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# Wide home ranges for widely foraging lizards

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## Abstract

Space usage by animals may be influenced by a range of factors. In this study we investigate whether foraging behaviour affects the home range size of lizards. Two distinct tactics of foraging have been recognized in predators: sit-and-wait foraging (SW) and active foraging (AF). Foraging activity level of a data set of lizard species, mainly compiled from literature, is compared with their home range sizes. Two opposite predictions can be made about foraging in connection with home range area: on the one hand, SW species may exhibit larger home ranges due to their mating system; on the other hand, AF species have higher metabolic energy and thus food requirements and can be expected to have larger home ranges that have to yield this food. This study shows that percentage of the time moving (as an index of foraging mode) correlates positively with home range, even after correcting for body mass, and these patterns remain when phylogenetic relationships are taken into account. We thus conclude that home range areas parallel activity levels in lizards.

***Keywords:*** Home range size; Foraging mode; Sit-and-wait foraging; Active foraging

## Introduction

### Lizard home ranges (HRs)

The HR is the area that is crossed by an individual animal during its activities in normal circumstances and that has to satisfy its requirements, including: food (Schoener, 1968; Waser and Homewood, 1979), shelter (Stamps, 1983a), suitable thermal conditions (Christian et al., 1984) and mates (Owen-Smith, 1977; Stamps, 1983b). Energetic requirements have always been central in the attempt to rationalize HR size (McNab, 1963; Harestad and Bunnell, 1979; Mace et al., 1983; Reiss, 1988). Energetic needs in turn vary with body mass according to some allometric power law (Mace and Harvey, 1983). HR size is further influenced by the density of available food (McNab, 1963; Mace and Harvey, 1983), and thus by the diet of an animal. Animal prey is generally a scarce food resource compared to fruit or foliage. An herbivore is therefore able to satisfy its energy requirements by exploiting a smaller area than a carnivore of similar size (Schoener, 1968; Harestad and Bunnell, 1979). Within trophic levels, HR size might further be influenced by foraging style (Harestad and Bunnell, 1979; Mysterud et al., 2001). This may actually go with differences in the distribution of specific food items (Mysterud et al., 2001).

In this study, the relationship between foraging mode and HR area will be investigated among lizard species. Lizards have been fairly popular as model systems in

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ecology in general and foraging ecology in particular (Huey et al., 1983; Vitt and Pianka, 1994) and there exists a rather extensive literature concerning their HR size (reviews in Turner et al., 1969; Christian and Waldschmidt, 1984; Perry and Garland, 2002).

## Lizard foraging modes

Pianka (1966) discerned two distinct tactics of foraging in carnivorous lizards, sit-and-wait or ambush foraging (SW) and wide or active foraging (AF). SW foragers remain sedentary most of their activity period until a suitable prey item comes within range, while AF predators devote much time to wandering in active search for prey. This grouping has also been applied to many other kinds of animals (for example, spiders: Enders, 1975; Janetos, 1982; birds: Eckhardt, 1979; amphibians: Toft, 1981), although the dichotomous nature of foraging mode distribution has sometimes been questioned (e.g. Pianka, 1973; Regal, 1983; Perry, 1999). Foraging activity seems associated with a broad range of morphological, ecological and behavioural characteristics (Vitt and Congdon, 1978; Huey and Pianka, 1981; Anderson and Karasov, 1981; Vitt and Price, 1982; Huey et al., 1984; Nagy et al., 1984; Magnusson et al., 1985; Vitt, 1990; Cooper, 1994).

As far as space usage is concerned, actively foraging lizards probably travel further and use more area than comparably sized lizards that ambush prey (Warrick et al., 1998). SW lizards only rarely move between different feeding patches, while AF lizards frequently move and do not stay long at the patches where they find their food (Anderson, 1993). SW foragers typically use a more limited number of patches with high food density, thus requiring smaller HR than active foragers that search for food more randomly and whose HR also encompasses less productive areas (Harestad and Bunnell, 1979). Magnusson et al. (1985) even included the area used while foraging in the measures they used to estimate foraging intensity.

Further, since movement results in a 2- to 10-fold increase in energy metabolism for terrestrial vertebrates (Schmidt-Nielsen, 1972; Taylor, 1973; White and Anderson, 1994), AF predators, moving more, can be expected to have higher metabolic energy requirements than SW predators. This simple idea is corroborated by several empiric studies. Anderson and Karasov (1981) showed that, compared to the syntopic SW lizard *Callisaurus draconoides*, the AF species *Aspidoscelis tigris* must compensate for its higher energy expenditure by sustaining a feeding rate that is more than two-fold. Nagy et al. (1984) found a similar result comparing a wide forager (*Heliobolus lugubris*) with a syntopic closely related ambushing species (*Pedioplanis lineoocellata*). AF lizards also tend to have higher field body temperatures than SW species (Magnusson et al., 1985; Bowker et al., 1986; Bergallo and Rocha, 1993). Interspecific comparisons show that the (resting) metabolic rate generally correlates positively with the temperature at which the species are actually living, further increasing metabolic requirements in the field (see Gillooly et al., 2001; Clarke and Fraser, 2004; but see Addo-Bediako et al., 2002). It can be expected that these higher energy and thus food requirements of AF species (see Nagy, 2001) will force them to have larger HR.

