

## SPATIAL AWARENESS BY THE LIZARD *ANOLIS CRISTATELLUS*: WHY SHOULD A NON-RANGING SPECIES DEMONSTRATE HOMING BEHAVIOR?

THOMAS A. JENSSEN<sup>1</sup>

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

**ABSTRACT:** I performed a displacement experiment with free-ranging adults of *Anolis cristatellus*, a tropical lizard species whose year-around space-use requirements are limited to small arboreal territories. Because *A. cristatellus* is a relatively sedentary species, selection for a generalized spatial orientation would seem unlikely. However, more than two-thirds of 25 lizards returned to home territories within an average of 3 d when relocated 11–62 m (equivalent to 2–26 territory diameters) to presumably unfamiliar release localities. Within the conditions of the study, there was no significant effect on returning success by displacement distance, sex, or body size. The returning performance of *A. cristatellus* supported two inferences. First, considering the costs and risks of traveling through unfamiliar habitat, returning to a specific location from a distant release point indicated the relative importance of a familiar home range to survival and reproduction by both sexes. Second, returning performance indicated that *A. cristatellus* can at least generalize between familiar and unfamiliar views of landmarks to determine a novel route between its displaced site and its home locality (i.e., pilotage). I suggest that the spatial ability demonstrated by *A. cristatellus* has not been selected in the context of “homing,” a phenomenon absent to this non-ranging species. Instead, the spatial cognition demonstrated by pilotage could be selected as a social mechanism, whereby a resident can spatially place itself, mates, competitors, and predators relative to its three-dimensional home range. By avoiding surprise, a resident who can anticipate encountering specific individuals at particular localities within its home range will gain a social advantage.

**Key words:** Displacement experiment; Homing; Spatial cognition; Squamata

THE ABILITY of mobile animals to place themselves within their habitat relative to biotic and abiotic resources is critical for survival and reproduction. As animals move about, the scale of oriented movement patterns varies greatly between species, from several meters in the homing behavior of chiton (Chelazzi et al., 1987) to thousands of kilometers in marine turtles (Green, 1984). Not surprising, the ecological and life-history traits of species (e.g., diet, mode of locomotion, sensory modalities, body size, lifespan) are generally related to the capacity and means by which animals encode and derive spatial relationships from landmarks and other cues (Dingle, 1996; Dyer, 1998; Gallistel, 1990). In particular, size of activity range and relative familiarization with surroundings are two prominent factors that tend to reflect most ecological and life-history factors (Baker, 1978) and that influence selection for particular orientation/navigation mechanisms (Table 1).

In the evolution of sensory cues and information-processing mechanisms for spatial orientation, a basic premise is made that system complexity should not extend beyond the performance requirements of a species (i.e., “principle of least navigation”; Baker, 1978; Dyer, 1998). Consequently, animals whose lifetime activity ranges are small and mostly restricted to familiar habitat should adequately function using self-referenced orientation systems based on egocentric coordinates (i.e., objects and places specified with reference to the animal's own body). However, animals that range or migrate over large and frequently unfamiliar areas must incorporate externally-referenced orientation systems based on allocentric coordinates (i.e., objects, places, and the animal's own position specified with reference to an external set of positional cues). As a test of this logic, I chose to examine a small, diurnal, non-ranging species of lizard, *Anolis cristatellus*, which I predicted would be limited to an egocentric-based orientation system.

My hypothesis, that *A. cristatellus*

<sup>1</sup> CORRESPONDENCE: e-mail, tjenssen@vt.edu

TABLE 1.—Classification of homing phenomena (adapted from Papi, 1992 and Shuttleworth, 1998).

