Home-range ecology, aggressive behaviour, and survival in juvenile lizards, *Psammodromus algirus*

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Abstract: Individual animals are assumed to gain possession of areas where they win fights or chases, while those that lose agonistic interactions leave areas where they were defeated. Thus, the more dominant animal secures the territory, often excluding subordinates from optimal habitat. This assumption forms the basis for concluding that the degree of aggressiveness or relative dominance of an individual may be important in determining the size or quality of a territory that it can secure. I examined in the field the relationships between home-range size, quality of home range, and degree of aggressiveness and their effects on survivorship in juvenile male lizards (*Psammodromus algirus*). The degree of aggressiveness was determined using tethered intruders presented to resident individuals in the field. The more aggressive individuals had larger home ranges than the less aggressive ones. Furthermore, home-range size and vegetative cover in the home range also influenced the probability of survival: survivors had larger home ranges, with a greater amount of vegetative cover, than nonsurvivors.

Résumé : On suppose généralement que les individus prennent possession des sites sur lesquels ils gagnent les batailles ou les poursuites, alors que les animaux perdants au cours d'interactions agonistiques quittent les sites où ils ont été vaincus. Il s'ensuit que l'animal dominant occupe le territoire, ce qui signifie que souvent les animaux subordonnés sont exclus des habitats optimaux. Cette supposition est à la base de l'hypothèse selon laquelle le degré d'agressivité d'un individu ou sa dominance relative peut influencer fortement la taille ou la qualité du territoire qu'il peut acquérir. J'ai examiné en nature la relation entre la taille du domaine vital, sa qualité et le degré d'agressivité et leurs effets sur la survie chez des lézards juvéniles (*Psammodromus algirus*).Le degré d'agressivité a été évalué en présentant des intrus attachés à des individus résidants sur le terrain. Les individus les plus agressifs avaient des domaines plus grands que les individus moins agressifs. De plus, la taille du domaine et la structure de la végétation dans le domaine influençaient également la probabilité de survie : les survivants avaient des domaines plus grands avec une plus grande couverture de végétation que les individus qui n'ont pas survécu.

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Introduction

Home-range size in lizards may be affected by many factors, such as sex, body size, foraging behaviour, population density, energetic requirements, and social behaviour (Rose 1982). However, little is known about the patterns of territory acquisition and the factors that affect the success of territory acquisition by juveniles (see Stamps 1994). One of the most common assumptions about territorial animals is that individuals acquire space by winning contests (Maynard Smith and Parker 1976; Krebs 1982; Maynard Smith 1982; review in Stamps 1994; Stamps and Krishnan 1994). That is, individuals are assumed to gain possession and become owners of areas where they win fights or chases, while animals that lose agonistic interactions leave areas where they were defeated. Thus, the more dominant animal secures the territory, often excluding subordinates from optimal habitat (Krebs 1971; King 1973). This assumption forms the basis for concluding that the degree of aggressiveness or relative dominance of a lizard may be important in determining the size or quality of a territory that it can secure.

Body size is strongly associated with home-range size in lizards (Turner et al. 1969; Christian and Waldschmidt 1984). Various authors have explained this close relationship between home-range size and body size on the basis of such factors as food requirements, foraging costs, and food density (MacNab 1963; Schoener 1968). Some studies have examined the effects of body size on survival of juvenile lizards and showed that larger individuals have an advantage over smaller ones (Fox 1978; Ferguson and Fox 1984; Civantos et al. 1999). Aggressiveness may also be influenced by body size, and differences in body size among juveniles are likely to affect their interactions with conspecifics during the acquisition of optimal home ranges. A larger body size and a greater degree of aggressiveness usually influence dominance relationships and confer an advantage in gaining access to resources (Archer 1988). Body size is correlated with strength and is an important factor in explaining the outcome of animal conflicts (Beaugrand and Zajan 1985).

Social factors can greatly influence home-range size and use of space in lizards (Stamps 1977*b*; Rose 1982; Schoener and Schoener 1982) and may be responsible for much of the observed variation in home-range size. A larger home range may be an indicator of a higher survival rate, because home-range size may be influenced by some characters that

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improve fitness. A few lizard studies also indicate that the degree of aggressiveness may be related to territory size or quality. In some species, more aggressive individuals are more successful in resource competition. For example, more aggressive side-blotched lizards (*Uta stansburiana*) increased the size and quality of their home ranges (Fox 1983).