On the other hand, available prey density (prey mass/unit area) may be different for SW or AF species. Because they use both chemoreception and vision in search for prey, daytime-active AF may encounter prey as hidden eggs, larvae, pupae, and daytime-inactive adults (Lewis, 1989) in addition to the typical prey of diurnal ambushers, i.e. arthropods which are day-active and mobile. Indeed, AF species show a higher encounter rate with prey (Nagy et al., 1984). AF lizards may even have a higher capture rate per encounter, because many of their prey are inactive, immobile and relatively easy to capture (Anderson, 1993). This would cause AF species to have a higher prey availability per unit HR area at their disposal, and could counter the effect of needing a larger HR as a function of the higher energetic needs or more scattered availability of prey.

It has also been suggested that differences in mating strategies (see Stamps, 1977, 1983b; Martins, 1994) would induce SW lizards to have larger HR sizes than AF species (Perry and Garland, 2002). Stamps (1977) explicitly linked territorial behaviour with SW foraging and the lack of HR defence and the presence of extensive HR overlaps with AF foraging. While a male AF lizard usually defends its immediate surroundings and during the mating season will try to monopolize females by following them, a typical male SW lizard tries to encompass in its territory as many females and their HR as possible. This would lead to larger HR sizes than would be expected on metabolic needs alone, at least for males.

To investigate whether HR size is larger in AF lizards, due to their higher food requirements, or in SW lizards, due to their mating system, data on HR size are here combined with measures that characterize foraging mode. Although Perry and Garland (2002) compared HR sizes between taxa that generally differ in foraging behaviour, a direct correlation of HR size with mobility indices used to quantify foraging mode was not included in their analysis.

## Material and methods

Data on HR size and foraging mode of lizards (Squamata exclusive of Serpentes) were collected from the literature (for a detailed overview of sources see Table 1). Because there are significant effects of diet on HR size (Perry and Garland, 2002), we excluded from our analyses all species that are not predominantly carnivorous. Only daytime-active species were included.

If more than one study was available, we selected what was interpreted as the most reliable HR size data for that species. Criteria for this selection were (1) availability of information on the methods used, (2) number of sightings used to estimate HR size, and (3) sample size. HR size estimates obtained by the convex polygon method (see Rose, 1982) were preferred, because this method is most commonly used and because it does not make assumptions about the distribution of data points (as e.g. statistical methods involving probability density functions do). However, this method does require a sufficient number of sightings. Only data of adult animals were used. As HR size differs between males and females (Perry and Garland, 2002), we performed the following analyses separately for each sex. Body mass data were taken from Perry and Garland (2002).

Two measures originally proposed by Pianka et al. (1979) are most commonly used for the characterisation of foraging mode: mean number of moves per minute (MPM) and percentage of the time spent moving (PTM) (see Perry, 1999).

Our own observations followed the methodology described in Cooper and Whiting (1999), with the difference that we used a PSION Workabout MX (Psion Teklogix, Inc.) handheld minicomputer, on which was installed a custom-written OVAL program to record movements, and that we only included observations that lasted at least 3 min. Whenever