Term or strategy	Source of spatial information for an object or place with respect to mechanism
I. Egocentric Systems	Object information referenced relative to individual's coordinates
Random/systematic Search	Information unavailable
Genetic-based Orientation	Innately fixed vectors (sometimes distance) and non-memory taxis responses
Trail Following	Trail left from previous journey
Route-based Orientation	Outward journey (stimulus-response based navigation)
Route Reversal	Reversing a chained sequence of learned landmarks
Course Reversal	Reversing a compass direction without integration
Path Integration	Vectorial integration of distance and direction of each outward leg to plot a straight-line return (dead-reckoning)
II. Allocentric Systems	Object information referenced relative to external coordinates
Pilotage	Acquired topographic or cognitive map without a compass
True Navigation	Location-specific stimuli relative to a cognitive map, with compass-selected direction

should have no need for sophisticated means of orientation beyond that of egocentric localization (Table 1), was based on the following traits that tend to suggest limited movement: small body size, terrestrially bound to a tropical arboreal habitat, sit-and-wait insectivore, and year-around foraging and mating within a small defended home range (Fitch et al., 1989; Gorman and Licht, 1974; Philibosian, 1972, 1975; Schwartz and Henderson, 1991). These diurnal lizards rely on acute eyesight (typical of anoline lizards) for monitoring and interacting with prey, predators, conspecifics, and competitors (Fleishman, 1992; Leal and Rodriguez-Robles, 1997; Ortiz and Jenssen, 1982; Underwood, 1970). Because individuals could conceivably function within their territories by simply using immediate, visual landmarks, I anticipated that a displacement experiment would overwhelm their immediate spatial cues; the result would be the inability of relocated lizards to place themselves spatially at their new positions with respect to their now distant territories. Furthermore, if *A. cristatellus* is dependent on egocentric mechanisms for spatial orientation, then females, who are smaller than males (i.e., sexually dimorphic) and have smaller territories than males (Philibosian, 1975; Schwartz and Henderson, 1991), should become lost at shorter displacement distances than males. Without intending to examine specific proximate mechanisms, I systematically

displaced adults of *A. cristatellus* to find the limit to the hypothesized egocentric-based coordinate system by testing the following four alternative hypotheses ( $H_{1-4}$ ):

$H_1$ —Though males and females of *A. cristatellus* are territorial, site fidelity and/or orientation skills are weakly selected, such that no lizard displaced outside its territory will return;

$H_2$ —Homing ability is demonstrated by *A. cristatellus*, but displacement outside the immediate area of familiarization disrupts homing performance because spatial information and processing are restricted to immediate habitat cues;

$H_3$ —Homing ability is demonstrated by *A. cristatellus*, but it is limited in scope and more developed in males than in females because males have a broader landmark familiarization due to their larger territories than females (Philibosian, 1975) and are more capable of traversing longer distances due to being larger than females; and

$H_4$ —Homing ability is demonstrated by *A. cristatellus*, with some individuals of both sexes returning from all displacement distances of the study, suggesting that a familiar territory conveys a significant benefit and that *A. cristatellus* has a more generalized spatial ability than might be predicted from the immediate needs of the species.

#### METHODS

Relocation trials were run on 12 adult females (SVL  $\bar{x} \pm SE = 44.9 \pm 0.85$  mm)

and 13 adult males (SVL  $\bar{x} \pm \text{SE} = 61.7 \pm 1.12$  mm) of *A. cristatellus* during 17–24 December 1998 in dry coastal habitat at the southeast end (Punta Soldado) of Culebra (18° 17' N, 65° 18' W), a small island 28 km east of Puerto Rico. Relocations were made in subtropical dry forest/thorn shrub-land. Physically, the habitat was relatively homogeneous. Extensive clumps of shrubs (1–3 m high), containing scattered trees (3–7 m high), were separated by narrow strips of bare ground, grasses, and cacti.

Baseline space-use by *A. cristatellus* comes from observations in coastal vegetation in nearby Puerto Rico and St. Johns (Jenssen et al., 1984; Philibosian, 1972, 1975). Typically, a single, semi-isolated clump of arboreal habitat (e.g., a tree or shrub complex) serves as a permanent territory for an adult male and up to several adult females. Philibosian (1975) found the average surface area of the arboreal male and female territories to be 19 and 1.5 m<sup>2</sup>, respectively; if the surface areas are visualized as circles, the territorial diameters would be 4.9 and 1.6 m, respectively. These diameter estimates are similar to unpublished values for canopy diameters of territories recorded for *A. cristatellus* during a behavioral ecology study (Jenssen et al., 1984). For the basis of the present study, I consider 6 and 2.5 m as conservatively large estimated mean distances across male and female territories of *A. cristatellus*. These estimates are larger than or similar to area data of other anoles in coastal Caribbean habitat (e.g., Schoener and Schoener, 1982).

