory would merely unlock the evolutionary pathway. Some of my results hint in the latter direction: in lacertid lizards, large lizards do not seem more likely to evolve herbivory than do small lizards. However, lacertids that evolved herbivory, eventually (though not immediately) seem to grow larger.

Body Size and Insularity—Dramatic examples of dwarfism and gigantism on islands have prompted much research on the evolution of body size in insular populations. Until now, theoretical models based on interspecific competition (e.g., Soulé, 1966; Schoener, 1969b, 1974; Lister, 1976), intraspecific competition (e.g., Schoener, 1969b; Ghiselin, 1974; Stamps and Buechner, 1985), timing of maturation (e.g., Dunham et al., 1978), predator-prey interactions (e.g., Case, 1978; Childs, 1986; King, 1991) or energetics (e.g., Foster, 1964; Millar and Hickling, 1996) have offered explanations for the observed trends in body size, but the major outcome seems to be that in unpredictable environments such as islands, the direction of selection on body size is extremely difficult to foresee. Each environment and each island may have an optimal body size that reflects the trade-off in all selective pressures mentioned above (Speakman, 1992). This finding is mirrored in the absence of a clear body size trend in insular lacertids. The lack of such a trend was suspected from contrary reports on size differences between island and mainland populations of lacertids (decrease in body size on islands: Clark 1967; increase: Castilla and Bauwens, 1991) and was confirmed by my analyses. Lacertids differ in this aspect from other lizard groups such as Scincidae, Gekkonidae, and Agamidae (Mertens, 1934, *in* Case, 1978), Anoles in the Lesser Antilles (Schoener, 1969a), and macroteid species in Central and South America (Case, 1978), that all show a general trend towards larger body size in islands. The adaptive forces that drive body size evolution in insular lacertid lizards (if any) remain to be identified.

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APPENDIX

Studies on diets of lacertid lizards on islands and continent. Lizard populations are labelled 'herbivore' if a substantial amount of stomachs or faeces examined contained plant parts; and 'insectivore' if plants were never found or judged to be taken 'by accident' while swallowing animal prey. The numbers preceding the species name correspond to the numbers in Fig. 1

- 1: *Mesalina guttulata* (Northern Africa, mainland, insectivore), Bons, 1957 in Schleich et al., 1996; 2: *M. guttulata* (SE-Morocco, mainland, insectivore), Pérez-Mellado, 1992; 3: *M. olivieri* (Kerkennah Islands, Tunisia, island, insectivore), Nouira and Mou, 1982; Nouira, 1983; 4: *M. olivieri* (SE-Morocco, mainland, insectivore), Pérez-Mellado, 1992; 5: *O. elegans* (Lesbos, Greece, island, insectivore), Perez-Mellado et al., 1993; 6: *Acanthodactylus schmidti* (eastern United Arab Emirates, mainland, insectivore), Arnold, 1984; 7: *A. boskianus* (Northern Africa, mainland, herbivore), Schleich et al., 1996; 8: *A. boskianus* (SE-Morocco, mainland, insectivore), Pérez-Mellado, 1992; 9: *A. pardalis* (Kerkennah Islands, Tunisia, island, insectivore), Nouira, 1983; 10: *A. scutellatus* (SE-Morocco, mainland, insectivore), Pérez-Mellado, 1992; 11: *A. longipes* (SE-Morocco, mainland, insectivore), Pérez-Mellado, 1992; 12: *A. erythrurus* (Ebro delta, Spain, mainland, insectivore), Carretero and Llorente, 1993; 13: *A. erythrurus* (S-Spain, mainland, herbivore), Valverde 1967 in Schleich et al., 1996, Busack and Jaksic, 1982; 14: *A. erythrurus* (Salamanca, Spain, mainland, herbivore), Pollo and Perez-Mellado, 1988; 15: *A. erythrurus* (Central Spain, mainland, insectivore), Gil et al., 1993; 16: *A. erythrurus* (Sistema Central, Spain, mainland, insectivore), Pérez-Mellado, 1982; 17: *Eremias arguta deserti* (Ukraine, mainland, insectivore), Kotenko, 1986; 18: *Pedioplanis lineocellata* (Kalahari, South Africa, mainland, insectivore), Nagy et al., 1984; 19: *Merolius cuneirostris* (Kuseb River floodplain, Namibia, mainland, insectivore), Robinson and Cunningham, 1978; 20: *Aporosaurus anchietae* (Namib desert, SW-Africa, mainland, herbivore), Robinson and Cunningham, 1978; Robinson, 1987; 21: *Heliobolus lugubris* (Kalahari, South Africa, mainland, insectivore), Nagy et al., 1984; 22: *Lacerta vivipara* (Somerset, UK, mainland, insectivore), Avery, 1962, 1971; 23: *L. vivipara* (Wiltshire, UK, mainland, insectivore), Avery, 1973; 24: *L. vivipara* (Turku, Finland, mainland, insectivore), Itämielä and Koskela, 1971; 25: *L. vivipara* (Puy-de-Dôme, France, mainland, insectivore), Pilorge, 1982; 26: *L. vivipara* (Rauma, Finland, mainland, insectivore), Koponen and Hietakangas, 1972; 27: *L. vivipara* (Nijmegen, The Netherlands, mainland, insectivore), Strijbosch, 1986; 28: *L. schreiberi* (Sistema Central, Spain, mainland, insectivore), Pérez-Mellado, 1982; Llorente