**Table 1.** Overview of sources used in this study

| GENUS | SPECIES | Source home range | Source foraging |
|---|---|---|---|
| *Crotaphytus* | *collaris* | Baird et al., 1996 | Cooper et al., 2001 |
| *Heloderma* | *suspectum* | Beck, 1990 | Grant, 1983 |
| *Acanthodactylus* | *boskianus* | Al-Johany and Spellerberg, 1989 | Perry et al., 1990 |
| *Lacerta* | *agilis* | Nicholson and Spellerberg, 1989 | Nemes, 2002 |
| *Lacerta* | *monticola* | Pérez-Mellado et al., 1988 | Verwaijen, D., unpubl. data |
| *Lacerta* | *vivipara* | Ortega-Rubio et al., 1988 | Verwaijen, D., unpubl. data |
| *Mesalina* | *guttulata* | Orr et al., 1979 | Perry et al., 1990 |
| *Podarcis* | *hispanica* | Swallow and Castilla, 1996 | Verwaijen, D., unpubl. data |
| *Podarcis* | *muralis* | Boag, 1973 | Verwaijen, D., unpubl. data |
| *Psammodromus* | *algirus* | Salvador et al., 1996 | Verwaijen, D., unpubl. data |
| *Cophosaurus* | *texanus* | Engeling, 1972 | Perry, 1999 |
| *Phrynosoma* | *modestum* | Munger, 1984 | Shaffer and Whitford, 1981 |
| *Sceloporus* | *graciosus* | Guyer, 1991 | Perry, 1999 |
| *Sceloporus* | *jarrovii* | Simon, 1975 | Cooper et al., 2001 |
| *Sceloporus* | *merriami* | Ruby and Dunham, 1987 | Perry, 1999 |
| *Sceloporus* | *olivaceus* | Blair, 1960 | Perry, 1999 |
| *Sceloporus* | *scalaris* | Gutiérrez and Ortega, 1985 | Cooper, W.E., pers. comm. |
| *Sceloporus* | *undulatus* | Jones and Droge, 1980 | Perry, 1999 |
| *Sceloporus* | *virgatus* | Rose, 1981, 1982 | Cooper et al., 2001 |
| *Urosaurus* | *ornatus* | Mahrt, 1998 | Perry, 1999 |
| *Uta* | *stansburiana* | Parker, 1974 | Cooper et al., 2001 |
| *Anolis* | *angusticeps* | Stamps and Eason, 1989 | Irschick, 2000 |
| *Anolis* | *carolinensis* | Jenssen and Nunez, 1998 | Perry, 1999 |
| *Anolis* | *cristatellus* | Schoener and Schoener, 1982 | Perry, 1999 |
| *Anolis* | *distichus* | Schoener and Schoener, 1982 | Moermond, 1979 |
| *Norops* | *limifrons* | Andrews and Rand, 1983 | Perry, 1999 |
| *Norops* | *lineatopus* | Schoener and Schoener, 1982 | Irschick, 2000 |
| *Norops* | *nebulosus* | Schoener and Schoener, 1982 | Lister and Garcia Aguayo, 1992 |
| *Norops* | *polylepis* | Schoener and Schoener, 1982 | Perry, 1999 |
| *Norops* | *sagrei* | Schoener and Schoener, 1982 | Irschick, 2000 |
| *Norops* | *valencienni* | Andrews and Rand, 1983 | Irschick, 2000 |
| *Oligosoma* | *grande* | Eifler and Eifler, 1999 | Eifler and Eifler, 1999 |
| *Ameiva* | *exsul* | Lewis and Saliva, 1987 | Perry, 1999 |
| *Ameiva* | *quadrilineata* | Hirth, 1963 | Perry, 1999 |
| *Aspidoscelis* | *hyperythra* | Rowland, 1992 | Karasov and Anderson, 1984 |
| *Aspidoscelis* | *tigris* | Jorgensen and Tanner, 1963 | Anderson and Karasov, 1988 |

multiple resources were available for the same species, the data that were based on longer observations and larger sample sizes were retained.

In order to achieve a more normal distribution in all measures, to correct the heavily right-skewed distribution of both HR size and body mass and to linearize their relationship (see Williamson and Gaston, 1999), all data were $\log_{10}$-transformed before being analysed.

## Conventional statistical analyses

We performed traditional Pearson correlation analyses between body mass, HR size and the foraging mode variables. Because HR size is dependent on body mass (Schoener, 1968; Perry and Garland, 2002), partial correlations were executed between HR size and PTM and HR size and MPM with body mass as controlling variable. All analyses were conducted using SPSS 12.0 for Windows.

## Phylogenetically based statistical analyses

Closely related species that share a common ancestry cannot be regarded as statistically independent. To account for this historical dependence of species, the method of standardized independent contrasts was used (Felsenstein, 1985), using the PDTREE program/PDAP package (Garland et al., 1999; Garland and Ives, 2000). The phylogenetic tree used in our analyses (see Fig. 1) is based on the most recent available phylogenies. The position of the families follows Townsend et al. (2004). The position of iguanian families is based on Schulte et al. (2003). Topology of the phrynosomatid lizard genera was taken from the combined data tree of Reeder and Wiens (1996). The phylogeny within *Sceloporus* was based on Wiens and Reeder (1997). Phylogeny of the anoles was taken from Nicholson et al. (2005). Phylogeny of the Teiidae is based on Reeder et al. (2002). The relationships among the *Ameiva* species follow Hower and Hedges (2003). Phylogeny of the Lacertidae follows Fu (2000). Some unresolved polytomies remain. This was taken into account by subtracting one degree of freedom for each unresolved node (Purvis and Garland, 1993).

Mostly, only rough estimates of divergence times or genetic distances are available. We therefore set all branch lengths to unity. It has been shown that the actual length of the branches does not usually have substantial effects on the results of phylogenetic analyses (Martins and Garland, 1991; Díaz-Uriarte and Garland, 1998). Checking branch lengths with the PDTREE program did not show any significant correlation between the absolute values of the standardized contrasts and their standard deviations (Garland et al., 1992).