I initiated displacement trials in the mornings (0900–1100 h) of the first 5 d of the 8-d experiment. Each morning, about five lizards from separate habitat clusters were caught by noosing, their snout–vent lengths (SVL) were measured and recorded, their capture sites were flagged and uniquely numbered, their capture sites were placed on a rough map of the area, and their individual-unique numbers were coded on their backs (water-based latex artist paint). Immediately after capture, each subject was singularly relocated to its own novel habitat cluster outside its esti-

mated territory (i.e., >6 m). During transport, I enclosed the subject's head within a wrapped hand grip to eliminate visual cues. A circuitous route was taken, not only to skirt thick clumps of vegetation, but also to avoid straight-line displacement routes that might simplify possible cues of angular inertia.

Each release point had two criteria. First, the release site was of similar vegetative complexity as the capture site, so that the displaced lizard could potentially colonize the new habitat cluster if it so chose. Second, the release point had at least one or more major habitat clusters that disrupted the line-of-sight to the capture site. Each release point was flagged, marked with the subject's identification number, and recorded on the map; straight-line displacement distances were paced off at the end of the experiment. Release sites were chosen to create a range of displacement distances (11–62 m) whose means and ranges for displacement distances of female and male subjects were similar ( $\bar{x} \pm \text{SE} = 31.8 \pm 5.8$  m, range 11–60 m; and  $\bar{x} \pm \text{SE} = 31.1 \pm 4.6$  m, range 11–62 m, respectively). Though lizards were relocated in various directions from their capture sites, randomizing a compass heading for displacement from each capture site was not part of the experimental design due to the limited release sites that met the above criteria.

During the afternoons (1500–1700 h) of the 8-d experiment, I visually searched the vicinity of each capture site for returning subjects (until known to have returned) and the vicinity of each release site for the presence or absence of the displaced subject (if not already known to have returned). This permitted estimates of return durations and number of relocated subjects that colonized new home ranges.

I statistically tested my basic premise, that modest displacement distances will disrupt the homing ability of *A. cristatellus*, by using the logistic regression procedure (Hosmer and Lemeshow, 1989). The logistic regression complements my experimental design because the procedure is structured for a binary outcome (dependent) variable; in my application, it

was whether a lizard returned (yes) or not (no). The logistic model is non-linear and does not carry restrictive normality assumptions. The procedure estimates the probabilities that lizards would return from the displacement distances established in my study. The tested null hypothesis is whether the slope of the experimental data significantly deviates from 0 (i.e., displacement distance has no effect on the probability of returning). Additional class comparisons were tested using the nonparametric Wilcoxon rank-sum test, which carries no data distribution assumptions and is preferable to parametric procedures when dealing with small sample sizes (Siegel and Castellan, 1988). All procedures were run using SAS statistical analysis software (SAS, 1999).

### RESULTS

*Hypothesis H<sub>1</sub>*.—The first hypothesis, that no relocated lizard would return to its home territory, was not supported. Seven of 12 females and 9 of 13 males (64%) returned from the entire range of relocation distances. Of the non-returnees, a lizard of each sex remained at or near its release point, and four females and three males were not seen again after their release.

*Hypothesis H<sub>2</sub>*.—The second hypothesis, that homing ability is limited and easily disrupted, was not supported. Within the range of displacement distances of this study, a logistic regression analysis indicated that the slope resulting from displacement distances plotted against the likelihood of lizards returning to their home sites was not significantly different from 0 (i.e., no relationship between displacement distance and the likelihood of returning; Likelihood ratio test, *chi-square* = 1.07, *P* = 0.30). To visualize the distribution of returnees and non-returnees relative to displacement distance (Fig. 1), I pooled the relocated lizards into three distance classes of similar sample sizes: near (10–19 m, *n* = 9), moderate (20–49 m, *n* = 9), and far (50–62 m, *n* = 7). The class means essentially doubled with each successive displacement class: near—14 m ( $\pm$  SE 0.88 m), moderate—31 m ( $\pm$  SE 3.61

