Ecology, 83(7), 2002, pp. 1870–1885

LIZARD HOME RANGES REVISITED: EFFECTS OF SEX, BODY SIZE, DIET, HABITAT, AND PHYLOGENY

GAD PERRY[1,2] AND THEODORE GARLAND, JR.[1,3]

[1]*Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison, Wisconsin 53706 USA*

Abstract. The area traversed by an animal during food gathering, mating, and other routine activities is termed the home range (HR), and its size is believed to reflect behavioral and physiological requirements (e.g., access to mates and food). We evaluated both biological and methodological factors that may affect estimated HR sizes of lizards. We compiled a database of nearly 500 published sex × population data sets. These yielded usable data for 108 populations from 60 species, all with both sexes represented. Initial analyses indicated pervasive sex differences, so sexes were analyzed separately with both conventional and phylogenetically based statistical methods. First, we conducted conventional analyses of covariance, which treat each data point as statistically independent. Second, we repeated these analyses while comparing members of two major clades represented in our database, Iguania and Autarchoglossa. Third, we repeated the analyses after designating smaller clades, nested within major clades. Fourth, we performed a fully phylogenetic analysis via independent contrasts and a composite phylogeny assembled from published studies. All analyses showed highly significant effects of both biological (body size, diet, habitat type) and most methodological (calculation method and minimum number of sightings per individual, but not study duration) factors and covariates tested. The conventional analysis comparing Iguania and Autarchoglossa en toto indicated a significant difference, as has been suggested in the literature. The analysis with nested minor clades, however, revealed differences among these but not between the two major clades. The analysis with phylogenetically independent contrasts indicated no statistically significant differences either among minor clades or between major clades. We also used our database to compare the scaling of HR area to body mass, using recently published allometric equations for field metabolic rates of lizards. The similarity of allometric slopes suggests that, interspecifically, HR size scales directly with energetic requirements. Intraspecifically, however, we found that males in both Autarchoglossa and Iguania consistently had larger HRs than did females. This difference, presumably related to the need to maximize access to females, may impose a ''cost of reproduction'' on males.

Key words: allometry; Autarchoglossa; body size; diet; energetics; habitat; home range; Iguania; lizards; methodology; phylogeny; sex.

INTRODUCTION

Home range (hereafter, HR) was defined by Burt (1943) as the area traversed during the natural activities of food gathering, mating, and caring for young, and this definition is still widely used. All of an animal's routine requirements must be found within the HR, including shelter and suitable thermal conditions (e.g., Christian et al. 1984, Huey et al. 1989), but most studies emphasize two main types of resources: food (e.g., Trivers 1976) and mates (e.g., Stamps 1983). In general, HR size is considered an important indicator of the behavioral and resource requirements of an animal, in relation to their availability in the environment. Hence, ecologists have long been interested in understanding factors that predict HR size.

Starting in the 1960s (McNab 1963, Armstrong 1965, Schoener 1968, Turner et al. 1969), studies of HR in relation to body size indicated that larger bodied species tend to possess larger HRs. The most commonly invoked explanation is that larger animals require more food and must therefore have larger food-gathering areas (Mace and Harvey 1983, Mace et al. 1983, Reiss 1988, Nunn and Barton 2000, Kelt and Van Vuren 2001, Mysterud et al. 2001). In addition, HR size may depend on diet. With each move up the trophic ladder, ~90% of available energy is lost. Therefore, a carnivore would need a larger HR to support itself than would an herbivore. The available data generally support this prediction (McNab 1963, Schoener 1968, Mace and Harvey 1983, Mace et al. 1983, Nunn and Barton 2000, Kelt and Van Vuren 2001; but see Swihart et al. 1988, Garland et al. 1993). Within trophic categories, specific food type or foraging style may also affect HR size. For example, frugivorous primates have relatively larger HRs than do foliage eaters (Milton and May 1976), and browsing ungulates have relatively

Manuscript received 2 January 2001; revised 7 July 2001; accepted 12 July 2001; final version received 6 November 2001.

[2] E-mail: Gperry@facstaff.wisc.edu

[3] Present address: Department of Biology, University of California, Riverside, California 92521 USA.

larger HRs than do grazers (Mysterud et al. 2001); both of these studies attributed the pattern to the relative commonness of different food types. Other factors shown to affect HR size include season, weather, age, sex, habitat quality, and activity pattern (Stickel 1968, Mysterud et al. 2001), although the effects of some of these factors might be mediated by dietary needs and food availability.

Lizards have been used often as model systems in ecology (Huey et al. 1983, Vitt and Pianka 1994). They show extensive inter- and intraspecific variation in patterns of space usage (for reviews, see Stamps 1983, Christian and Waldschmidt 1984, Martins 1994). They also rarely engage in social behaviors such as parental activities (Somma 1990) and do not normally live in well-defined social groups. This eliminates the complications that emerge in social animals that share a HR (for a recent phylogenetic analysis in primates, see Nunn and Barton 2000). Lizards may thus be especially appropriate models for studies of factors that affect HR size.

Two previous reviews (Turner et al. 1969, Christian and Waldschmidt 1984) examined the relationship between HR and body size in lizards (squamates exclusive of snakes). Unfortunately, statistical methods that explicitly incorporate phylogenetic information were not then available. Because they descend from common ancestors, species are related in a hierarchical fashion and may not represent statistically independent data points, a phenomenon termed phylogenetic pseudoreplication by Perry and Pianka (1997; see also Garland and Adolph 1994). Consequently, conventional statistical analyses, which assume independence and identical distributions, may lead to incorrect conclusions (e.g., Felsenstein 1985, Harvey and Pagel 1981, Martins 1996, Garland et al. 1999, Garland and Ives 2000, Nunn and Barton 2000). This is especially true when ecology and phylogeny are highly confounded (e.g., Ackerly 1999, Vanhooydonck and Van Damme 1999, Purvis and Webster 1999, Brashares et al. 2000, Cruz-Neto et al. 2001). For example, in a recent analysis of mammalian home ranges (Garland et al. 1993), all carnivores were members of Carnivora and all herbivores were members of Ungulata. Although conventional statistical analysis showed that carnivores had larger mass-adjusted home ranges, reanalysis with phylogenetically based statistical methods showed no significant difference (Garland et al. 1993). This makes suspect the conclusions of studies that ignore phylogeny (e.g., Kelt and Van Vuren 2001).

The availability of many additional data on lizard HR, compared to past reviews, as well as modern phylogenetically based statistical methods, provided the impetus for the present study. We hypothesized that HR area would be related to diet after the effects of body size are controlled. A second goal was to determine whether HR size varied among the major lizard lineages. Although early work (Turner et al. 1969) identified no such differences, lizard clades more recently have been shown to differ in foraging behavior (Cooper 1995, Perry 1999) and life history relationships (Clobert et al. 1998). Moreover, Stamps (1977, 1983) has shown differences between members of the two major lizard clades, Iguania and Autarchoglossa, in social behavior, territorial behavior, and use of the HR. These differences could, in turn, result in differences in HR size, or possibly differences in the scaling relationship of HR size in relation to body size (Stamps 1977, 1983, Clobert et al. 1998). Third, we wished to identify clades and questions that require additional data collection before a definitive analysis is possible. Fourth, our compilation of HR information sets the stage for future studies on the physiological correlates of interspecific variation in field movement patterns of lizards, such as locomotor performance (e.g., Losos 1990, Garland 1999, Perry 1999, Irschick 2000). Finally, we ask whether HR size and field metabolic rate show similar scaling relationships with body size.

METHODS

We followed previous authors in excluding snakes from the analysis for three main reasons. First, the phylogenetic position of snakes within lizards remains unclear. Second, phylogenetic relationships within snakes are often unresolved. Third, the body plan and locomotor modality of snakes differ radically from those of all taxa included in the study; this may, in principle, cause qualitative differences in the relationship between HR and various biological factors. Nevertheless, we recognize the clear desirability of phylogenetic analyses that are not paraphyletic in scope (see Bininda-Emonds and Gittleman 2000).

Acquisition of home range and methodological data

Raw data for the analyses that follow are provided in Appendix A for the 489 entries, each containing information for one sex or age group, studied in one population at one time. These data were drawn from published and unpublished sources (Appendix B). Four reviews (Stamps 1977, 1983, Christian and Waldschmidt 1984, Turner et al. 1969) formed the starting point for a comprehensive literature search. Additionally, we contacted colleagues around the world for assistance in locating obscure and unpublished sources. All data from studies reporting HR as previously defined were included in the analyses (with the exceptions listed in *Data distribution and quality*). Studies that used conceptually different definitions (e.g., Burrage 1974) were omitted. Similarly, the HR values calculated by Iverson (1979: Table 18) were omitted because the authors providing the original data did not themselves measure HR. Studies not possessing sufficient methodological information were also omitted.

For each of the sources listed in Appendix B, we recorded HR size, as well as biological and methodological details that might be relevant. Methodological details included computation method (for descriptions, see Jennrich and Turner 1969, Waldschmidt 1979, Schoener 1981, Powell 2000) and the number of locations (sightings) used for calculating HR (Jennrich and Turner 1969, Waldschmidt 1979, Ford and Myers 1981, Schoener 1981, Rose 1982). We used the minimum number of sightings in our analyses (range = 3–147). Some studies only reported the range or mean value, and these were omitted from the final analyses. We also noted study duration; however, data on duration were only available for 87 of the 108 data sets. In initial analyses that included this variable, it was never a statistically significant predictor of HR ($P > 0.1$ in all cases). Therefore, we only report the results for analyses without this variable. Because larger sample sizes should result in more accurate estimates of HR, we used the number of individuals as a weighing factor in all of our analyses.