Then, correlations among the independent contrasts of the logarithmically transformed body mass, HR size, PTM and MPM were calculated. The multiple regression model used for this was forced through the origin (see Garland et al., 1992). To account for the dependence of HR size on body mass, the residuals of the regression of standardized contrasts of HR size on the standardized contrasts of body mass were correlated with the contrasts of PTM and the contrasts of MPM, forcing this regression through the origin.

Finally, in order to summarize the analyses mentioned above, we combined the probabilities for males and females of all previous tests (see Fisher, 1954).

# Results

For 36 species in our foraging mode data set, HR data were available in the literature. For 35 of those species, we found HR estimates for both sexes. For one species, *Psammodromus algirus*, only HR data of males were available.

Not all foraging studies reported both MPM and PTM. Estimates of MPM (in combination with HR data) were available for 34 species, as were values for PTM data (see Table 2 for the values used in the analyses).

## Conventional analyses

In both sexes similar patterns were found in the relations between variables: MPM correlates positively with PTM; larger species had larger HR and lizards with high values of PTM had larger HR. No correlation was found between MPM and HR size (see Table 3).

The partial correlation between $\log_{10}$(HR), corrected for body mass, and $\log_{10}$(PTM) was significant in females ($\mathrm{df} = 27$; $r = 0.43$; $p = 0.02$) and nearly significant in males ($\mathrm{df} = 28$; $r = 0.35$; $p = 0.056$). When corrected for body mass, $\log_{10}$(HR) and $\log_{10}$(MPM) were not correlated (males: $\mathrm{df} = 28$; $r = 0.003$; $p = 0.99$; females: $\mathrm{df} = 27$; $r = 0.13$; $p = 0.50$).

## Phylogenetic analyses

The independent contrasts of mass and HR size correlated positively in both males and females, as did the contrasts of $\log_{10}$(PTM) and $\log_{10}$(MPM). Also, the contrasts of PTM and HR size correlated positively in both sexes (see Table 4).

The residuals of the contrasts of $\log_{10}$(HR) versus the contrasts of $\log_{10}$(mass) correlated positively and nearly significantly with the contrasts of $\log_{10}$(PTM) in males ($F = 3.73$; $r = 0.34$; $\mathrm{df} = 1,28$; $p = 0.063$) and

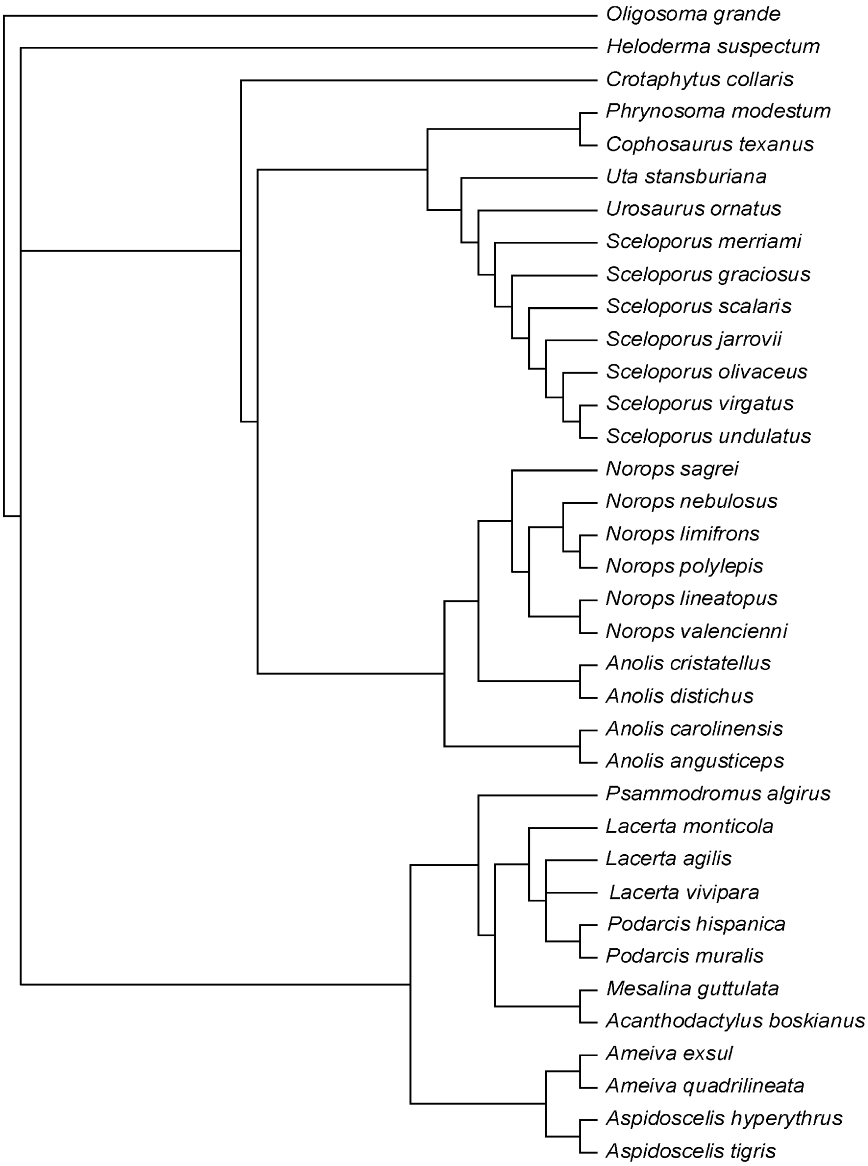

**Fig. 1.** Phylogenetic tree used in our analyses. This composite tree is a currently best approximation (see text for references). The depicted branch lengths are arbitrary in the analyses, all branch lengths were set to unity.