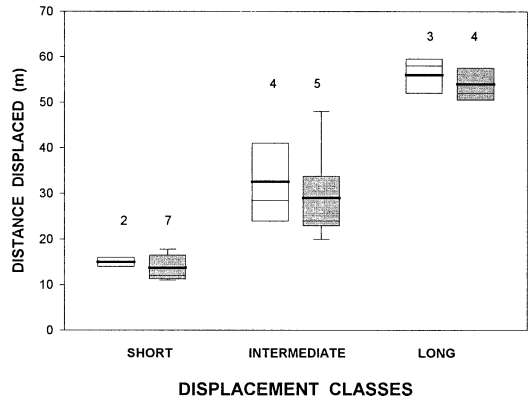


FIG. 1.—Box plots for comparing the displacement distances for which *Anolis cristatellus* did not return (white boxes) and for which they did return (grey boxes) within three classes of displacement distances. Ends of boxes provide 25th and 75th percentiles; thick and thin horizontal lines in each box provide the mean and median, respectively; and numbers over the boxes give sample sizes.

m), and far—55 m ( $\pm$  SE 1.91 m). Respective class returning success was 89%, 67%, and 71%.

*Hypothesis H<sub>3</sub>*.—The third hypothesis, that returning success is biased toward males and their larger territories and body sizes than females, was not supported. The samples of females and males were displaced over a similar range of distances (Wilcoxon test, *Z* = -0.191; *P* = 0.85), and the returning success was not sex biased (7/12 females, 9/13 males; *chi-square* 2  $\times$  2 test,  $\chi^2$  = 0.322, *P* = 0.57). The logistic regression analysis made the same inference, where the slopes resulting from both sex and SVL plotted against the likelihood of lizards returning to their home sites were not significantly different from 0 (i.e., no relationship between sex or SVL and the likelihood of returning; Likelihood ratio test, *chi-square* = 1.06, *P* = 0.81 and 0.001, *P* = 0.97, respectively). The returned females and males showed no significant differences (Wilcoxon test) in either respective displacement distance ( $\bar{x}$  = 24 m, seven females;  $\bar{x}$  = 31 m, nine males; *Z* = -0.849, *P* = 0.41) or time to return ( $\bar{x}$  = 1.8 d, seven females;  $\bar{x}$  = 2.7 d, nine males; *Z* = -0.870, *P* = 0.39).

*Hypothesis H<sub>4</sub>*.—The last hypothesis, that at least some males and females

would return from all displacement distances, was supported. From the above data, most males and females of *A. cristatellus* returned to their original territories, including some from distances equivalent to 10 male and 26 female territorial diameters.

Homing success, particularly that of lizards displaced the greatest distances, may have been negatively affected by two factors. First, predator pressure was indicated by a male and female returning with half or more of their tails missing. Second, some lizards may have been in transit when the 8-d experiment was concluded. Of the last five lizards released (on day 5), the three non-returnees had been displaced >50 m.

#### DISCUSSION

The phenomenon of spatial orientation and navigation has been little studied in lizards (see reviews of Baker, 1978; Chelazzi, 1992). Of the few species examined, displacement experiments show that most can home. Depending on the study and species, the longest straight-line distances of returning individuals ranged between 50–280 m within 20 d of release (Chelazzi, 1992; Hein and Whitaker, 1997; Stanley, 1998); most sleepy lizards (*Tiliqua rugosa*), when displaced 800 m (approximately four home range diameters), showed orientation movements in the direction of their capture sites (Freake, 1998). From my study, males and females of *A. cristatellus* also demonstrated the ability to return to their territories from presumably unfamiliar release points (support of hypothesis,  $H_4$ ). These results diverge from my a priori prediction for *A. cristatellus* (see Introduction) and lead me to question both the nature and the function of orientation behavior by *A. cristatellus*.