Sources of other ecological data

For each data point, we noted current phylogenetic position as well as a variety of ecologically relevant or potentially confounding factors, including diet, body size, sex, and age (adult vs. juvenile). Body size was represented by data on snout–vent length (SVL, also known as rostrum–anus length, or ra; Werner 1971) and body mass. Because body size is often different for males and females (e.g., Fitch 1981), and because allometry may be different for different taxa (e.g., Abouheif and Fairbairn 1997), we analyzed separate values for the sexes. Lizard diet is often categorized as herbivorous, insectivorous, carnivorous, or omnivorous. However, the diet of most species is not fully within such categories (e.g., Lazell and Perry 1997, Perry and Lazell 1997; for a review, see Peters 1977). To account for this, we followed Peters (1977) and Harestad and Bunnell (1979) in employing a 90% rule. For example, animals categorized as herbivorous had ≥90% vegetable material in their diets. Diet can vary among lizard populations (Perry and Brandeis 1992), as can body size and other traits. Whenever possible, therefore, biological data were taken from the primary authors and represent the specific population included. (In several cases, authors kindly made unpublished data available to us.) When this was not possible, we preferentially used data recorded at the same site as the original study. In the absence of such data, we used more general summaries such as field guides (e.g., Stebbins 1985) or topical reviews (e.g., Fitch 1981, Pianka 1986, Dunham et al. 1988), and finally more general summaries (e.g., Obst et al. 1988, Rogner 1997*a*, *b*). Given the broad dietary categories that we used, such sources are likely to provide sufficient information. In some cases, we estimated missing size information using SVL–mass conversion formulas based on multispecies allometric equations. We used the equations of Stamps et al. (1994) for members of the genus *Anolis*, of Perry (1989) for lacertid lizards, and of Pough (1980) for all other species (for additional sources of such data, see Blob 2000).

Data distribution and quality

Sampling effort has clearly been far from uniform for lizards. For example, we found 104 data points (representing 20 species) for *Anolis* (which includes about 400 species; Pough et al. 2001), 57 data points (representing 10 species) for *Sceloporus* (which includes 80 species), and 24 data points (representing 12 species) for *Varanus* (about 40 species). In contrast, there were 28 entries for all skinks (out of ~1100 species; Pough et al. 2001) combined (of which nine were from a single species), six for all geckos (of ~960 species), and none for any anguid species (of ~100 species). The bias was not only taxonomic, but also geographic. Within *Anolis*, for example, most of the data were for Caribbean species. Finally, phylogeny and ecology were confounded because, for example, all anoles for which HR data were available are insectivorous.

The studies that we located varied greatly in the methods used and the degree of methodological information provided, and some had to be omitted. Many of the located studies provided only partial methodological information. Of the original entries (Appendix A), ~10% were omitted because the methods used to calculate HR were not known with certainty. Missing cells and highly unbalanced designs can be problematical in ANOVAs, reducing the statistical power of the analysis (Sokal and Rohlf 1995). Because some of the categories chosen beforehand introduced such problems (Tables 1 and 2), we omitted from the analyses that follow those data from the ''juveniles'' and ''all'' age categories, and from the ''leaf litter'' and ''near stream'' habitat categories. Populations for which data were only available for one sex ($N = 9$), the least informative data set from two populations that were each represented by three data sets, and three studies lacking information on the number of individuals studied, were also removed. The resulting database, encompassing 108 populations (as indicated in Appendix A) from each sex and representing 60 species, was used in both the traditional and phylogenetic analyses that follow, with the exception of initial analyses of study duration. Despite this pruning, the current database is much larger than any previously analyzed. For example, the most recent review (Christian and Waldschmidt 1984) contained 52 data lines representing 16 species.

Following conventional treatment (e.g., Williamson and Gaston 1999), both SVL and HR data were $\log_{10}$-transformed at the outset to correct the heavily right-skewed distributions and to linearize their relationship. Other variables were visually inspected for the presence of outliers and skewness, and were transformed as needed, following Sokal and Rohlf (1995). The number of individuals in each study served as a weighting factor.

TABLE 1. Division of lizard home range data based on habitat type and sex or age group.

Habitat type	Juvenile	Male	Female	All†	Adult‡	Total
Near water	1	1	1	1	···	4
Leaf litter	···	3	3	···	···	6
Saxicolous	9	21	16	6	···	52
Arboreal	22	50	46	3	···	121
Ground (dense)	14	48	44	19	3	128
Ground (open)	13	73	70	23	1	180
Total	59	196	180	52	4	491

Note: Each value represents the number of entries in Appendix A for a single category × location × period.

† Studies that lumped all individuals together.

‡ Studies that lumped both sexes of adults.

Conventional statistical analyses

Fully nonphylogenetic analyses, assume a ''star'' phylogeny and do not incorporate information on relatedness (Felsenstein 1985, Garland and Adolph 1994, Garland and Carter 1994, Garland et al. 1999). We therefore began our analysis by treating each population as an independent data point, in effect stipulating a perfect ''star'' phylogeny with no hierarchical relationships. This is an extreme approach, however, and a long tradition exists for separating data, at least in relation to taxonomy, although the taxonomic breakdown may not reflect cladistic relationships (e.g., passerine vs. nonpasserine birds, reptiles vs. mammals).

Differences between males and females are often biologically important, and this is also true for HR (e.g., Stamps 1983). We therefore first tested for sex effects using Wilcoxon's tests for paired comparisons. This approach avoids confounding methodological issues because each compared pair is drawn from a single study. Moreover, because methods are internally consistent within each study, this approach allows a larger data set to be analyzed. Tests were conducted on the complete data set, as well as on smaller clades.

We incorporated phylogenetic information into our analyses at two levels. First, the three main lizard clades (Iguania, Gekkota, and Autarchoglossa) are often biologically very different, e.g., in social structure (Stamps 1977, 1983); foraging behavior (Cooper 1995, Perry 1999); and life-history allometry (Clobert et al. 1998). Sufficient data for analysis exist for two of these, Iguania and Autarchoglossa (Fig. 1), and we included this distinction in our second analysis. Our third analysis also included information on 13 clades contained within Iguania or Autarchoglossa, using a nested ANOVA design (reviewed in Harvey and Pagel 1991) to account for the relatedness of smaller clades within the two major clades. Populations of the same species were still treated as independent entities. Because of unequal cell size, degrees of freedom and mean squares were estimated using the Satterthwaite approximation where needed (Sokal and Rohlf 1995). Choice of statistical methods followed Sokal and Rohlf (1995) and SPSS (1999*b*). All analyses were conducted using SPSS 10.0 (SPSS 1999*a*).

Phylogeny construction

No comprehensive estimate of phylogeny for all lizard species exists (cf. Bininda-Emonds et al. 1999). We therefore created a composite phylogeny for all lizard species for which HR data existed (Fig. 1), using the most recent or comprehensive available phylogenies. Thus, large-scale tree topology follows Estes et al. (1988), rather than the single-gene-based analysis of Harris et al. (1999*a*). For major radiations within Iguania, we followed convention in using the family-rich nomenclature of Frost and Etheridge (1989). The taxonomic view of Iguanidae advocated by Macey et al. (1997; see also Schulte et al. 1998) might be more appropriate than the one used here. However, the distinction makes no difference within the context of the current analysis, as current views regarding the relationships among taxa are not affected. Relationships of phrynosomatid lizards were drawn from Reeder and Wiens (1996), Wiens and Reeder (1997), and Schulte et al. (1998), rather than from the DNA/DNA hybridization work of Changchien (1996). *Anolis* phylogeny follows Jackman et al. (1999), that of crotaphytids follows McGuire (1996), and that of the Iguanidae follows Rassmann (1997) and Wiens and Hollingsworth (2000). Agamid phylogeny follows the outlines provided by Joger (1991) and Honda et al. (2000*a*), and the much more detailed phylogeny of Macey et al. (2000). Tropidurid relationships follow Frost (1992) and Harvey and Gutberlet (2000), and relationships of geckos are based on Kluge (1987). The hypothesis used for Lacertidae was drawn from Fu (1998, 2000), Vanhooydonck and Van Damme (1999), and especially the extensive work of Arnold (Arnold 1973, 1989*a*, *b*, 1997, Harris and Arnold 1999, Harris et al. 1999*b*). The phylogeny of varanids follows Fuller et al. (1998), that of skinks follows Greer (1970) and Honda (1999*a*, *b*, 2000*b*), and teiid phylogeny was based on Presch (1974).

TABLE 2. Division of lizard home range data based on diet and sex or age group.

Diet	Juvenile	Male	Female	All†	Total
Herbivore	4	25	21	3	53
Insectivore	51	149	139	35	374
Carnivore	1	11	10	7	29
Omnivore	2	7	6	6	21
Total	58	192	176	51	477

Notes: Each value represents the number of single category × location × period entries in Appendix A. As compared with Table 1, data for two habitat categories, ''leaf litter'' and ''near water,'' each containing a small number of entries, were omitted before tabulation. The ''Adult'' category was also omitted.

† Studies that lumped all individuals together.