marginally in females ($F = 3.12$; $r = 0.32$; df = 1,27; $p = 0.089$). The contrasts of MPM correlated negatively, but not significantly with the contrasts of HR size (see Table 4). The residuals of the contrasts of $\log_{10}$(HR) versus the contrasts of $\log_{10}$(mass) did not correlate with the contrasts of $\log_{10}$(MPM) in either sex (males: $F = 1.77$; $r = 0.24$; df = 1,28; $p = 0.19$; females: $F = 0.95$; $r = 0.18$; df = 1,27; $p = 0.34$).

Combining probabilities yielded similar results. However, the relationship between PTM and HR size, when corrected for body mass, appeared to be significant ($\chi^2 = 13{,}59$; df = 4; $p < 0.01$), also when taking phylogenetic relationships into account ($\chi^2 = 10.37$; df = 4; $p < 0.05$).

## Discussion

When considering the possible relationship between foraging mode and HR size, our first expectation was that the more active species might need larger HR areas to meet their higher energetic requirements inherent to their higher level of activity than SW species with the same body mass. Other specific characteristics of an AF mode might amplify this trend still further (see the Introduction). However, other foraging mode characteristics as its efficiency and prey encounter rate might dim or even counter this effect. An entirely opposite view on the foraging activity/HR size relationship has also been put forward by considering typical

**Table 2.** Species included in this study. Mass (in g), home range (in m$^2$), home range computation method, number of individuals used in the home range study (#ind), MPM, PTM. Abbrev.: Sex: M = male; F = female; home range computation method: 1 = (maximum) convex polygon; 2 = minimum polygon; 3 = Jennrich and Turner (1969) correction; 4 = radii recapture; 5 = density; 6 = by hand; 7 = ellipse; 8 = Schoener (1981) regression; 9 = unknown; FAM = family: 1 = Crotaphytidae; 2 = Helodermatidae; 3 = Lacertidae; 4 = Phrynosomatidae; 5 = Polychrotidae; 6 = Scincidae; 7 = Teiidae; mass = mean body mass; home range = mean home range size