#### *Nature of the Orientation Behavior*

From an experimental perspective, the displacement protocol for *A. cristatellus* should have effectively broken the link between egocentric-limited spatial cues and the lizard's ability to update its specific position after relocation. First, individuals do not normally venture outside their terri-

ories, neither daily nor seasonally. Therefore, voluntary relocation of any significant distance is not a normal context for which there may be a selected navigational mechanism. Likewise, subjects are not expected to have recent route familiarization with landmarks beyond their local view from within territorial boundaries. By the same logic, incidental movement as a juvenile would not be a source of immediate cues for an egocentric-dependent coordinate system. Second, I attempted to deprive visual, kinesthetic, directional, and distance cues from the subjects on the trip away from familiar landmark views. Theoretically, deprivation of these cues should be relatively effective in uncoupling the egocentric-based mechanisms of *A. cristatellus*, particularly since lizards travel on a fixed substrata. Thus, in comparison with swimming or flying species that must compensate for natural displacement by the movement of water and air (e.g., Srygley, 2001), a moving *A. cristatellus* can reliably update its spatial position from visual, kinesthetic, and inertial cues, with minimal or no redundancy from other orientation cues.

Some inferences can be drawn with regard to the nature of the spatial ability of *A. cristatellus* by comparing the behavioral ecology and homing performance of the species with the orientation/navigation mechanisms listed in Table 1. The first three strategies seem unlikely for *A. cristatellus*. If a random heading or a systematic search pattern were used to return to home territories, I would expect either a very low success rate or a success rate that significantly decreased with increasing displacement distances; neither was the case for *A. cristatellus* where the majority of lizards returned from each of the three displacement classes (Fig. 1). If a genetic-based directional heading (e.g., innate vectors or taxic responses) were used, there would be little or no homing success given the unpredictable directions of experimental displacement. Trail following, a non-memory mechanism, is improbable because species of *Anolis* are visually-oriented with no morphological or behavioral evidence of pheromones (e.g., Jenssen et al.,

1995). Moreover, when subjects are carried to relocation positions, any mechanism based on an exudate trail would be disrupted.

Route-based orientation (route-reversal, dead reckoning, course-reversal), while potentially selected for operating within a territory, does not exclusively explain the homing success of *A. cristatellus*. Route-reversal requires that the lizard memorize a sequence of reference points (i.e., visual cues) during the outward journey, then reverse the order of cues to find its starting point. But the opportunity for *A. cristatellus* to memorize the initial sequence of cues during the outward journey was deprived during relocation trials. Dead reckoning by path integration uses memorized velocity and vector cues on the outward journey, then the nervous system double integrates these cues to plot a direct return course. However, by carrying a visually shielded subject, the lizard's own kinesthetic and visual inputs were deprived. Thus, velocity and vector cues would be disrupted as well as possible sun-compass cues for determining directional vectors. The carried lizard might still obtain some information on angular deflections from its vestibular canals based on movements by the investigator. However, jostling, random holding positions, unknown initial headings, and unknown transport velocity would combine to confound reliability. Course-reversal is independent of landmarks and relies on reversing a compass heading to get home. There is evidence that the parietal eye of a lizard receives celestial cues relative to homing (Ellis-Quinn and Simon, 1991), but shielding the parietal eye will prevent orientation to a trained direction (Adler and Phillips, 1985). With its head shielded on the outward journey, *A. cristatellus* would not have a compass bearing, per se, to simply reverse for the return trip. Furthermore, potential compass information during the outward trip was complicated by an unknown initial heading and a non-linear route.

In contrast to the above-mentioned egocentric mechanisms for localization (i.e., orientation relative to the subject) listed in

Table 1, the remaining mechanisms of pilotage and true navigation are allocentric (i.e., orientation relative to a map). Pilotage is the most parsimonious explanation for the homing performance by *A. cristatellus*. With pilotage, a lizard may use an array of visual landmarks, but must be able to generalize between familiar and unfamiliar views of those landmarks. Consider that after cue deprivation, the lizard is abruptly exposed to a new set of habitat features. In order to determine a novel route home, the lizard must allocentrically locate its present position relative to its home location. Pilotage may also extend to a spatial memory acquired as a juvenile should the release point have occurred fortuitously in an area previously occupied, but such past experiences would not be applicable to route-based mechanisms that depend on real time sequences of directional cues. In summary, despite relocation that should disrupt egocentric-based coordinates, the lizards continued to know both their new locations and that of their home territories within an expanded spatial context. This is evidence of a cognitive map (e.g., Gallistel, 1990; Shuttleworth, 1998), but see also Bennett (1996) for additional considerations.