However, few studies address the hypothetical benefits of a larger and (or) higher quality home range (Schoener and Schoener 1982). The evaluation of habitat quality is a central topic in contemporary ecological studies and requires the integration of a large number of synergistic factors (e.g., physical constraints, predation risk, mating opportunities, resource availability) (Huey 1991). A high-quality home range may be defined by its greater microhabitat diversity or the prevalence of favourable microhabitat characteristics (Fox 1978). Selective exploitation of microhabitats allows many lizards to maintain body temperature within a range that optimizes physiological capacities and, ultimately, ecological performance (Huey 1991). Also, some microhabitats may provide better refuge against predators or access to higher quality food (Martin and Salvador 1992). Thus, microhabitat use may have a direct effect on lizard survival (Tracy 1982). Additionally, activity levels may impinge on survival. Activity is vital for resource acquisition by lizards. However, in few studies have data on the activity of juveniles been collected because the small size of juveniles makes them difficult to locate.

I examined the relationships between degree of aggressiveness, home-range size, and vegetative cover in the home range and their effects on survival of juvenile male *Psammodromus algirus*. Juvenile *P. algirus* that are territory owners typically defend their entire home range against unfamiliar intruders, and defend most or all of their home range against neighbouring territory owners (E. Civantos, unpublished data). This paper relates aggressive behaviour of residents to home-range ecology and survival.

Material and methods

Psammodromus algirus is a medium-sized terrestrial, diurnal, oviparous lizard that inhabits the Iberian Peninsula, southern France, and northwestern Africa. *Psammodromus algirus* in my study population inhabiting a mountain area in central Spain (see below) enter hibernation in late October and emerge in early March. Hatchlings hatch between late August and early October, with variation among years, depending on weather conditions. Individuals become sexually mature in their second spring, when the snout–vent length (SVL) is 65–70 mm (E. Civantos, unpublished data). Adult body size varies among populations, but SVL seldom exceeds 90 mm.

The study was conducted in a deciduous oak forest near Navacerrada, Madrid Province, central Spain, during March–May 1997. Vegetation included small deciduous oak trees (*Quercus pyrenaica*), well-developed low sapling scrub oaks (*Q. pyrenaica*), and less abundant and dispersed perennial evergreen bushes (*Cistus laurifolius*). The forest contains some isolated patches of large rocks, bare ground, and grass.

The entire study period extended from February to June 1997. In February 1997, I delimited a 30 × 30 m plot that was divided into a grid with markers every 5 m. I visited the plot 5 days a week between 26 February and 16 March, and searched for juvenile male lizards (born in 1996) by walking over the plot between 09:30–13:30 and 16:00–17:00. Individuals were captured by hand and marked by toe-clipping for permanent identification. At each census, the point where individuals were first sighted was mapped. All individuals were taken to El Ventorrillo field station, where they were weighed to the nearest 0.01 g with an electronic balance and their SVL was measured to the nearest 0.5 mm with a ruler. Individuals were given two or three paint spots on the back for individual identification. They were released during the same day at the capture point. Only individuals sighted inside the plot during March were considered residents.

Between 26 February and 16 March, I performed several censuses per day over the study plot and mapped the position of each individual sighted with respect to the grid markers. I attempted to randomize the time of day and direction of these censuses. The home range of each lizard was defined by the convex polygon surrounding all observation points (Rose 1982). To minimize dependency between repeated observations of single individuals, I recorded the location of each individual only once each day. I estimated that six points per individual were enough to encompass the home range (Rose 1982). The number of points per individual was 9.5 ± 0.77 (mean ± SE) and ranged from 6 to 15. Thus, home-range areas were determined from consecutive resightings of individuals, and not from points of defense. I refer to these areas, therefore, as home ranges rather than territories.