| GENUS | SPECIES | FAM | Sex | Mass | Home range | Method | #ind | MPM | PTM |
|---|---|---|---|---|---|---|---|---|---|
| *Crotaphytus* | *collaris* | 1 | M | 35 | 1311 | 2 | 15 | 0.09 | 0.40 |
| *Crotaphytus* | *collaris* | 1 | F | 35 | 367.9 | 2 | 38 | | |
| *Heloderma* | *suspectum* | 2 | M | 600 | 494000 | 1 | 2 | | 21.50 |
| *Heloderma* | *suspectum* | 2 | F | 600 | 56000 | 1 | 1 | | |
| *Acanthodactylus* | *boskianus* | 3 | M | 8.3 | 469.5 | 1 | 9 | 2.01 | 28.80 |
| *Acanthodactylus* | *boskianus* | 3 | F | 8.3 | 264.4 | 1 | 3 | | |
| *Lacerta* | *agilis* | 3 | M | 31.4 | 648 | 1 | 7 | 0.21 | 1.59 |
| *Lacerta* | *agilis* | 3 | F | 31.4 | 398 | 1 | 7 | | |
| *Lacerta* | *monticola* | 3 | M | 8.6 | 62.3 | 1 | 12 | 3.04 | 19.10 |
| *Lacerta* | *monticola* | 3 | F | 6.5 | 50.3 | 1 | 39 | | |
| *Lacerta* | *vivipara* | 3 | M | 3.1 | 584.2 | 3 | 8 | 4.20 | 33.20 |
| *Lacerta* | *vivipara* | 3 | F | 3.7 | 563.9 | 3 | 18 | | |
| *Mesalina* | *guttulata* | 3 | M | 2.5 | 626.7 | 4 | 15 | 0.15 | 30.50 |
| *Mesalina* | *guttulata* | 3 | F | 2.5 | 472.7 | 4 | 11 | | |
| *Podarcis* | *hispanica* | 3 | M | 5.4 | 132.3 | 1 | 17 | 3.12 | 21.39 |
| *Podarcis* | *hispanica* | 3 | F | 4 | 86.5 | 1 | 4 | | |
| *Podarcis* | *muralis* | 3 | M | 7.6 | 26 | 6 | 18 | 3.05 | 20.54 |
| *Podarcis* | *muralis* | 3 | F | 5 | 23 | 6 | 65 | | |
| *Psammodromus* | *algirus* | 3 | M | 12.9 | 397.4 | 1 | 11 | 2.95 | 20.68 |
| *Cophosaurus* | *texanus* | 4 | M | 9.1 | 194.3 | 2 | 2 | 0.46 | 2.30 |
| *Cophosaurus* | *texanus* | 4 | F | 7.1 | 263 | 2 | 4 | | |
| *Phrynosoma* | *modestum* | 4 | M | 17 | 4101 | 7 | 15 | 0.12 | 15.10 |
| *Phrynosoma* | *modestum* | 4 | F | 17 | 1355 | 7 | 11 | | |
| *Sceloporus* | *graciosus* | 4 | M | 6.5 | 425 | 1 | 3 | 1.31 | 5.84 |
| *Sceloporus* | *graciosus* | 4 | F | 6.5 | 463.3 | 1 | 3 | | |
| *Sceloporus* | *jarrovii* | 4 | M | 11.5 | 132 | 1 | 11 | 0.34 | 0.90 |
| *Sceloporus* | *jarrovii* | 4 | F | 11.5 | 39 | 1 | 16 | | |
| *Sceloporus* | *merriami* | 4 | M | 4.3 | 138.2 | 2 | 57 | 1.07 | 2.51 |
| *Sceloporus* | *merriami* | 4 | F | 3.7 | 53.7 | 2 | 29 | | |
| *Sceloporus* | *olivaceus* | 4 | M | | 683.9 | 1 | 141 | 0.62 | 1.98 |
| *Sceloporus* | *olivaceus* | 4 | F | | 291.4 | 1 | 265 | | |
| *Sceloporus* | *scalaris* | 4 | M | 2.8 | 144.5 | 1 | 13 | 0.24 | 0.42 |
| *Sceloporus* | *scalaris* | 4 | F | 4.1 | 76.8 | 1 | 19 | | |
| *Sceloporus* | *undulatus* | 4 | M | 3.8 | 121.1 | 1 | 15 | 0.29 | 0.81 |
| *Sceloporus* | *undulatus* | 4 | F | 3.8 | 101.1 | 1 | 19 | | |
| *Sceloporus* | *virgatus* | 4 | M | 5.5 | 287 | 1 | 9 | 0.38 | 0.8 |
| *Sceloporus* | *virgatus* | 4 | F | 5.5 | 102.0 | 1 | 12 | | |
| *Urosaurus* | *ornatus* | 4 | M | 4.1 | 30.99 | 1 | 11 | 0.66 | 2.30 |
| *Urosaurus* | *ornatus* | 4 | F | 3 | 19.2 | 1 | 23 | | |
| *Uta* | *stansburiana* | 4 | M | 1.5 | 446 | 1 | 15 | 0.18 | 0.60 |
| *Uta* | *stansburiana* | 4 | F | 2.3 | 121 | 1 | 15 | | |
| *Anolis* | *angusticeps* | 5 | M | 2.6 | 11.5 | 8 | 7 | 0.72 | 2.12 |
| *Anolis* | *angusticeps* | 5 | F | 1.5 | 5 | 8 | 4 | | |
| *Anolis* | *carolinensis* | 5 | M | 5.5 | 51 | 1 | 7 | 0.86 | 7.04 |
| *Anolis* | *carolinensis* | 5 | F | 2.9 | 8 | 1 | 23 | | |
| *Anolis* | *cristatellus* | 5 | M | 7.7 | 3.4 | 1 | 19 | 0.36 | 0.83 |
| *Anolis* | *cristatellus* | 5 | F | 1.9 | 4.4 | 1 | 4 | | |
| *Anolis* | *distichus* | 5 | M | 2.5 | 19 | 8 | 9 | 0.24 | |
| *Anolis* | *distichus* | 5 | F | 1.8 | 15.4 | 8 | 10 | | |
| *Norops* | *limifrons* | 5 | M | 2.7 | 8.5 | 4 | 21 | 0.61 | 1.59 |
| *Norops* | *limifrons* | 5 | F | 2.7 | 3.7 | 4 | 30 | | |
| *Norops* | *lineatopus* | 5 | M | 6.7 | 0.6 | 1 | 8 | 0.38 | 0.48 |