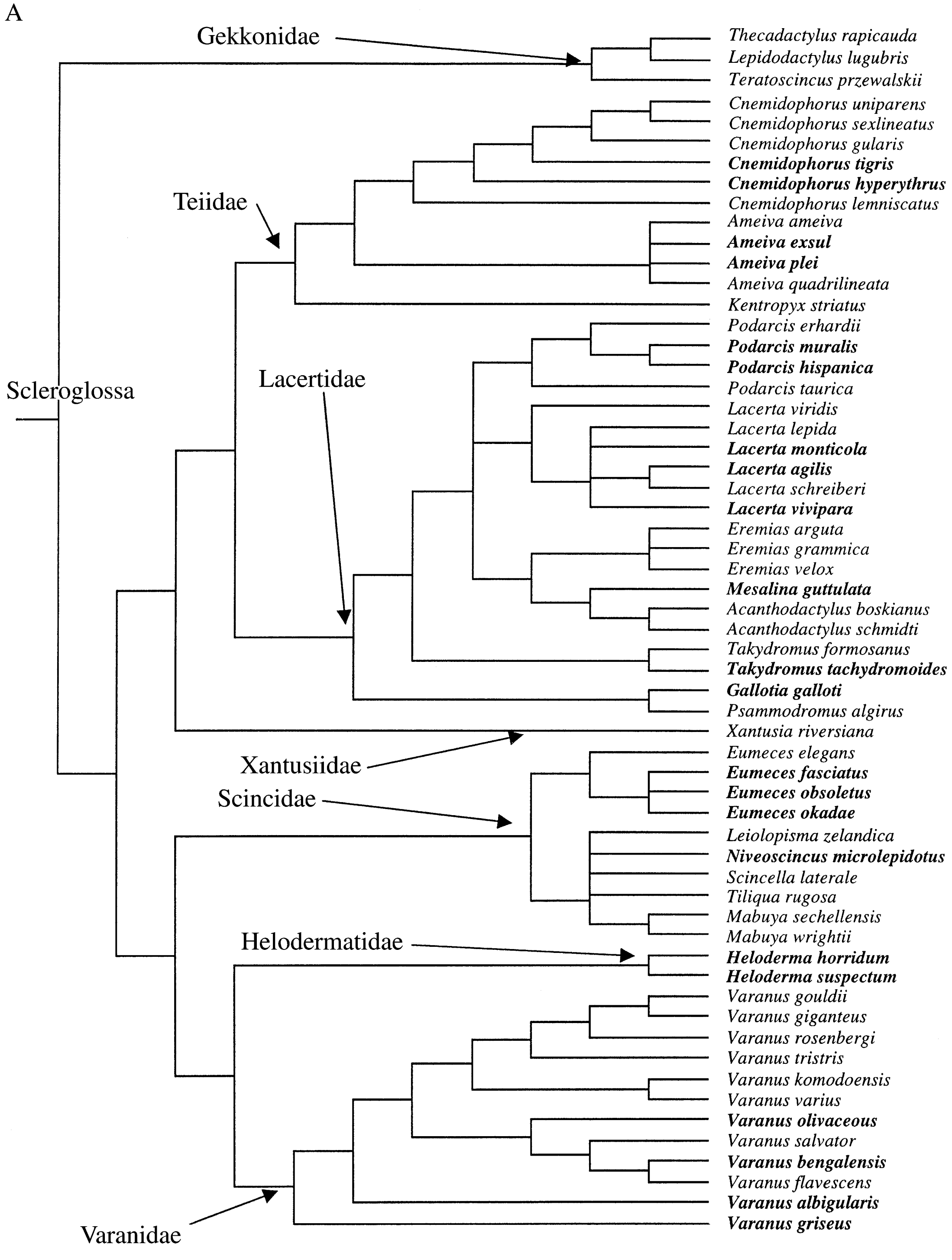

FIG. 1. Composite phylogeny for the lizards species in the full database, as listed in Appendix A (where several species are represented by data for multiple populations). Because of missing data for some variables, not all species or populations were included in the final analysis of 108 taxa. Taxa included in the final analysis are given in boldface, and their phylogeny is presented in Appendix D. (A) Scleroglossa (=Gekkota and Autarchoglossa). (B) (facing page) Iguania. Arrows indicate minor clades used for statistical analyses. Branch lengths are arbitrary.

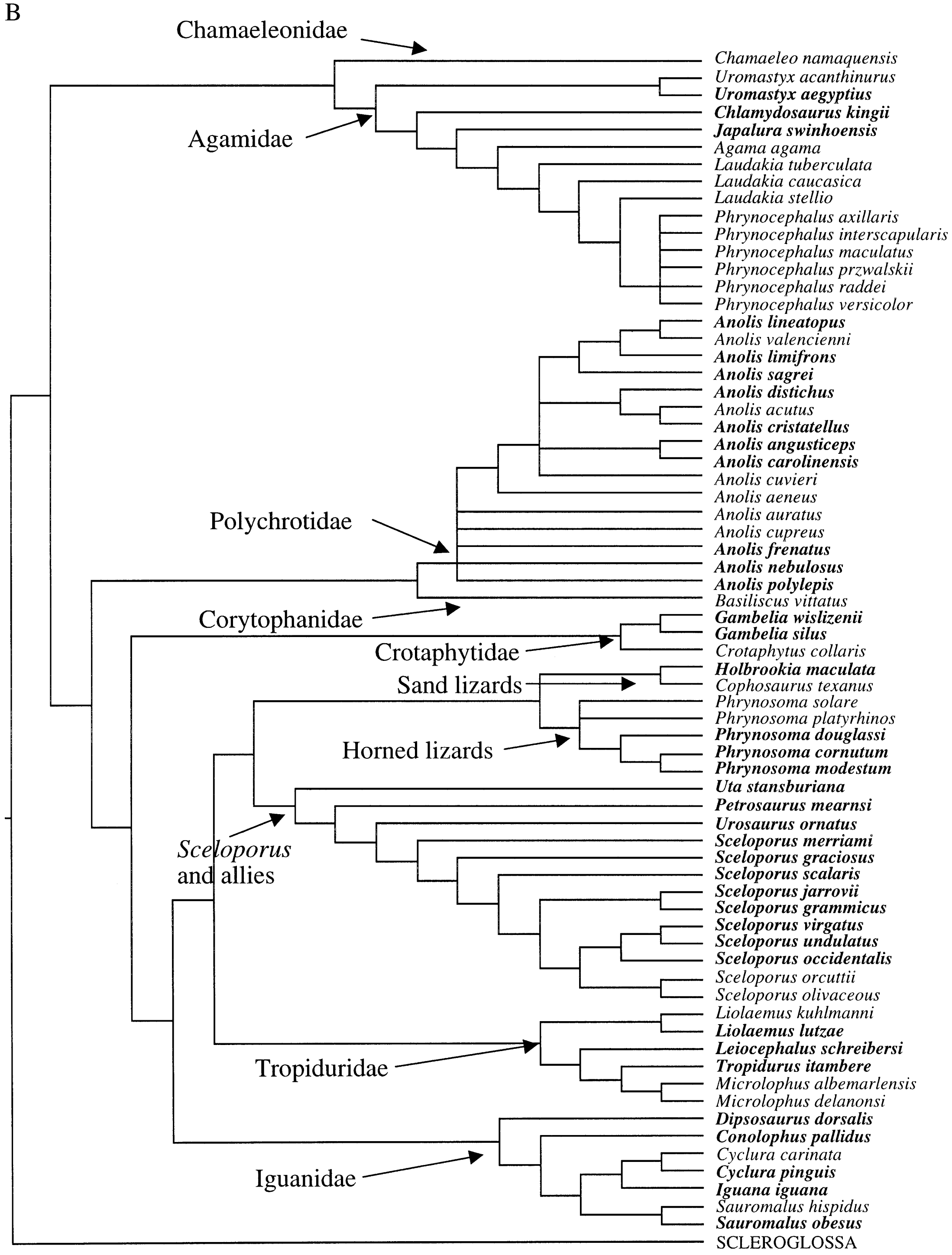

FIG. 1. Continued.

Phylogenetically based statistical analyses

To account fully for hypothesized evolutionary relationships (Fig. 1), we repeated the analyses using phylogenetically independent contrasts (Felsenstein 1985), calculated using the program PDTREE (Garland et al. 1999, Garland and Ives 2000). Species with multiple data were represented by polytomies, with no hierarchical arrangement of populations, and the phylogeny used in these analyses is presented in Appendix D.

Because estimates of divergence time or genetic distance for all of the taxa included here are not available, we used Grafen's (1989) arbitrary branch lengths. The diagnostic recommended by Garland et al. (1992) and Garland and Diaz-Uriarte (1999) indicated that these branch lengths provided adequate standardization of the contrasts for log SVL (the correlation between the absolute value of standardized contrasts and their standard deviation is -0.080 for males and -0.110 for females). These diagnostic correlations were somewhat more negative for log HR. However, HR in these diagnostics is uncorrected for the various biological and nonbiological variables that may affect it (see *Results*), making this finding hard to interpret.

Three of the variables (number of sightings, study duration, and calculation method) are nonbiological and should be independent of phylogeny. Therefore, prior to computing contrasts for these variables, we collapsed the phylogeny to a star with equal branch lengths (Wolf et al. 1998). The same procedure was followed for the square root of the number of individuals per study, and then the reconstructed nodal value was used as an estimate of the average square root of sample size for each contrast (Bonine and Garland 1999). To analyze the categorical variables (diet, habitat, and calculation method), we first computed $N - 1$ dummy variables, where N is the number of categories within a given variable, and then computed standardized contrasts of these (Garland et al. 1992, 1993). For each dummy variable, one category (e.g., herbivore) was coded as 1, and 0 was used for all other tips in the phylogeny. To test whether clades differed in HR size after adjusting for all other variables, we used additional dummy variables. For the major clades ($N = 2$), this required a single dummy variable. For minor clades ($N = 13$), 12 dummy variables were computed.

All standardized contrasts were then entered into a multiple regression model (computed through the origin) treating number of sightings, calculation method, SVL, diet, habitat, major clade, or minor clade as independent variables predicting HR. Because minor clades coded as previously described are not nested within the major-clade dummy variable, we did not test dummy variables for both major and minor clade simultaneously in a single analysis. Rather, we performed two otherwise identical analyses, one for major clade (single dummy variable) and the other for the minor clades (12 dummy variables). Note that, as discussed in Clobert et al. (1998), the comparison of major clades in this fashion is mathematically identical to the method shown in Garland et al. (1993: Fig. 5). For simplicity, we followed Garland and Diaz-Uriarte (1999) in not subtracting degrees of freedom for soft polytomies.

One goal of this study was to test the hypothesis that HR size is primarily a function of energetic requirements. Nagy et al. (1999) recently compiled information on the field metabolic rates, FMR (as determined by doubly labeled water) of a variety of lizard species and calculated both conventional and phylogenetic allometric equations for the relationship of FMR with body size. We therefore repeated our analysis, omitting those covariates not accounted for in their study: diet, habitat, and major or minor clade. To make our allometry fully comparable with that of Nagy et al. (1999), we used body mass as a covariate for this analysis. The number of taxa shared by our database and that of Nagy et al. (1999) was small. We therefore expanded our analysis to include all 108 taxa from Appendix A included in the previous analyses.