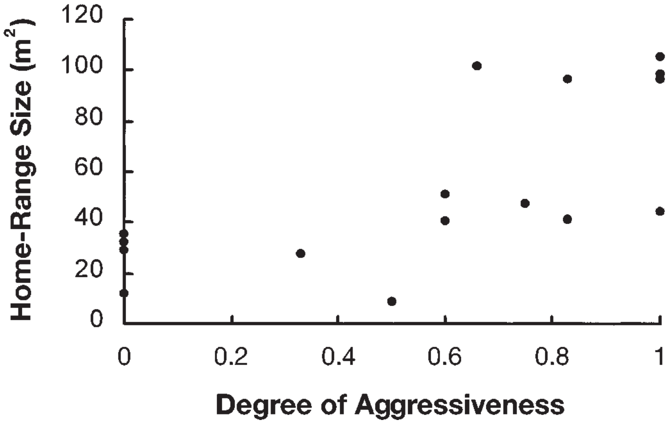
In March, after I had delineated the home range of each individual, I used four transects (one in each of the four cardinal directions from the center of home range) over it to quantify its microhabitat features. I used a scored stick held vertically at 1-m intervals and recorded contacts of the stick with grass, leaf litter, bare soil, or rocks at ground level. Rocks were scored according to size, as <50 cm or >50 cm in diameter. Using the same procedure I recorded the number of plant contacts with the stick at heights of 5, 10, 25, 50, and 100 cm. This procedure allowed me to calculate for each home range the percent cover values for each habitat variable (i.e., percentage of contacts with each substratum and with vegetation at each height). For each lizard, a standard Shannon's diversity index (H) (Shannon and Weaver 1949) value of microhabitat diversity at ground level and diversity of vegetation heights over the five heights was calculated.

Focal observations of marked lizards were made in the field (during 15-min periods) with binoculars from a distance of 3–4 m between 31 March and 15 April. Observations were made on sunny days between 11:00–1300 and 16:00–17:00. Observation time per individual was 30.69 ± 1.50 min (mean ± 1 SE), ranging from 15 to 45 min. During each observation period I recorded the time spent by each individual in each microhabitat at substratum level (bare soil, grass, leaf litter, and rocks). I also noted the total number of movements, the number of movements within each type of microhabitat, total distance moved, and total distance moved in each microhabitat. I tallied a movement when a lizard moved for more than 2 s and walked more than 3 cm. I expressed time spent in each microhabitat as the percentage of total observation time and activity as frequency of movement (moves/s); distance moved is given in centimetres.

During May–June 1997, I searched the plot and the surroundings (in a 50 m wide band) on 5 days a week to identify surviving lizards. All vegetation was shaken and debris lifted on each walk to ensure as complete a search as possible.

Because I saw few agonistic interactions between juvenile lizards during focal observations, I quantified the degree of intraspecific aggressiveness using tethered intruders presented to residents, following Stamps (1977*a*, 1978). I used individuals of the same age-class captured at least 200 m from the study plot as intruders. The intruder was tethered around the abdomen with a dark nylon thread, 2 m long and 0.1 mm thick, attached to a stick, and then placed 20 cm from a resident; the stick was fixed to restrict the intruder's movements. I moved back 3 m and observed the resident for 5 min through binoculars, recording the first response of the resident. In

Fig. 1. Relationship between home-range size and degree of aggressiveness (frequency of aggressive responses to intruders).



the first test, I introduced an intruder matched in size to the resident (<5% difference in SVL). I recorded the resident's first response to the intruder as aggression (if the resident chased, displayed toward, bit, or approached the intruder) or nonaggressive (if the resident avoided or ignored the intruder or fled). In a second test conducted 1 week later, I presented several intruders of various sizes (range 27–41.5 mm SVL) to each resident. In this test I recorded the first response of residents to the tethered intruder, and I expressed degree of aggressiveness as the frequency of aggressive responses to all intruders. The goal of this second test was to determine if individuals that were aggressive in the first test were also aggressive toward other intruders that were not matched in size. I presented 3.5 ± 0.6 (mean ± 1 SE) intruders to each resident (range 2–8) at the rate of one intruder per day. The number of presentations did not differ significantly between eventual survivors and nonsurvivors (Mann–Whitney *U* test, $U = 19.5$, $P = 0.25$).