**Table 2.** (*continued*)

| GENUS | SPECIES | FAM | Sex | Mass | Home range | Method | #ind | MPM | PTM |
|---|---|---|---|---|---|---|---|---|---|
| *Norops* | *lineatopus* | 5 | F | 0.7 | 1.4 | 1 | 2 | | |
| *Norops* | *nebulosus* | 5 | M | 1.7 | 2 | 1 | 25 | 0.07 | |
| *Norops* | *nebulosus* | 5 | F | 1 | 0.6 | 1 | 27 | | |
| *Norops* | *polylepis* | 5 | M | 3.9 | 34 | 1 | 6 | 0.36 | 1.20 |
| *Norops* | *polylepis* | 5 | F | 2.5 | 7 | 1 | 9 | | |
| *Norops* | *sagrei* | 5 | M | 3.2 | 10.1 | 8 | 13 | 0.25 | 0.64 |
| *Norops* | *sagrei* | 5 | F | 1.4 | 1.6 | 8 | 29 | | |
| *Norops* | *valencienni* | 5 | M | 8.6 | 25 | 9 | 1 | 0.82 | 7.15 |
| *Norops* | *valencienni* | 5 | F | 6.1 | 30.1 | 9 | 6 | | |
| *Oligosoma* | *grande* | 6 | M | | 39.1 | 2 | 10 | 1.5 | 4.60 |
| *Oligosoma* | *grande* | 6 | F | | 31.3 | 2 | 22 | | |
| *Ameiva* | *exsul* | 7 | M | | 376.8 | 1 | 15 | 2.18 | 32.10 |
| *Ameiva* | *exsul* | 7 | F | | 173.7 | 1 | 13 | | |
| *Ameiva* | *quadrilineata* | 7 | M | 14.7 | 445.2 | 1 | 8 | 1.56 | 31.90 |
| *Ameiva* | *quadrilineata* | 7 | F | 14.1 | 187.7 | 1 | 13 | | |
| *Aspidoscelis* | *hyperythra* | 7 | M | 5.5 | 421.2 | 1 | 8 | | 67.97 |
| *Aspidoscelis* | *hyperythra* | 7 | F | 5 | 306 | 1 | 7 | | |
| *Aspidoscelis* | *tigris* | 7 | M | 20 | 720 | 1 | 15 | 0.14 | 87.00 |
| *Aspidoscelis* | *tigris* | 7 | F | 16.5 | 400 | 1 | 8 | | |

reproductive strategies. Perry and Garland (2002) found larger HRs in territorial families that are also generally SW and they made reference to Stamps (1977 and 1983b) to ground this. Stamps (1977) found that territoriality mostly occurs among SW foragers, while AF species are generally non-territorial or defend only specific sites within their HRs. During the reproductive season, male AF lizards rather try to pursue and guard females instead of keeping watch over a territory. The result is that male and female HR sizes are more or less the same, or can be understood as primarily reflecting metabolic needs. SW males, on the other hand, try to occupy a territory that encloses more female HRs, thus possessing larger HRs than can be expected on the base of energetic needs alone. In this way, one could indeed expect male SW lizards to have larger HRs than male AF lizards, but for females there is no reason why this should also be the case.

On the other hand, AF males might still move widely to court more females, if they have the opportunity to do so (for example when reproductive synchronicity is low among females). Female AF lizards might be spaced out more widely than comparable-sized SW females, in accordance with our first expectation. This would induce the AF male willing to court more females to wander around more widely than a comparable-sized SW male trying to monopolise a certain number of relatively compact female territories. Further, such an SW male could not afford a territory that is too large, without increasing substantially its patrolling activity, and thereby adopting a lifestyle that is more AF-like, as has actually been reported (Pietruszka, 1986). It would be most welcome if these differences in mating systems were linked quantitatively with foraging activity (PTM and MPM). Anyway, when taking into account more detailed phylogenetic information Perry and Garland (2002) found no difference in HR size going with a broad foraging mode classification and they concluded that energetics (through body mass), rather than foraging mode, might be determinative for HR size.

However, our analysis shows that foraging activity might exert a considerable influence on HR area. When corrected for body mass, PTM shows a positive relationship with HR size. An AF lizard thus occupies a larger HR size than an SW lizard of the same size. On the other hand, MPM does not at all show such a relation with HR size. Although SW lizards in general tend to have lower MPM values than AF species, PTM may be the better comparative measure to describe foraging activity (Cooper et al., 2001), and because it partly reflects energy investment in foraging, it is probably the more relevant in a comparison with HR size, which largely reflects energetic requirements as well. MPM, on the other hand, does not say anything about the nature of the movements it describes: movements may be scarce, but take a lot of time (going with a high PTM), or may be numerous but short, with the total time in movement limited. So, some AF species may display low MPM, while some SW lizards may exhibit relatively high MPM. In the first case, high energy consumption and covering of a substantial distance while on the move may be expected to go with large HR, while this does not necessarily apply to the second case. Clearly, in order to account for energetic