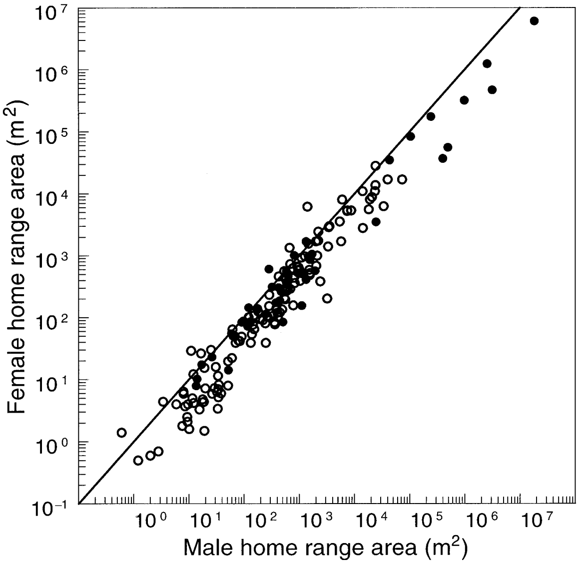

FIG. 2. The relationship between female and male home range area in Iguania (open circles) and Autarchoglossa (solid circles). Note the log scales. Each data point represents a single study in which both sexes were simultaneously observed using the same methods ($N = 173$ pairs).

RESULTS

Conventional analyses

For the sample of 222 lizard data sets, average SVL ranged from ~18 mm to >100 cm, and HR size varied between 0.5 m^2 and 18 300 000 m^2. Males had significantly larger HRs when all data were combined (Fig. 2; Wilcoxon's test of paired comparisons; $N = 173$ pairs, $Z = 9.29$, $P < 0.001$); when only Iguania ($N = 129$ pairs, $Z = 7.96$, $P < 0.001$) or Autarchoglossa ($N = 44$ pairs, $Z = 4.69$, $P < 0.001$) were analyzed; and in all five clades with $N > 8$ pairs (Agamidae, Iguanidae, Lacertidae, the *Sceloporus* group, and *Anolis*; $P < 0.015$ in all cases). However, males were also larger, overall, than females, as measured by SVL ($N = 160$ pairs, $Z = 6.81$, $P < 0.001$). To account for that, we repeated the test with HR corrected for body size. Both male and female HR size scale to SVL with an exponent of ~1.8; therefore, we divided HR by SVL raised to the 1.8 power. Mean size-corrected male HR was considerably larger than that of females (0.72 m^2/mm$^{1.8}$

TABLE 3. Results of first conventional ANCOVA, with log home range area as the dependent variable (weighted by the square root of the number of individuals included in each study).

		Males					Females				
Source	df	F	Slope	95% CI	Partial r^2	P	F	Slope	95% CI	Partial r^2	P
Diet	3	10.31			0.25	<0.001	12.90			0.30	<0.001
Habitat	3	22.38			0.43	<0.001	17.93			0.37	<0.001
Method	7	4.91			0.28	<0.001	4.98			0.28	<0.001
Log SVL	1	44.35	2.57	(1.8, 3.3)	0.33	<0.001	41.29	2.52	(1.7, 3.3)	0.31	<0.001
Log sightings	1	14.77	−0.39	(−0.6, −0.2)	0.14	<0.001	9.26	−0.69	(−1.1, −0.2)	0.09	0.003
(Zlogsight)^2†	1	8.12	0.16	(0.0, 0.3)	0.08	0.005	4.66	0.12	(0.0, 0.2)	0.05	0.034
Error	91										

Note: For both males and females, 108 data points were used.

† The square of the Z-transformed log of the number of sightings.

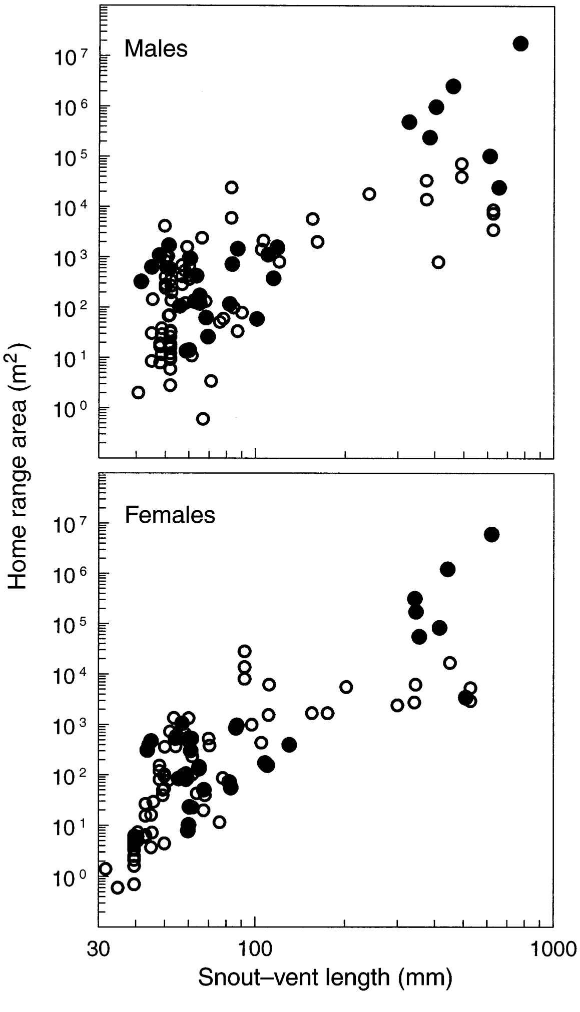

FIG. 3. Home range area as a function of snout–vent length (SVL) in lizards, separated by major clade, in Iguania (open circles) and Autarchoglossa (solid circles). Note the log scales. Pooling data for both clades ($N = 108$), conventional least-squares regression slopes are 3.01 ± 0.256 (all data expressed as mean ± 1 SE) for males and 3.32 ± 0.232 for females. Slopes with phylogenetically independent contrasts (Grafen's [1989] arbitrary branch lengths) are 2.96 ± 0.481 for males and 2.97 ± 0.459 for females.

and 0.63 m^2/mm$^{1.8}$, respectively), and the difference was highly significant ($N = 160$ pairs, $Z = 9.10$, $P < 0.001$). As with nonstandardized analyses, the same conclusion was reached when only Iguania ($N = 129$ pairs, $Z = 7.84$, $P < 0.001$) or Autarchoglossa ($N = 44$ pairs, $Z = 4.60$, $P < 0.001$) were analyzed, and in all five clades with $N > 8$ pairs ($P < 0.015$ in all cases). Males and females were therefore analyzed separately in the analyses that follow.

Conventional ANCOVAs indicated significant effects of all biological and methodological factors and covariates tested, in both sexes (Table 3). There were also significant differences between the two major clades in size-adjusted HR area (Fig. 3). Addition of major clade yielded similar results for all of these factors and covariates, and indicated that the HRs of Iguania were larger, on average, than those of Autarchoglossa (Table 4), once all other factors are accounted for. However, inclusion of subclades nested within the two major clades invalidated this finding, showing significant differences among subclades, but not between the two major clades (Table 5). This analysis also indicated that omnivores had smaller HRs than species with other diets, and nearly all analyses indicated that carnivores had the largest HRs (e.g., see Fig. 4). Additionally, all analyses indicated that terrestrial species had larger HRs than did arboreal and saxicolous species. Finally, the most complete conventional model (Table 5) indicated that the convex polygon and ellipse methods produced the smallest estimates of HR area. The correction recommended by Jennrich and Turner (1969) and the radii recapture method of Schoener (1981) produced the highest HR estimates.

To test for differences in the scaling of log HR with log SVL between the major clades, we repeated the analyses presented in Table 4, adding an interaction term. The interaction between clade and log SVL was not statistically significant for either females ($F_{1,89} = 0.17$, $P = 0.68$) or males ($F_{1,89} = 3.42$, $P = 0.07$).

Phylogenetically independent contrasts

The use of a fully explicit phylogenetic framework for analysis (Table 6) did not greatly change the con-

TABLE 4. Conventional ANCOVA results, with log home range area as the dependent variable (weighted by the square root of the number of individuals included in each study) and major clade (Iguania vs. Autarchoglossa) included in the analysis.

		Males					Females				
Source	df	*F*	Slope	95% CI	Partial r^2	*P*	*F*	Slope	95% CI	Partial r^2	*P*
Diet	3	13.07			0.30	<0.001	15.65			0.34	<0.001
Habitat	3	26.28			0.47	<0.001	21.10			0.41	<0.001
Major clade	1	7.18			0.07	0.009	6.38			0.07	0.013
Method	7	5.60			0.30	<0.001	5.82			0.31	<0.001
Log SVL	1	52.08	2.71	(2.0, 3.5)	0.37	<0.001	47.53	2.65	(1.9, 3.4)	0.35	<0.001
Log sightings	1	16.37	−0.98	(−1.5, −0.5)	0.15	<0.001	11.15	−0.74	(−1.2, −0.3)	0.11	0.001
(Zlogsight)^2†	1	10.23	0.17	(0.0, 0.3)	0.10	0.002	6.42	0.14	(0.0, 0.2)	0.07	0.013
Error	90										

† The square of the *Z*-transformed log of the number of sightings.

clusions reached when we used major and minor clade information in a more traditional analysis. Overall, omnivores had smaller HRs than did species with other diets, and carnivores had the largest HRs, although this difference was not significant in males. Terrestrial species had larger HRs than arboreal and saxicolous species, but there was no significant difference between ground-dwelling species from dense vs. open habitats. HRs estimated using the Jennrich and Turner (1969) correction and the radii recapture method (Schoener 1981) were the largest. Finally, the minimum number of sightings was significantly negatively related to estimated HR size in this interspecific comparison. The main departure from conventional analyses was the absence of a significant overall clade effect in either sex. This was true at the level of the two major clades ($P > 0.75$ in both sexes; results are not shown) and minor clades (Table 6). Thus, this analysis did not identify consistent differences between the two major clades, nor among the subclades nested within them.