I used the results of the first test to classify each resident as aggressive or nonaggressive because each subject was given a comparable stimulus (a same-sized tethered intruder). I used nonparametric statistics to analyze all variables with the exception of home-range area (log-transformed), which was normally distributed according to the Lillieford's test. Reported probabilities are not adjusted for multiple comparisons, but the reported significance was verified, where appropriate, using the sequential Bonferroni adjustment of Rice (1989) for multiple comparisons (Chandler 1995).

Results

Between 26 February and 16 March, I captured 16 juveniles on the plot. Their initial SVL was 33.4 ± 0.66 mm (mean ± SE) (range 27–39 mm) and their mass 0.9 ± 0.06 g (range 0.47–1.55 g). In March and April all 16 individuals were still on the plot, but in June only 10 remained. During May I did not find any marked individuals in the 50 m wide band surrounding the plot, therefore I assumed that the missing individuals had not survived.

Home range and aggressiveness

Of the 16 residents, 9 were classified as aggressive and 7 as nonaggressive. SVL and mass of aggressive individuals (35.16 ± 1.28 mm (mean ± SE) and 1.08 ± 0.13 g, respectively; $n = 9$) and nonaggressive individuals (32.6 ± 1 mm and 0.79 ± 0.06 g, respectively; $n = 7$) did not differ significantly (Mann–Whitney *U* test, SVL: $U = 22.5$, $P = 0.32$; mass: $U = 20$, $P = 0.22$). The home-range area of aggressive individuals (68.5 ± 9.3 m^2) was greater than that of nonaggressive individuals (35.9 ± 12.16 m^2) (one-way ANOVA, $F_{[1,15]} = 7.63$, $P = 0.015$). The correlation between home-range size and frequency of aggressive response also was statistically significant ($r_s = 0.5$, $P = 0.04$, $n = 16$; Fig. 1).

Home range, morphology, activity, and survival

The home-range area for survivors (72.22 ± 9.15 m^2; $n = 10$) was significantly greater than that for nonsurvivors (27.44 ± 4.12 m^2; $n = 6$) (independent *t* test, $t = –4.18$, df = 14, $P = 0.001$). Home-range size was not significantly correlated with SVL ($r_s = 0.05$, $n = 16$, $P = 0.8$), nor with mass ($r_s = 0.24$, $n = 16$, $P = 0.37$). SVL and mass were not different between survivors and nonsurvivors (SVL: 34 ± 0.75 mm, $n = 10$, vs. 32.5 ± 1.18 mm, $n = 6$, Mann–Whitney *U* test, $U = 24.5$, $P = 0.76$; mass: 1.06 ± 0.12 vs. 0.78 ± 0.08 g, Mann–Whitney *U* test, $U = 17.5$, $P = 0.17$).

There were no differences in microhabitat diversity at ground level between home ranges of survivors ($H = 0.60$, $n = 10$) and nonsurvivors ($H = 0.61$, $n = 6$) (Mann–Whitney *U* test, $U = 27$, $P = 0.74$). However, the diversity of vegetation height within home ranges was significantly greater for survivors ($H = 0.79$, $n = 10$) than for nonsurvivors ($H = 0.66$, $n = 6$) (Mann–Whitney *U* test, $U = 4.5$, $P = 0.0054$). Diversity of vegetation heights was significantly correlated with home-range size ($r_s = 0.63$, $n = 16$, $P = 0.008$). Microhabitat use, activity (moves/s), and distance moved (cm/s) did not differ significantly between survivors and nonsurvivors (Mann–Whitney *U* test, $P > 0.1$ in all cases).

Discussion

The more aggressive individuals in this study established larger home ranges than the less aggressive ones. Furthermore, the home ranges of survivors were larger, and had a greater diversity of vegetation heights (i.e., more complex cover), than those of nonsurvivors.

The significant correlation between home-range size and degree of aggressiveness suggests that more aggressive individuals might acquire more space by displacing neighbours. It seems likely that less aggressive individuals were competitively excluded and forced to remain in high-risk areas or in poor-quality habitat, and this could have affected their survival. In my study of 16 resident individuals, only 6 had disappeared from the study area by the end of May. It is possible that these six animals moved to another area, but it is more likely that they did not survive. Careful searching of areas near the study plot did not reveal them, and the normal death rate for this species (E. Civantos, unpublished data) could more than account for the disappearance of these juveniles. Of the 10 animals that remained within the study area, none moved to another area. This suggests that, at least in spring, once home ranges are established, most juveniles shift their use of space very little. Juveniles emigrating through unfamiliar areas might suffer a higher rate of predation than sedentary individuals. Emigration could occur later, if necessary. Ruby (1986), for example, suggested that mature *Sceloporus jarrovi* may shift their home ranges during the breeding season.