- and Pérez-Mellado, 1988; 29: *L. viridis* (Romania, mainland, insectivore), Vancea and Fuhn, 1959 in Nettmann and Rykena, 1984a; 30: *L. viridis* (Central France, mainland, herbivore), Rollinat, 1934 in Nettmann and Rykena, 1984a; 31: *L. trilineata* (Bulgaria, mainland, insectivore), Peters, 1963 in Nettmann and Rykena, 1984b; 32: *L. strigata* (Dagestan, mainland, insectivore), Ferchatowa, unpubl. in Darewskij, 1984; 33: *L. agilis* (Russia, mainland, insectivore), Jablokow, 1976 in Bischoff, 1984; 34: *L. agilis* (Nijmegen, The Netherlands, mainland, insectivore), Strijbosch, 1986; 35: *L. lepida* (Almeria, Spain, mainland, herbivore), Valverde, 1967 in Bischoff et al., 1984; 36: *L. lepida* (Huelva, Spain, mainland, herbivore), Mellado et al., 1975 in Bischoff et al., 1984; 37: *L. lepida* (Vaucluse, France, mainland, herbivore), Cheylan unpubl. in Bischoff et al., 1984; 38: *L. lepida* (Central Spain, mainland, herbivore), Castilla et al., 1991; 39: *L. lepida* (Sistema Central, Spain, mainland, insectivore), Pérez-Mellado, 1982; 40: *L. danfordi* (Icaria, Greece, island, insectivore), Valakos, 1986; 41: *L. perspicillata* (Oran, Algeria, mainland, insectivore), Doumergue, 1901 in Richter, 1986; 42: *L. dugesii* (Madeira, Portugal, island, herbivore), Sadek, 1981; 43: *L. andreanskyi* (Atlas, Morocco, mainland, herbivore), Busack, 1987 in Schleich et al., 1996; 44: *Podarcis sicula* (Venice, Italy, mainland, insectivore), Marcuzzi, 1959 in Henle and Klaver, 1986; 45: *P. sicula* (Dubrovnik, Yugoslavia, mainland, herbivore), Bol-kay, 1923, 1925 in Henle and Klaver, 1986; 46: *P. sicula* (Dalmatia, Yugoslavia, mainland, herbivore), Tomasi-ni, 1905 in Henle and Klaver, 1986; 47: *P. sicula* (Fragli-ioni, Italy, island, herbivore), Butz and Kuenzer, 1956 in Henle and Klaver, 1986; 48: *P. sicula* (Tuscan Archipelago, Italy, island, herbivore), Pérez-Mellado and Corti, 1993; 49: *P. sicula* (Menorca, Spain, island, herbivore), Pérez-Mellado and Corti, 1993; 50: *P. sicula* (Sicily, Italy, island, herbivore), Sorci, 1990; 51: *P. sicula salffi* (Vivaro di Nerano, Italy, island, herbivore), Oub-oter, 1981; 52: *P. hispanica* (Salamanca, Spain, main-land, insectivore), Perez-Mellado, 1983 in Salvador, 1986; 53: *P. hispanica* (Alicante, Spain, mainland, insectivore), Escarre and Vericad, 1981 in Salvador, 1986; 54: *P. hispanica* (Sierra Morena, mainland, insectivore), Mellado et al., 1975 in Salvador, 1986; 55: *P. hispanica* (Sistema Central, Spain, mainland, insectivore), Pérez-Mellado, 1982; 56: *P. hispanica* (Benidom Island, Spain, island, herbivore), Pérez-Mellado and Corti, 1993; 57: *P. hispanica atrata* (Columbretes Islands, Spain, island, herbivore), Castilla and Bauwens, 1991; 58: *P. bocagei* (Sistema Central, Spain, mainland, insectivore), Pérez-Mellado, 1982, 1983; 59: *P. muralis* (Maastricht, The Netherlands, mainland, insectivore), Strijbosch et al., 1980; 60: *P. muralis* (Juillac, France, mainland, insectivore), Mou and Barbault, 1986; 61: *P. muralis* (Chizé, France, mainland, insectivore), Mou, 1987; 62: *P. muralis* (Bulgaria, mainland, herbivore), Kabisch and Engelmann, 1969 in Gruschwitz and Böhme, 1986; 63: *P. muralis* (Tuscan Archipelago, Italy, island, herbivore), Pérez-Mellado and Corti, 1993; 64: *P. melisellensis* (Jugoslavia, mainland, insectivore), Radovanovic 1956, 1959 in Tiedemann and Henle, 1986; 65: *P. melisellensis* (Adriatic Island, Yugoslavia, island, herbivore), Radovanovic, 1956 in Tiedemann and Henle, 1986; 66: *P. erhardii* (Ios, Greece, island, insectivore), Quayle, 1983; 67: *P. erhardii naxensis* (Naxos, Greece, island, insectivore), Valakos, 1986; 68: *P. peloponnesiaca* (Greece, mainland, insectivore), Bringsoe, 1986; 69: *P. lilfordi* (Cabrera, Menorca, Spain, island, herbivore), Pérez-Mellado, 1989; 70: *P. lilfordi* (Balearic Islands, Spain, island, herbivore), Pérez-Mellado and Corti, 1993; 71: *P. pityusensis* (Balearic Islands, Spain, island, herbivore), Pérez-Mellado and Corti, 1993; 72: *P. taurica* (Ionian islands, Greece, island, herbivore), Chondropoulos et al., 1993; 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