For comparison with the data of Nagy et al. (1999) (see *Discussion*), we repeated the analysis with a smaller number of covariates (log SVL, number of sightings, and calculation method, weighed by the number of individuals observed). All 108 taxa included in previous analyses were included in this study (see Appendix A). This analysis produced allometric slopes that were similar to those shown in Tables 3–6. The partial regression slope of the relationship between HR and body mass was 1.05 ± 0.121 for males (mean ± 1 SE; 95% CI = 0.8–1.3; df = 1, 98; partial $r^2 = 0.44$; $P < 0.001$) and 0.785 ± 0.114 for females (95% CI = 0.6–1.0; df = 1, 98; partial $r^2 = 0.33$; $P < 0.001$). Slopes for males and females were not significantly different ($F_{1,212} = 1.22$, $P \approx 0.25$; Sokal and Rohlf 1995:493–499).

DISCUSSION

As in other groups (e.g., Kelt and Van Vuren 2001 for mammals), HR size is strongly positively correlated with body size across species of lizards. Also, males have larger HRs than do females, even when the effects of body size are controlled statistically. Diet affects HR size: carnivores have the largest HRs, omnivores have the smallest, and herbivores have slightly smaller HRs than do insectivores. In addition, various methodological variables affect estimates of HR size.

TABLE 5. Conventional nested ANCOVA results, with log home range area as the dependent variable (weighted by square root of the number of individuals included in each study).

		Males					Females				
Source	df	*F*	Slope	95% CI	Partial r^2	*P*	*F*	Slope	95% CI	Partial r^2	*P*
Diet	3	4.90			0.16	0.004	7.68			0.23	<0.011
Habitat	3	6.25			0.19	0.001	3.93			0.13	0.011
Major clade	1	1.05			0.04	0.317	0.001			0.00	0.972
Minor clade†	11	6.14			0.46	<0.001	6.31			0.47	<0.001
Method	7	6.14			0.35	<0.001	7.20			0.39	<0.001
Log SVL	1	32.31	2.38	(1.5, 3.2)	0.29	<0.001	39.79	2.46	(1.7, 3.2)	0.34	<0.001
Log sightings	1	31.12	−1.16	(−1.6, −0.7)	0.28	<0.001	13.60	−0.70	(−1.1, −0.3)	0.15	<0.001
(Zlogsight)^2‡	1	9.74	0.19	(0.1, 0.3)	0.18	<0.001	5.43	0.11	(0.0, 0.2)	0.06	0.022
Error	79§										

† Minor clades ($N = 13$ families or closely allied genera) were nested within the major clades (Iguania and Autarchoglossa) previously examined.

‡ The square of the *Z*-transformed log of the number of sightings.

§ For major clade, error is 22.9 for males and 25.4 for females.

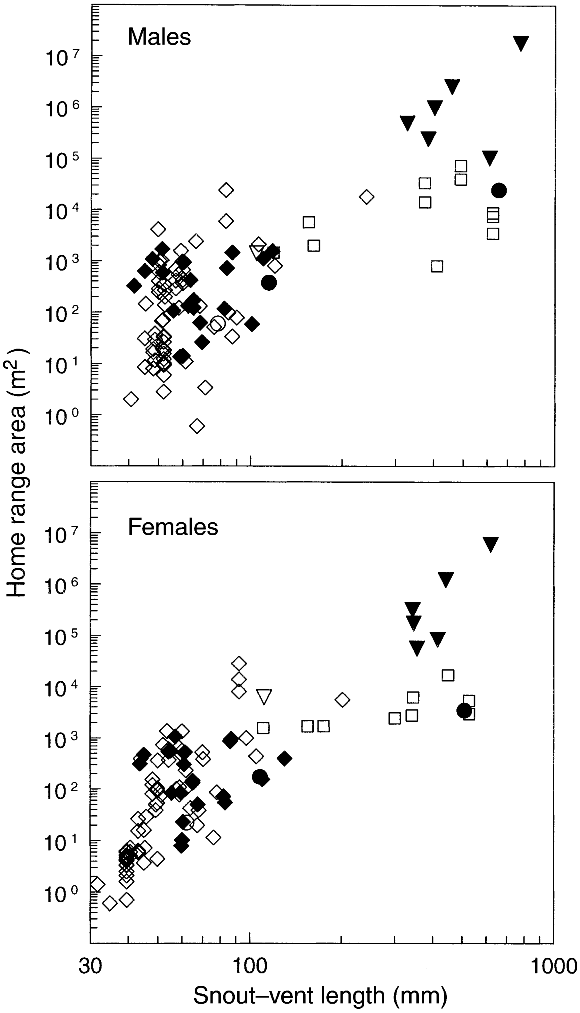

FIG. 4. Home range area as a function of snout–vent length (SVL) in lizards, separated by diet (N = 108). Note the log scales. For a given body size, carnivores (triangles) have relatively large home ranges, and herbivores (squares) have relatively small ones. Circles represent omnivores, and diamonds represent insectivores. Iguania, open symbols; Autarchoglossa, closed symbols.

Data distribution and quality

The lack of information from many studies, some of it very basic (e.g., sample size, the method used to calculate HR), was a limiting factor in our analyses. Harris et al. (1990) identified a similar problem in the HR literature for mammals. Moreover, although items such as total study duration are provided by most authors, few report the observation duration for individual animals, which may be quite different. Thus, not all of the values that we used for study duration may have been comparable. The phylogenetically and geographically biased sampling effort represented in the data and the tendency of related species to share many biological traits were also limiting factors. The strong ties between phylogeny and ecology reflect a larger trend of phylogenetic conservatism. Closely related lizards also show extensive similarities in body size (Pough 1980, Greene 1982), territorial behavior (Stamps 1977, 1983), chemosensory abilities (Cooper 1995), foraging behavior (Perry 1999), diet (Greene 1982), and such life-history traits as clutch size (Clobert et al. 1998 and references therein). A diversification of taxonomic and geographic efforts is clearly needed.

Methodological issues in home range estimation

A bewildering array of methods for estimating HR has been developed over the years, and our study encompasses a large number of these. Each makes important assumptions about the cognitive map used by the organism, the completeness of the data, and the animal's use of space both inside the HR and at its periphery (for a recent review, see Powell 2000). An HR is not uniformly used, and parts of it are likely to be more heavily utilized than others (Christian et al. 1986, Powell 2000). As a result, a method such as minimum convex polygon may underestimate the HR by missing seldom-used areas, whereas some of the larger estimates may give the erroneous impression that a larger area is regularly used. Discussions of the most appropriate techniques for calculating HR began decades ago (e.g., Jennrich and Turner 1969) and are still ongoing. Our analyses, both traditional and phylogenetically informed, support previous work (Waldschmidt 1979, Powell 2000) in showing a significant effect of the method used to estimate HR. The correction suggested by Jennrich and Turner (1969) and the estimator of Schoener (1981) consistently produce the largest estimates, whereas HRs estimated by the more commonly used polygon method are significantly smaller. Yet, evaluating the absolute utility of these methods is impossible in the absence of data on ''true'' HR size (Schoener 1981). Because the true HR size is generally unknowable, it may be neither desirable nor possible to formulate a general answer to the question of which calculation method is best. Indeed, Robertson et al. (1998), who used empirical data and simulations to evaluate several methods for birds, concluded that different methods are most appropriate under different conditions and for different purposes. To facilitate comparisons, we suggest that the estimate produced by the minimum convex polygon method always be provided in future work, in addition to other method(s) deemed most appropriate to the specific system. Convex polygon estimates are the most widely reported values, and therefore the most comparable across taxa and studies and the most often used in large-scale analyses (e.g., Kelt and Van Vuren 2001). Moreover, this method appears to be relatively insensitive to sample size and periphery information (Robertson et al. 1998).

Theory (see e.g., Schoener 1981, Powell 2000) suggests that the number of sightings used should affect the resulting estimate of HR size. Specifically, additional sightings should initially greatly increase the es-

TABLE 6. ANCOVA through the origin, implemented with phylogenetically independent contrasts and the regression procedure in SPSS.

		Males					Females				
Source	df	*F* or *t*‡	Slope	95% CI	Partial r^2	*P*	*F* or *t*†	Slope	95% CI	Partial r^2	*P*
Diet	3	4.34				0.007	11.32				<0.001
Habitat	3	15.21				<0.001	18.13				<0.001
Minor clade	12	0.55				0.876	0.38				0.967
Method	7	2.94				0.009	2.64				0.017
Log SVL	1	4.13	2.50	(1.3, 3.7)	0.18	<0.001	2.92	1.52	(0.5, 2.6)	0.09	0.005
Log sighting	1	−5.15	−0.43	(−0.6, −0.3)	0.25	<0.001	−3.24	−0.23	(−0.4, −0.1)	−0.12	<0.002
(Zlogsight)^2†	1	5.13	0.19	(0.1, 0.3)	0.25	<0.001	3.51	0.14	(0.1, 0.2)	0.14	0.001
Error	79										

Note: Log home range area was the dependent variable, weighted by the square root of number of individuals included in each study.

† The square of the *Z*-transformed log of the number of sightings.

‡ For the first four rows (Diet–Method), *F* is the test statistic; for the last three rows (Log SVL–(*Z*logsight)^2), *t* is the test statistic.

timate, but a plateau will ultimately be reached past which additional data will make little difference. Many empirical examples conform to this expectation (e.g., Schoener 1981, Alberts 1993, Powell 2000). Much discussion has centered on the point at which this asymptote is reached, as an indicator of determining how best to apportion effort between increasing sample size within vs. among individuals (e.g., see Gautestad and Mysterud 1995). Recent work suggests that, at the intrapopulation level, the asymptotic number may be large (Gautestad and Mysterud 1995). Our findings indicate that increasing the number of sightings does not necessarily result in increased estimated HR size when comparisons are performed among species. One possible explanation for this discrepancy is that asymptotic curves may be highly sensitive to species characteristics and study methods. In that case, reliance on asymptotic values obtained in other species, a technique used in some of the studies that we reviewed, may not be advisable.