In studies with adult lizards, home-range size and body mass were significantly correlated (Turner et al. 1969; Christian and Waldschmidt 1984), but in this study with juveniles, although energy requirements increase with body size, home-range size and body mass (and SVL) were not significantly correlated. Other factors, such as variation in habitat productivity (Simon 1975; Ferguson et al. 1983) and distribution and variation in lizard density (Rose 1982), can affect home-range size. Also important is the degree of aggression. Despite the fact that body size and degree of aggression are usually correlated in lizards (Fox and Rostker 1982; Fox 1983), I found that SVL did not differ significantly between the aggressive and nonaggressive lizards in my study, but that the aggressive ones inhabited larger home ranges and survived better.

Advantages derived from holding a territory include access to an exclusive food supply and to choice basking sites, and other benefits not associated with reproduction. For example, territories are important to *S. jarrovi* for maintaining an adequate food supply (Simon 1975). Stamps (1978, 1984*a*, 1984*b*) identified at least four factors that might affect the value of a territory for juvenile *Anolis aeneus*: availability of food, availability of perches, insolation and temperature, and distance from potential predators. In my study, enhanced complexity of vegetative cover may well have been the aspect that directly impinged on survival of juveniles with larger home ranges, and not home-range size itself. Enhanced complexity of vegetative cover can influence the four factors mentioned above by making available a higher quality home range and this may explain why juvenile lizards compete for better space (i.e., higher quality home range). Fox (1978) showed that home ranges of surviving juvenile *U. stansburiana* contained a significantly greater diversity of plants and refuges than those of nonsurvivors. In my study, individuals having home ranges with more complex vegetative cover likewise survived better, and perhaps did so because they had access to a greater abundance of resources like prey, basking sites, and thermoregulatory refuges, and better opportunities to escape from predators. Individuals living in areas with low diversity of vegetation heights and more open spaces suffered higher mortality. Although there are many habitat-quality factors that can affect the fitness of a particular individual on its home range, in this study the difference in diversity of vegetation heights seems to be an important one.

The level of individual aggressiveness or relative dominance may be important in determining the size or quality of a territory an animal can secure and retain. This appears to be the case in some territorial birds (Watson and Miller 1971) and lizards (Brattstrom 1974; Ferner 1974; Fox 1978; Fox et al. 1981). My study shows differences between home ranges of surviving and nonsurviving juveniles, and indicates the importance of agonistic interactions in bringing about these differences. I suggest that aggressive behaviour might partly determine the size and quality of home range a juvenile lizard can procure, and the size and quality of the home range may influence the expressed behaviour of the lizard living there, and subsequently its survival.

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References

Archer, J. 1988. The behavioural biology of aggression. Cambridge University Press, Cambridge.

Beaugrand, J.P., and Zajan, R.C. 1985. An experimental model of aggressive dominance in *Xiphophorus helleri* (Pisces, Poeciliidae). Behav. Processes, **10**: 1–52.

Brattstrom, B.H. 1974. The evolution of reptilian social organization. Am. Zool. **14**: 35–49.

Chandler, C.R. 1995. Practical considerations in the use of simultaneous inference for multiple tests. Anim. Behav. **49**: 524–527.

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

Civantos E., Salvador A., and Veiga, J.P. 1999. Body size and microhabitat affect winter survival of hatchlings *Psammodromus algirus*. Copeia, 1999: 1112–1117.

Ferguson, G.W., and Fox, S.F. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. Evolution, **38**: 342–349.

Ferguson, G.W., Huges, J.L., and Brown, K.L. 1983. Food availability and territorial establishment of juvenile *Sceloporus undulatus*. *In* Lizard ecology: studies of a model organism. *Edited by* R.B. Huey, E.R. Pianka, and T.W. Schoener. Harvard University Press, Cambridge, Mass. pp. 134–148.