#### *Possible Function*

Because many lizard species are territorial (e.g., reviewed by Turner et al., 1969), it follows that there should be selection for at least limited spatial orientation to find refuge, to exploit local resources, and to defend consistent territorial boundaries. Such functions for spatial orientation apply to *A. cristatellus* and could be adequately supported by egocentric-based mechanisms. However, the responses of *A. cristatellus* to relocation suggest that the species has a greater spatial awareness (i.e., pilotage) than predicted. What, then, might select for pilotage as a component to the spatial referencing system in *A. cristatellus*? The displacement experiment infers that the "homing" response is the adapted function, but this may be a misleading assumption.

A homing function for an allocentric orientation system in a non-migratory and

non-ranging species could have evolved due to an errant juvenile stage, where individuals disperse widely and then return to settle in the best suitable habitat that was encountered. However, not having any evidence for such a dispersal pattern in *A. cristatellus*, I suggest that the selective advantage for a cognitive spatial mechanism may be independent of large-scale spatial orientation and navigation. Instead, the mechanism may have a social context that functions within the boundaries of the territory. Spatial learning and memory (i.e., spatial cognition) would permit a territorial resident to place allocentrically itself and other individuals in space and time. A mental map of one's surroundings, perhaps initially constructed from data gathered by route-based mechanisms, would be a much more flexible system than if orientation were limited to motor or cue sequence learning (O'Keefe and Nadel, 1978). Thus, by recognizing and remembering mates, competitors, and potential predators relative to its spatial association within a three-dimensional territory, a resident *A. cristatellus* could gain a selected advantage by anticipating social interactions or avoiding risky encounters with specific individuals.

*Acknowledgments.*—Field assistance was provided by L. Jenssen and G. Jenssen, with facilitation from T. Tallevast, refuge manager of the Culebra National Wildlife Refuge. Data analysis was reviewed and improved by suggestions from G. Terrell of the Virginia Tech Statistical Consulting Center. The manuscript benefitted through the comments by M. Lovern, K. Passek, and J. Phillips. The author adhered to the Guidelines for the Use of Animals in Research.