Our analyses consistently suggest that HR sizes of terrestrial species are larger than those of species occupying a more vertically complex habitat. We believe that this may simply reflect the methodological difficulty of accurately calculating HR size for a species using a three-dimensional environment (Milstead 1972). For example, is the appropriate HR for an *Anolis* lizard living on a tree the area underneath that tree? A composite of the area actually utilized? A three-dimensional representation? To the best of our knowledge, Jenssen and Nunez (1998) have been the only authors to make a direct attempt to account for this problem, which clearly deserves additional attention. For arboreal and saxicolous species, traditional estimates may be comparable within species, and perhaps even among species inhabiting similar habitats, but are clearly not equivalent to those of terrestrial species.

Biological factors affecting home range size

Not surprisingly, body size and HR size exhibit a strong positive relationship across species of lizards. After accounting for the effects of body size, our initial analysis indicated a difference in HR between iguanian and autarchoglossan lizards (comparisons with Gekkota were not possible because of the paucity of data for this group). This matches early work by Stamps (1977), who found that Iguania, which are typically territorial, have larger HRs than do the nonterritorial Autarchoglossa. Similarly, Stamps (1983) compared HR size in territorial (all in Iguania) and nonterritorial (all in Autarchoglossa) lizard species. She found that the two groups differed: iguanian males had larger HRs than females during the reproductive season, whereas autarchoglossan males did not. We therefore expected to find a difference between the two clades, which often differ in other important ways. This was supported in the analysis containing phylogenetic information in the form of major clade only, which was similar to analyses conducted by Stamps (1977, 1983). However, the studies of Stamps (1977, 1983) were not designed to explicitly compare the two clades, and were conducted before phylogenetic pseudoreplication emerged as a major concern for such work.

Surprisingly, analyses incorporating more elaborate phylogenetic information did not show a difference between the two major clades in HR area adjusted for body size. When minor clades were added to the conventional analysis, it became clear that the appearance of a difference between the major clades was an artifact of methodology. Most likely, the limited phylogenetic scope of earlier work contributed to this problem. The analysis with phylogenetically independent contrasts suggests that there are neither higher level differences between the two major clades, nor differences among the subclades nested within them (at least as coded in our analyses). In other words, once all other factors are accounted for, iguanids (territorial species of previous analyses) do not appear to have larger HRs than autarchoglossans (nonterritorial taxa). We did not, however, test for the effects of territorial behavior separate from other factors, and HR may indeed differ between territorial and nonterritorial taxa, once other factors are accounted for.

Several recent studies suggest that Iguania and Autarchoglossa may not be as dichotomous as once thought. For example, Perry (1999) found that lizard foraging behaviors were not bimodal, contrary to some suggestions. The data of Perry (1999) do not show the presence of bimodality within either clade, nor among them, although members of Iguania tend to be more sedentary than are members of Autarchoglossa. In a complementary manner, neither clade appears as constrained in its evolution as seems to have been presumed. For example, Martins et al. (1998) demonstrated rapid changes in structure and function related to communicative displays among populations of *Sceloporus graciosus*, and Martins (1993) and Martins and Lamont (1998) showed substantial and sometimes rapid divergence in head bob displays among species and populations of *Cyclura*. Similarly, Bonine and Garland (1999) and Bonine et al. (2001) showed that locomotor performance and underlying morphologies are highly diverse among species within Phrynosomatidae.

The lack of overall differences between the two clades suggests that lizard HR size may largely be determined by energetics, as has been suggested for a variety of taxa (e.g., McNab 1963, Turner et al. 1969, Schoener 1971, Milton and May 1976, Harestad and Bunnell 1979, Gompper and Gittleman 1991, Nagy et al. 1999, Kelt and Van Vuren 2001, Mysterud et al. 2001; but see Swihart et al. 1988, Garland et al. 1993). Significant differences among species exhibiting different diets also support this interpretation. We consistently found that carnivores had the largest HRs, as would be expected for species whose diet is the highest on the food chain. Interestingly, omnivores had the smallest HRs, suggesting that their ability to utilize diverse food types may result in a biologically significant energetic benefit. Relatively few such species exist, suggesting that other disadvantages accrue to omnivores. For example, Drummond (1983) has shown that generalist garter snakes are less effective aquatic foragers than specialists.

Two previous studies examined the allometry of metabolic rate in lizards. Andrews and Pough (1985) used traditional statistical approaches to compare lizard families with respect to standard metabolic rate, and Nagy et al. (1999) used phylogenetically independent contrasts to compare field metabolic rates. Nagy et al. (1999) also published an allometric equation relating field metabolic rates to body mass for all lizards. Their analysis of phylogenetically independent contrasts yielded a slope of 0.787, with a 95% CI of 0.695–0.879 (their conventional analysis yielded a slope of 0.92). Our analyses with independent contrasts indicated a similar relationship, with slopes of 1.1 for males (95% CI = 0.8–1.3) and 0.8 for females (95% CI = 0.6–1.0). Thus, evidence from this and previous studies suggests that energetic needs may be of paramount importance in determining the size of lizard HRs. However, this conclusion remains tentative because a similarity in slopes does not necessarily require the causality that we are proposing.

Male lizards had larger HRs, relative to their body sizes, than did females, and this difference held across both territorial and nonterritorial taxa (Fig. 2). This significant difference also matches previous findings (Andrews 1971, Schoener and Schoener 1982, Stamps 1983), although these resulted from much more limited studies. The difference strongly suggests that social factors do impact HR size. Several authors have suggested that the size of the HR in females is primarily determined by energetic needs. In contrast, the larger HRs of males are also determined by availability of females, and are structured to increase reproductive success (Andrews 1971, Schoener and Schoener 1982, Stamps 1983, Hews 1993). Our data suggest that this conclusion may be appropriate to other lizard taxa as well. Reproduction is commonly treated as being especially costly for females, for example because being gravid reduces their locomotor performance and chances of survival (e.g., Miles et al. 2000). Our findings suggest that males also incur a considerable reproductive cost, although it is harder to measure. Traits that increase male reproductive success often have survival costs (e.g., Clinton and Le Boeuf 1993). Indeed, Marler et al. (1995) have shown that artificially augmented testosterone levels cause an increase in territorial behavior in male *Sceloporus jarrovii*, but also elevate energetic and survival costs. Similarly, additional testosterone increases HR size in male *Uta stansburiana* (DeNardo and Sinervo 1994); males with high testosterone levels hold larger territories and enjoy high access to females (Sinervo and Lively 1996).

The main difference between our findings and previous work is the lack of a difference in size-adjusted HR area between Iguania and Autarchoglossa, once phylogenetic relationships were accounted for by use of independent contrasts (or even by use of conventional nested ANCOVA). Overall, our reanalysis suggests that earlier studies, although smaller in scope and lacking in phylogenetic context, generally correctly identified nonphylogenetic biological factors that affect HR size in lizards. We confirmed that larger bodied species have larger HRs, and that diet influences HR size such that carnivores have especially large HRs. Our findings provide support for earlier conclusions that methodological issues can greatly affect HR estimates. We also support the suggestion that habitat type can be an important methodological, as well as biological, factor, because typical methods for estimating HR size are not ideally suited for use in habitats with a strong vertical component. Moreover, the scaling of HR size with body mass is very similar to the scaling of field metabolic rate. Thus, various findings support the conclusion that, at the interspecific level, HR size is driven primarily by energetic needs. However, males consistently have larger HRs than do females of similar body size. This suggests that additional selection acts at the intraspecific level, presumably via sexual selection on males.

ACKNOWLEDGMENTS

We thank J. G. Swallow for beginning the compilation of home ranges and L.-L. Changchien for assistance with the phylogeny for this early data set. L. J. Vitt, A. C. Alberts, A. Bouskila, T. K. Brown, E. J. Censky, T. H. Fritts, W. B. Jennings, J. D. Lazell, J. B. Losos, W. E. Magnusson, E. R. Pianka, M. Tayab, and Y. L. Werner shared unpublished information or helped us to locate hard-to-find lizard home range data. E. R. Pianka, J. A. Schulte, and especially J. J. Wiens provided invaluable advice on phylogenetic relationships. R. W. Sutherland, I. Girard, and two anonymous reviewers provided helpful comments on the manuscript. We also thank R. E. Espinosa for discussions of lizard diets and G. Lapina for helping to translate articles from the Russian. This study was supported by NSF grants IBN-9723758 and DEB-9981967 to T. Garland, Jr. and a Michael Guyer postdoctoral fellowship to G. Perry.

LITERATURE CITED

Abouheif, E., and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensche's rule. American Naturalist **149**:540–562.

Ackerly, D. D. 1999. Comparative plant ecology and the role of phylogenetic information. Pages 391–413 *in* M. C. Press, J. D. Scholes, and M. G. Braker, editors. Physiological plant ecology. The 39th Symposium of the British Ecological Society held at the University of York, 7–9 September 1998. Blackwell Science, Oxford, UK.

Alberts, A. C. 1993. Relationship of space use to population density in an herbivorous lizard. Herpetologica **49**:469–479.

Andrews, R. M. 1971. Structural habitat and time budget of a tropical *Anolis* lizard. Ecology **52**:262–271.

Andrews, R. M., and F. H. Pough. 1985. Metabolism of squamate reptiles: allometric and ecological relationships. Physiological Zoology **58**:214–231.

Armstrong, J. T. 1965. Breeding home range in the nighthawk and other birds: its evolutionary and ecological significance. Ecology **46**:619–629.

Arnold, E. N. 1973. Relationships of the Palearctic lizards assigned to the genera *Lacerta*, *Algyroides*, and *Psammodromus* (Reptilia: Lacertidae). Bulletin of the British Museum (Natural History) Zoology **25**:292–366.