Ferner, J.W. 1974. Home range size and overlap in *Sceloporus undulatus erythrocheilus* (Reptilia: Iguanidae). Copeia, 1974: 332–337.

Fox, S.F. 1978. Natural selection on behavioral phenotypes of the lizard *Uta stansburiana*. Ecology, **59**: 834–847.

Fox, S.F. 1983. Fitness, home-range quality and aggression in *Uta stansburiana*. *In* Lizard ecology: studies of a model organism. *Edited by* R.B. Huey, E.R. Pianka, and T.W. Schoener. Harvard University Press, Cambridge, Mass. pp. 149–168.

Fox, S.F., Rose, E., and Myers, R. 1981. Dominance and the acquisition of superior home ranges in the lizard *Uta stansburiana*. Ecology, **62**: 888–893.

Fox, S.F., and Rostker, M.A. 1982. Social cost of tail loss in *Uta stansburiana*. Science (Washington, D.C.), **218**: 692–693.

Huey, R.B. 1991. Physiological consequences of habitat selection. Am. Nat. **137**: s95–s115.

King, J.A. 1973. The ecology of aggressive behavior. Annu. Rev. Ecol. Syst. **4**: 117–138.

Krebs, J.R. 1971. Territory and breeding density in the great tit, *Parus major.* Ecology, **52**: 1–22.

Krebs, J.R. 1982. Territorial defence in the great tit (*Parus major*): Do residents always win?. Behav. Ecol. Sociobiol. **11**: 185–194.

MacNab, B. 1963. Bioenergetics and determination of home range size. Am. Nat. **97**: 133–139.

Martin, J., and Salvador, A. 1992. Tail loss consequences on habitat use by the Iberian rock lizard, *Lacerta monticola*. Oikos, **65**: 328–333.

Maynard Smith, J. 1982. Evolution and theory of games. Cambridge University Press, Cambridge.

Maynard Smith, J., and Parker, G.A. 1976. The logic of asymmetric contests. Anim. Behav. **24**: 159–179.

Rice, W.R. 1989. Analysing tables of statistical tests. Evolution, **43**: 223–225.

Rose, B. 1982. Lizard home ranges: methodology and functions. J. Herpetol. **16**: 253–269.

Ruby, D.E. 1986. Selection of home range site by females of the lizard *Sceloporus jarrovi*. J. Herpetol. **20**: 466–469.

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

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

Simon, C.A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. Ecology, **56**: 993–998.

Shannon, C.E., and Weaver, W. 1949. The mathematical theory of communication. University of Illinois Press, Urbana.

Stamps, J.A. 1977*a*. The relationship between resource competition, risk and aggression in a tropical territorial lizard. Ecology, **58**: 349–358.

Stamps, J.A. 1977*b*. Social behavior and spacing patterns in lizards. *In* Biology of the Reptilia. Vol. 7. *Edited by* C. Gans and D. Tinkle. Academic Press, New York. pp. 265–334.

Stamps, J.A. 1978. A field study of the ontogeny of social behavior in the lizard *Anolis aeneus*. Behaviour, **66**: 1–31.

Stamps, J.A. 1984*a*. Rank dependent compromises between growth and predator protection in lizard dominance hierarchies. Anim. Behav. **32**: 1101–1107.

Stamps, J.A. 1984*b*. Growth cost of territorial overlap: experiments with juvenile lizards (*Anolis aeneus*). Behav. Ecol. Sociobiol. **15**: 115–119.

Stamps, J.A. 1994. Territorial behavior: testing the assumptions. Adv. Study Behav. **23**: 173–232.

Stamps, J.A., and Krishnan, V.V. 1994. Territory acquisition in lizards: II. Establishing social and spatial relationships. Anim. Behav. **47**: 1387–1400.

Tracy, C.R. 1982. Biophysical modelling in reptilian thermal physiology and ecology. *In* Biology of the Reptilia. Vol. 12. *Edited by* C. Gans and F.H. Pough. Academic Press, London. pp. 275–321.

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

Watson, A., and Miller, G.R. 1971. Territory size and aggression in a fluctuating red grouse population. J. Anim. Ecol. **40**: 367–383.