#### LITERATURE CITED

- ADLER, K., AND J. B. PHILLIPS. 1985. Orientation in a desert lizard (*Uma notata*): time-compensated compass movement and polarotaxis. *Journal of Comparative Physiology* 156:547–552.
- BAKER, R. R. 1978. *The Evolutionary Ecology of Animal Migration*. Hodder and Stoughton, London, U.K.
- BENNETT, A. T. D. 1996. Do animals have cognitive maps? *Journal of Experimental Biology* 199:219–224.
- CHELAZZI, C. 1992. Reptiles. Pp. 235–261. *In* F. Papi (Ed.), *Animal Homing*. Chapman and Hall, London, U.K.
- CHELAZZI, C., P. DELLA SANTINA, AND D. PAPPAGNOLI. 1987. Trail following in the chiton *Acanthopleura gemmata*: operational and ecological problems. *Marine Biology* 95:539–545.
- DINGLE, H. 1996. *Migration: the Biology of Life on the Move*. Oxford University Press, New York, New York, U.S.A.
- DYER, F. C. 1998. Cognitive ecology of navigation. Pp. 201–260. *In* R. Dukas (Ed.), *Cognitive Ecology*. University of Chicago Press, Chicago, Illinois, U.S.A.
- ELLIS-QUINN, B. A., AND C. A. SIMON. 1991. Lizard homing behavior: the role of the parietal eye during displacement and radio-tracking, and time-compensated celestial orientation in the lizard *Sceloporus jarrovi*. *Behavioural Ecology and Sociobiology* 28:397–407.
- FITCH, H. S., R. W. HENDERSON, AND H. GUARISCO. 1989. Aspects of the ecology of an introduced anole: *Anolis cristatellus* in the Dominican Republic. *Amphibia-Reptilia* 10:321–329.
- FLEISHMAN, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *American Naturalist* 139:36–61.
- FREAKE, M. J. 1998. Variation in homeward orientation performance in the sleepy lizard (*Tiliqua rugosa*): effects of sex and reproductive period. *Behavioural Ecology and Sociobiology* 43:339–344.
- GALLISTEL, C. R. 1990. *The Organization of Learning*. MIT Press, Cambridge, Massachusetts, U.S.A.
- GORMAN, G. C., AND P. LICHT. 1974. Seasonality in ovarian cycles among tropical *Anolis* lizards. *Ecology* 55:360–369.
- GREEN, D. 1984. Long-distance movements of the Galapagos green turtles. *Journal of Herpetology* 18:121–130.
- HEIN, E. W., AND S. J. WHITAKER. 1997. Homing the eastern fence lizards (*Sceloporus undulatus*) following short-distance translocation. *Great Basin Naturalist* 57:348–351.
- HOSMER, D. W., AND S. LEMESHOW. 1989. *Applied Logistic Regression*. John Wiley & Sons, New York, New York, U.S.A.
- LEAL, M., AND J. A. RODRIGUEZ-ROBLES. 1997. Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Animal Behaviour* 54:1147–1154.
- JENSSEN, T. A., D. L. MARCELLINI, C. PAGUE, AND L. A. JENSSEN. 1984. Competitive interference between Puerto Rican lizards, *Anolis cooki* and *A. cristatellus*. *Copeia* 1984:853–862.
- JENSSEN, T. A., N. GREENBERG, AND K. A. HOVDE. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs* 9:41–62.
- O'KEEFE, J., AND L. NADEL. 1978. *The Hippocampus as a Cognitive Map*. Oxford University Press, London, U.K.
- ORTIZ, P. R., AND T. A. JENSSEN. 1982. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. *Zeitschrift für Tierpsychologie* 60:227–238.
- PAPI, F. 1992. General aspects. Pp. 2–18. *In* F. Papi

- (Ed.), Animal Homing. Chapman and Hall, London, U.K.
- PHILIBOSIAN, R. 1972. Territorial behavior and population regulation in anoline lizards. Ph.D. Dissertation, University of California, Riverside, California, U.S.A.
- . 1975. Territorial behavior and population regulation in the lizards, *Anolis acutus* and *A. cristatellus*. *Copeia* 1975:428–444.
- SAS INSTITUTE. 1999. Statistical Analysis Systems, Release 6.12. SAS Institute, Cary, North Carolina, U.S.A.
- SCHOENER, T. W., AND A. SCHOENER. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology* 63:809–823.
- SHWARTZ, A., AND R. W. HENDERSON. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University of Florida Press, Gainesville, Florida, U.S.A.
- SHUTTLEWORTH, S. J. 1998. Cognition, Evolution and Behavior. Oxford University Press, New York, New York, U.S.A.
- SIEGEL, S., AND N. J. CASTELLAN, JR. 1988. Non-parametric Statistics for the Behavioral Sciences. McGraw-Hill, New York, New York, U.S.A.
- SRYGLEY, R. B. 2001. Compensation for fluctuations in crosswind drift without stationary landmarks in butterflies migrating over seas. *Animal Behaviour* 61:191–203.
- STANLEY, M. C. 1998. Homing in the skink, *Oligosoma grande*, within a fragmented habitat. *Journal of Herpetology* 32:461–464.
- TURNER, F. B., R. I. JENNRICH, AND J. D. WEINTRAUB. 1969. Home ranges and body sizes of lizards. *Ecology* 50:1076–1081.
- UNDERWOOD, G. 1970. The eye. Pp. 1–97. In C. Gans and T. S. Parsons (Eds.), *Biology of the Reptilia*, Vol. 2, Morphology. Academic Press, New York, New York, U.S.A.

Accepted: 5 October 2001

Associate Editor: Edmund Brodie III