Arnold, E. N. 1989*a*. Towards a phylogeny and biogeography of the Lacertidae: relationships within an old-world family of lizards derived from morphology. Bulletin of the British Museum of Natural History D **55**:209–251.

Arnold, E. N. 1989*b*. Systematic and adaptive radiation of Equatorial African lizards assigned to the genera *Adolphus*, *Bedriagaia*, *Gastropholis*, *Holapsis*, and *Lacerta* (Reptilia; Lacertidae). Journal of Natural History **23**:525–555.

Arnold, E. N. 1997. Interrelationships and evolution of the east Asian grass lizards, *Takydromus* (Squamata: Lacertidae). Zoological Journal of the Linnean Society **119**:267–296.

Bininda-Emonds, O. R. P., and J. L. Gittleman. 2000. Are pinnipeds functionally different from fissiped carnivores? The importance of phylogenetic comparative analyses. Evolution **54**:1011–1023.

Bininda-Emonds, O. R. P., J. L. Gittleman, and A. Purvis. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora. Biological Reviews **74**:143–175.

Blob, R. W. 2000. Interspecific scaling of the hindlimb skeleton in lizards, crocodilians, felids and canids: does limb bone shape correlate with limb posture? Journal of Zoology, London **250**:507–531.

Bonine, K. E., and T. Garland, Jr. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. Journal of Zoology, London **248**:255–265.

Bonine, K. E., T. T. Gleeson, and T. Garland, Jr. 2001. Comparative analysis of fiber-type composition in the iliofibularis muscle of phrynosomatid lizards (Sauria). Journal of Morphology **250**:265–280.

Brashares, J., T. Garland, Jr., and P. Arcese. 2000. Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. Behavioral Ecology **11**:452–463.

Burrage, B. R. 1974. Population structure in *Agama atra* and *Cordylus cordylus cordylus* in the vicinity of De Kelders, Cape Province. Annals of the South African Museum **66**:1–23.

Burt, W. H. 1943. Territoriality and home range concepts applied to mammals. Journal of Mammalogy **24**:346–352.

Changchien, L.-L. 1996. A phylogenetic study of sceloporine lizards and their relationships with other iguanid lizards based on DNA/DNA hybridization. Dissertation. University of Wisconsin, Madison, Wisconsin USA.

Christian, K. A., W. P. Porter, and C. R. Tracy. 1986. Core areas within the home ranges of Galapagos land iguanas, *Conolophus pallidus*. Journal of Herpetology **20**:272–276.

Christian, K. A., C. R. Tracy, and W. P. Porter. 1984. Physiological and ecological consequences of sleeping-site selection by the Galapagos land iguana *Conolophus pallidus*. Ecology **65**:752–758.

Christian, K. A., and S. Waldschmidt. 1984. The relationship between lizard home range and body size: a reanalysis of the data. Herpetologica **40**:68–75.

Clinton, W. L., and B. J. Le Boeuf. 1993. Sexual selection's effects on male life history and the pattern of male mortality. Ecology **74**:1884–1892.

Clobert, J., T. Garland, Jr., and R. Barbault. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. Journal of Evolutionary Biology **11**:329–364.

Cooper, W. E., Jr. 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. Animal Behaviour **50**:973–985.

Cruz-Neto, A. P., T. Garland, Jr., and A. S. Abe. 2001. Diet, phylogeny, and basal metabolic rate in phyllostomid bats. Zoology **104**:49–58.

DeNardo, D. F., and B. Sinervo. 1994. Effects of steroid–hormone interactions on activity and home-range size of male lizards. Hormones and Behavior **28**:273–287.

Drummond, H. 1983. Aquatic foraging in garter snakes: a comparison of specialists and generalists. Behaviour **86**:1–30.

Dunham, A. E., D. B. Miles, and D. N. Reznick. 1988. Life history patterns in squamate reptiles. Pages 441–522 *in* C. Gans and R. B. Huey, editors. Biology of the Reptilia. Volume 16. Ecology B. Alan R. Liss, New York, New York, USA.

Estes, R., K. de Quiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata. Pages 119–281 *in* R. Estes and G. Pregill, editors. Phylogenetic relationships of the lizard families. Stanford University Press, Stanford, California, USA.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist **125**:1–15.

Fitch, H. S. 1981. Sexual size differences in reptiles. University of Kansas Museum of Natural History Miscellaneous Publications **70**:1–72.

Ford, R. G., and J. P. Myers. 1981. An evaluation and comparison of techniques for estimating home range and territory size. Studies in Avian Biology **6**:461–465.

Frost, D. R. 1992. Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). American Museum Novitates **3033**.

Frost, D. R., and R. Etheridge. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). University of Kansas, Museum of Natural History Miscellaneous Publications **81**:1–65.

Fu, J. 1998. Toward the phylogeny of the family Lacertidae: implications from mitochondrial DNA 12S and 16S gene sequences (Reptilia: Squamata). Molecular Phylogenetics and Evolution **9**:118–130.

Fu, J. 2000. Toward the phylogeny of the family Lacertidae: why 4708 base pairs of mtDNA sequences cannot draw the picture. Biological Journal of the Linnean Society **71**:203–217.

Fuller, S., P. Baverstock, and D. King. 1998. Biogeographic origins of goannas (Varanidae): a molecular perspective. Molecular Phylogenetics and Evolution **9**:294–307.

Garland, T., Jr. 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. Animal Behaviour **57**:77–83.

Garland, T., Jr., and S. C. Adolph. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiological Zoology **67**:797–828.

Garland, T., Jr., and P. A. Carter. 1994. Evolutionary physiology. Annual Review of Physiology **56**:579–621.

Garland, T., Jr., and R. Díaz-Uriarte. 1999. Polytomies and phylogenetically independent contrasts: an examination of the bounded degrees of freedom approach. Systematic Biology **48**:547–558.

Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology **42**:265–292.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology **41**:18–32.

Garland, T., Jr., and A. R. Ives. 2000. Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. American Naturalist **155**:346–364.

Garland, T., Jr., P. E. Midford, and A. R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. American Zoologist **39**:374–388.

Gautestad, A. O., and I. Mysterud. 1995. The home range ghost. Oikos **74**:195–204.

Gompper, M. E., and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia **87**:343–348.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London B **326**:119–157.

Greene, H. W. 1982. Dietary and phenotypic diversity in lizards: why are some organisms specialized? Pages 107–128 *in* D. Mossakowski and G. Roth, editors. Environmental adaptation and evolution. Gustav Fischer, Stuttgart, Germany.

Greer, A. E. 1970. A subfamilial classification of scincid lizards. Bulletin of the Museum of Comparative Zoology **139**:151–184.

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight—a reevaluation. Ecology **60**:389–402.

Harris, D. J., and E. N. Arnold. 1999. Relationships of wall lizards, *Podarcis* (Reptilia: Lacertidae) based on mitochondrial DNA sequences. Copeia **1999**:749–754.

Harris, D. J., E. N. Arnold, and R. H. Thomas. 1999*a*. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. Proceedings of the Royal Society of London B **265**: 1939–1948.

Harris, D. J., E. A. Sinclair, N. L. Mercader, J. C. Marshall, and K. A. Crandall. 1999*b*. Squamate relationships based on C-*MOS* nuclear DNA sequences. Herpetological Journal **9**:147–151.

Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. Mammal Review **20**:97–123.

Harvey, M. B., and R. L. Gutberlet, Jr. 2000. A phylogenetic analysis of the tropidurine lizards (Squamata: Tropiduridae), including new characters of squamation and epidermal mircostructure. Zoological Journal of the Linnean Society **128**:189–233.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, UK.

Hews, D. K. 1993. Food resources affect female distribution and male mating opportunities in the iguanian lizard *Uta palmeri*. Animal Behaviour **46**:279–291.

Honda, M., H. Ota, M. Kobayashi, and T. Hikida. 1999*a*. Phylogenetic relationships of Australian skinks of the *Mabuya* group (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. Genes and Genetic Systems **74**:135–139.

Honda, M., H. Ota, M. Kobayashi, J. Nabhitabhata, H.-S. Yong, and T. Hikida. 1999*b*. Evolution of Asian and African lygosomine skinks of the *Mabuya* group (Reptilia: Scincidae): a molecular perspective. Zoological Science **16**: 979–984.

Honda, M., H. Ota, M. Kobayashi, J. Nabhitabhata, H.-S. Yong, S. Sengoku, and T. Hikida. 2000*a*. Phylogenetic relationships of the family Agamidae (Reptilia: Iguania) inferred from mitochondrial DNA sequences. Zoological Science **17**:527–537.

Honda, M., H. Ota, M. Kobayashi, J. Nabhitabhata, H.-S. Yong, and T. Hikida. 2000*b*. Phylogenetic relationships, character evolution, and biogeography of the subfamily Lygosominae (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. Molecular Phylogenetics and Evolution **15**:452–461.

Huey, R. B., C. R. Peterson, S. J. Arnold, and W. P. Porter. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. Ecology **70**: 931–944.

Huey, R. B., E. R. Pianka, and T. W. Schoener, editors. 1983. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, Massachusetts, USA.

Irschick, D. J. 2000. Comparative and behavioral analyses of preferred speed: *Anolis* lizards as a model system. Physiological and Biochemical Zoology **73**:428–437.

Iverson, J. B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum, Biological Sciences **24**:175–358.

Jackman, T. R., A. Larson, K. de Quiroz, and J. B. Losos. 1999. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. Systematic Biology **48**:254–285.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology **22**: 227–237.

Jenssen, T. A., and S. C. Nunez. 1998. Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intrasexual selection. Behaviour **135**:981–1003.

Joger, U. 1991. A molecular phylogeny of agamid lizards. Copeia **1991**:616–622.

Kelt, D. A., and D. H. Van Vuren. 2001. The ecology and macroecology of mammalian home range area. American Naturalist **157**:637–645.