**Table 3.** Conventional Pearson correlations between mass, HR size and foraging variables

| | Variable 1 | Variable 2 | $R$ | $N$ | $P$ |
|---|---|---|---|---|---|
| Males | $\log_{10}$mass | $\mathrm{Log}_{10}$HRsize | 0.68 | 33 | $<0.001$ |
| | $\log_{10}$PTM | $\mathrm{Log}_{10}$HRsize | 0.42 | 34 | 0.01 |
| | $\log_{10}$MPM | $\mathrm{Log}_{10}$HRsize | 0.03 | 34 | 0.87 |
| | $\log_{10}$PTM | $\mathrm{Log}_{10}$MPM | 0.53 | 32 | 0.002 |
| Females | $\log_{10}$mass | $\mathrm{Log}_{10}$HRsize | 0.83 | 32 | $<0.001$ |
| | $\log_{10}$PTM | $\mathrm{Log}_{10}$HRsize | 0.48 | 33 | 0.005 |
| | $\log_{10}$MPM | $\mathrm{Log}_{10}$HRsize | 0.09 | 33 | 0.63 |
| | $\log_{10}$PTM | $\mathrm{Log}_{10}$MPM | 0.51 | 31 | 0.004 |

consumption by movement, not only the time moving, but also the velocity of the movements would have to be known (Bennett and Gleeson, 1979), and this is sometimes reported to characterise foraging behaviour (e.g. Huey and Pianka, 1981; Cooper et al., 2005), but in general, such data are rare.

We found a positive correlation between PTM and HR size, corrected for body mass, in both sexes, although this relationship was not always statistically significant. This may be due to several reasons. Firstly, the data set we put together might just be too small to demonstrate this relationship between the variables. A quite impressive amount of data on both lizard foraging and lizard HR areas is by now available in the literature, but the overlap in species remains rather limited. Inclusion of more data might overcome this problem.

In the second place, noise in the type of data that constitute our data set may be considerable. In general, the attribution of one PTM and MPM value per species is an oversimplification of real behaviour. Foraging behaviour of a species or even an individual is not at all fixed and is related to spatiotemporal variation in resource availability (see Huey and Pianka, 1981; Pietruszka, 1986; Avery, 1993; Greeff and Whiting, 2000; Butler, 2005). Similar concerns apply to HR size estimates. HR size can be affected by a lot of ecological factors and space usage patterns can vary considerably within species and even populations (see reviews in Stamps, 1977, 1983b; Christian and Waldschmidt, 1984; Martins, 1994). Only the very broadest patterns may be detectable when using data collected on the base of such diverse methods, sample sizes, time intervals and in different environmental conditions as used in this study. Further, we largely left out of consideration other biological and ecological factors (morphotype, prey preferences, predatory pressure, microhabitat selection) that also may exert an influence on both foraging behaviour and HR characteristics of such different species as those constituting our data set. Clearly, the ideal comparative study would compare foraging mode and HR size of a range of closely related species controlling for environmental conditions and other factors that may act on both variables.

**Table 4.** Correlations between independent contrasts of mass, HR size and foraging variables

| | Contrast 1 | Contrast 2 | $r$ | $N$ | $P$ |
|---|---|---|---|---|---|
| Males | $\log_{10}$mass | $\log_{10}$HRsize | 0.66 | 31 | $<0.001$ |
| | $\log_{10}$PTM | $\log_{10}$HRsize | 0.37 | 32 | 0.03 |
| | $\log_{10}$MPM | $\log_{10}$HRsize | $-0.24$ | 32 | 0.22 |
| | $\log_{10}$PTM | $\log_{10}$MPM | 0.38 | 30 | 0.02 |
| Females | $\log_{10}$mass | $\log_{10}$HRsize | 0.8 | 30 | $<0.001$ |
| | $\log_{10}$PTM | $\log_{10}$HRsize | 0.41 | 31 | 0.02 |
| | $\log_{10}$MPM | $\log_{10}$HRsize | $-0.18$ | 31 | 0.37 |
| | $\log_{10}$PTM | $\log_{10}$MPM | 0.37 | 29 | 0.02 |

A third caveat might be that when looking for correlations of HR size with PTM and MPM in both sexes separately, we mostly used PTM and MPM values reported for the species, not taking into account the possible intersexual differences in foraging behaviour. Such differences have been reported (e.g. Anderson and Karasov, 1981; Karasov and Anderson, 1984; Durtsche, 1992; Perry, 1996; Eifler and Eifler, 1999), but only rarely, and most studies typify a species by one general MPM and PTM. For the species used in this study, such foraging data for both sexes are only available for very few species indeed (Karasov and Anderson, 1984; Perry, 1996; Eifler and Eifler, 1999; own observations). On the other hand, intersexual differences in mean foraging variables are mostly limited, at least outside the reproductive season (Karasov and Anderson, 1984; Perry, 1996; Eifler and Eifler, 1999).

Nevertheless, despite the possible pitfalls in such data, we believe the above tendencies indicate a real relationship in both male and female lizards, only to be substantiated when more available data will be included. In any case, combination of the results for both sexes yielded significant results, and we conclude that in lizards, HR size correlates positively with foraging activity level (PTM). This may as well apply to other animal groups.

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