Kluge, A. G. 1987. Cladistic relationships in the Gekkonoidea (Squamata, Sauria). Miscellaneous Publications of the Museum of Zoology, University of Michigan, **173**.

Lazell, J., and G. Perry. 1997. *Anolis cristatellus wileyae*: frugivory. Herpetological Review **28**:150.

Losos, J. B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. Ecological Monographs **60**:369–388.

Mace, G. M., and P. H. Harvey. 1983. Energetic constraints on home-range size. American Naturalist **121**:120–132.

Mace, G. M., P. H. Harvey, and T. H. Clutton-Brock. 1983. Vertebrate home-range size and energetic requirements. Pages 32–53 *in* I. R. Swingland and P. J. Greenwood, editors. The ecology of animal movement. Clarendon Press, Oxford, UK.

Macey, J. R., A. Larson, N. B. Ananjeva, and T. J. Papenfuss. 1997. Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. Journal of Molecular Evolution **44**:660–674.

Macey, J. R., J. A. Schulte, II, A. Larson, N. B. Ananjeva, Y. Wang, R. Pethiyagoda, N. Rastegar-Pouyani, and T. J. Papenfuss. 2000. Evaluating tras-Tethys migration: an example using acrodont lizard phylogenetics. Systematic Biology **49**:233–256.

Marler, C. A., G. Walsberg, M. L. White, and M. Moore. 1995. Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. Behavioral Ecology and Sociobiology **37**:225–231.

Martins, E. P. 1993. A comparative study of the evolution of *Sceloporus* push-up displays. American Naturalist **142**: 994–1018.

Martins, E. P. 1994. Phylogenetic perspectives on the evolution of lizard territoriality. Pages 117–144 *in* L. J. Vitt and E. R. Pianka, editors. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, New Jersey, USA.

Martins, E. P., editor. 1996. Phylogenies and the comparative method in animal behavior. Oxford University Press, Oxford, UK.

Martins, E. P., A. N. Bissell, and K. K. Morgan. 1998. Population differences in a lizard communicative display: evidence for rapid change in structure and function. Animal Behaviour **56**:1113–1119.

Martins, E. P., and J. Lamont. 1998. Estimating ancestral states of a communicative display: a comparative study of *Cyclura* rock iguanas. Animal Behaviour **55**:1685–1706.

McGuire, J. A. 1996. Phylogenetic systematics of crotaphytid lizards (Reptilia: Iguania: Crotaphytidae). Bulletin of the Carnagie Museum of Natural History **32**.

McNab, B. K. 1963. Bioenergetics and determinants of home range size. American Naturalist **97**:133–140.

Miles, D. B., B. Sinervo, and W. A. Frankino. 2000. Reproductive burden, locomotor performance, and the cost of reproduction in free ranging lizards. Evolution **54**:1386–1395.

Milstead, W. W. 1972. More on lizard home ranges. Herpetological Review **4**:83–84.

Milton, K., and M. L. May. 1976. Body weight, diet and home range area in primates. Nature **259**:459–462.

Mysterud, A., F. J. Pérez-Barbería, and I. J. Gordon. 2001. The effects of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. Oecologia **127**:30–39.

Nagy, K. A., I. A. Girard, and T. K. Brown. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annual Review of Nutrition **19**:247–277.

Nunn, C. L., and R. A. Barton. 2000. Allometric slopes and independent contrasts: a comparative test of Kleiber's Law in primate ranging patterns. American Naturalist **156**:519–533.

Obst, F. J., K. Richter, and U. Jacob. 1988. The completely illustrated atlas of reptiles and amphibians for the terrarium. T.F.H. Publishing, Neptune City, New Jersey, USA.

Perry, G. 1989. Size and mass in five Israeli lizards (Reptilia: Lacertidae). Israel Journal of Zoology **36**:129–132.

Perry, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. American Naturalist **153**: 98–109.

Perry, G., and M. Brandeis. 1992. Variation in stomach contents of the gecko *Ptyodactylus hasselquistii guttatus* in relation to sex, season and locality. Amphibia-Reptilia **13**: 275–287.

Perry, G., and J. Lazell. 1997. *Anolis stratulus*: nectivory. Herpetological Review **28**:150–151.

Perry, G., and E. R. Pianka. 1997. Animal foraging: past, present, and future. Trends in Ecology and Evolution **12**: 360–364.

Peters, R. H. 1977. Unpredictable problems with tropho-dynamics. Environmental Biology of Fishes **2**:97–102.

Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton, New Jersey, USA.

Pough, F. H. 1980. The advantages of ectothermy for tetrapods. American Naturalist **115**:92–112.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 2001. Herpetology. Second edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Presch, W. 1974. Evolutionary relationships and biogeography of the macroteiid lizards (Family Teiidae, Subfamily Teiinae). Bulletin of the Southern California Academy of Sciences **73**:23–32.

Purvis, A., and A. J. Webster. 1999. Phylogenetically independent comparisons and primate phylogeny. Pages 44–70 *in* P. C. Lee, editor. Comparative primate socioecology. Cambridge University Press, Cambridge, UK.

Rassmann, K. 1997. Evolutionary age of the Galapágos iguanas predates the age of the present Galapágos chain. Molecular Phylogenetics and Evolution **7**:158–172.

Reeder, T. W., and J. J. Wiens. 1996. Evolution of the lizard family Phrynosomatide as inferred from diverse types of data. Herpetological Monographs **10**:43–84.

Reiss, M. 1988. Scaling home range size: body size, metabolic needs and ecology. Trends in Ecology and Evolution **3**:85–86.

Robertson, P. A., N. J. Aebischer, R. E. Kenward, I. K. Hanski, and N. P. Williams. 1998. Simulation and jack-knifing assessment of home-range indices based on underlying trajectories. Journal of Applied Ecology **35**:928–940.

Rogner, M. 1997*a*. Lizards: husbandry and reproduction in the vivarium. Volume 1. Geckos, flap-footed lizards, agamas, chameleons, and iguanas. Krieger, Malabar, Florida, USA.

Rogner, M. 1997*b*. Lizards. Volume 2. Monitors, skinks, and other lizards including tuataras and crocodilians. Krieger, Malabar, Florida, USA.

Rose, B. 1982. Lizard home ranges: methodology and functions. Journal of Herpetology **16**:253–269.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology **49**:123–141.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics **2**:369–404.

Schoener, T. W. 1981. An empirically based estimate of home range. Theoretical Population Biology **20**:281–325.

Schoener, T. W., and A. Schoener. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. Ecology **63**:809–823.

Schulte, J. A., II, J. R. Macey, A. Larson, and T. J. Papenfuss. 1998. Molecular tests of phylogenetic taxonomies: a general procedure and example using four subfamilies of the lizard family Iguanidae. Molecular Phylogenetics and Evolution **10**:367–376.

Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature **380**:240–243.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. Freeman, New York, New York, USA.

Somma, L. A. 1990. A categorization and bibliographic survey of parental behavior in lepidosaurian reptiles. Smithsonian Herpetological Information Service **81**:1–53.

SPSS. 1999*a.* SPSS Base 10.0. SPSS, Chicago, Illinois, USA.

SPSS. 1999*b.* SPSS Base 10.0 applications guide. SPSS, Chicago, Illinois, USA.

Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. Pages 265–334 *in* C. Gans and D. W. Tinkle, editors. Biology of the Reptilia. Volume 7. Academic Press, London, UK.

Stamps, J. A. 1983. Sexual selection, sexual dimorphism, and territoriality. Pages 169–204 *in* R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, Massachusetts, USA.

Stamps, J. A., V. V. Krishnan, and R. M. Andrews. 1994. Analyses of sexual size dimorphism using null growth-based models. Copeia **1994**:598–613.

Stebbins, R. C. 1985. A Field guide to western amphibians and reptiles. Second edition. Houghton Mifflin, Boston, Massachusetts, USA.

Stickel, L. F. 1968. Home range and travels. Pages 373–411 *in* J. A. King, editor. Biology of *Peromyscus* (Rodentia). Special Publication Number 2. American Society of Mammalogists, Stillwater, Oklahoma, USA.

Swihart, R. K., N. A. Slade, and B. J. Bergstrom. 1988. Relating body size to the rate of home range use in mammals. Ecology **69**:393–399.

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution **30**:253–269.

Turner, F. B., R. I. Jennrich, and J. D. Weintraub. 1969. Home range and body size of lizards. Ecology **50**:1076–1081.

Vanhooydonck, B., and R. Van Damme. 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. Evolutionary Ecology Research **1**:785–805.

Vitt, L. J., and E. R. Pianka, editors. 1994. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, New Jersey, USA.

Waldschmidt, S. R. 1979. The effect of statistically based models on home range size estimate in *Uta stansburiana.* American Midland Naturalist **101**:236–240.

Werner, Y. L. 1971. Some suggestions for the standard expression of measurements. Systematic Zoology **20**:249–252.

Wiens, J. J., and B. D. Hollinsworth. 2000. War of the iguanas: conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. Systematic Biology **49**:143–159.

Wiens, J. J., and T. W. Reeder. 1997. Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. Herpetological Monographs **11**:1–101.

Williamson, M., and K. J. Gaston. 1999. A simple transformation for sets of range sizes. Ecography **22**:674–680.

Wolf, C. M., T. Garland, Jr., and B. Griffith. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. Biological Conservation **86**:243–255.

APPENDIX A

A table presenting source data used in the analyses is available in ESA's Electronic Data Archive: *Ecological Archives* E083-032-A1.

APPENDIX B

A list of bibliographic sources cited in Appendix A is available in ESA's Electronic Data Archive: *Ecological Archives* E083-032-A2.

APPENDIX C

A list of abbreviations used in Appendix A is available in ESA's Electronic Data Archive: *Ecological Archives* E083-032-A3.

APPENDIX D

A bracket representation of the phylogenetic tree representing the 108 data points used in independent contrasts analyses is available in ESA's Electronic Data Archive: *Ecological Archives* E083-032-A4.