Herpetologica, 61(3), 2005, 233–240

THE IMPORTANCE OF SOIL MOISTURE AND LEAF COVER IN A FEMALE LIZARD'S (*NOROPS POLYLEPIS*) EVALUATION OF POTENTIAL OVIPOSITION SITES

ANNE M. SOCCI[1], MARTIN A. SCHLAEPFER[1,2,3,4], AND THOMAS A. GAVIN[1,2]

[1]*Department of Natural Resources, and*
[2]*Field of Ecology and Evolutionary Biology, Fernow Hall, Cornell University, Ithaca, NY 14853-3001, USA*

ABSTRACT: The microenvironment surrounding a lizard egg will strongly influence its probability of hatching, yet little is known about which environmental cues females use to select favorable nest sites. We conducted three experiments using *Norops polylepis* (Polychrotidae) in semi-natural enclosures to determine a female's ability to assess soil moisture levels and the presence of leaf-litter cover when selecting an oviposition site. Females laid significantly more eggs in moist soil (42% water content) than in the dry (10%) and saturated (70%) soil treatments. Most eggs (72%) placed in moist soil treatments hatched, whereas none of the eggs in the dry and saturated soil treatments hatched. In a separate choice experiment, females laid significantly more eggs in a "soil-and-leaf-cover" treatment than in "soil-only" or "leaf-cover-only" treatments. Our results demonstrate that female *N. polyelpis* can detect variations in water content and leaf cover, and that females prefer microhabitats that likely maximize the survival of their eggs.

Key words: *Anolis*; Incubation; *Norops polylepis*; Nest-site selection; Ovipositioning behavior; Perceptual cues, Squamata

ABIOTIC conditions within a nest can strongly influence a reptile egg's probability of survival, as well as the subsequent fitness of the hatchling. Numerous field and laboratory studies have demonstrated the importance of factors such as soil temperature, humidity, respiratory gases (O_2, CO_2), and soil water content to squamate egg development and hatchling vigor (Elphick and Shine, 1998; Phillips and Packard, 1994; Shine et al., 1997; Van Damme et al., 1992; and reviews by Overall, 1994; Packard and Packard, 1988). We expect ovipositioning behavior to be under strong selective pressure because females can maximize the probability that their eggs will hatch, and thus their own inclusive fitness, by selecting microhabitats that protect eggs from predators and avoid sub-optimal abiotic conditions (Kolbe and Janzen, 2002; Wilson, 1998). We know relatively little, however, as to how female lizards perceive their environment and which environmental cues they integrate into their ovipositioning choices (Castilla, 1996; Warner and Andrews, 2002; Wilson, 1998). In particular, it is not known whether females rely upon one or several environmental cues to decide where to oviposit and, if several environmental cues are used, in which manner they are prioritized.

To elucidate the decision-making rules, or 'Darwinian algorithms' (Cosmides and Tooby, 1987), underlying oviposition behavior, we presented female anoles with a choice of nest sites that varied with respect to two of many potential environmental cues: soil moisture content and leaf cover. Parchment-shelled eggs experience transpirational water loss in the course of natural incubation but avoid desiccation by absorbing water from their surroundings (Andrews and Sexton, 1981; Packard and Packard, 1988; Packard et al., 1977). It is of particular importance, therefore, that a female selects a microhabitat with adequate moisture for proper development of an egg. Anecdotal observations suggest that females can detect moisture content of the soil and preferentially select areas with moisture levels conducive to normal egg development (Andrews and Rand, 1974; Brown and Sexton, 1973; Sexton et al., 1971; Stamps, 1976; Tokarz and Jones, 1979). Although Warner and Andrews (2002) have demonstrated experimentally that female *Sceloporus undulatus* will select soil moisture and temperatures most conducive to the survival of their eggs, this has

[3] PRESENT ADDRESS: Department of Integrative Biology, University of Texas at Austin, 1 University Station C0930, Austin, TX 78712, USA.
[4] CORRESPONDENCE: e-mail, mas50@mail.utexas.edu

not been experimentally demonstrated in species of *Norops/Anolis*. Leaf-litter also may play an important role in selection of a nest site by a female if it provides the female with cover from predators while ovipositing and reduces the probability of detection and desiccation for incubation of the egg. However, unlike soil moisture, the importance of leaf-litter in selection of a nest site by a female has not been tested experimentally. More generally, deciphering the Darwinian algorithms of female *Norops/Anolis* oviposition behavior may help us predict the behavior and survival of these species in human-disturbed habitats, where the traditional environmental cues may appear in novel ecological contexts (Schlaepfer and Gavin, 2001; Schlaepfer, 2003).

We used experiments in semi-natural enclosures to determine (1) if female *Norops polylepis* distinguish between three soil moisture levels (dry, moist, and saturated) for nest site selection, (2) egg survivorship and development time in each of these soil moisture treatments, and (3) the relative importance of leaf cover and soil when females select a nest site.

Materials and Methods

Study Species and Experimental Conditions

Norops polylepis (formerly *Anolis polylepis*) is a semi-arboreal, diurnal lizard from southern Costa Rica (Savage, 2002). Adult females of *N. polylepis* measure up to 53 mm in length from snout to vent (SVL) (Andrews,1983). In general, females of *Norops/Anolis* species lay their eggs near the surface of the forest floor soil, often covered by leaf litter, or in cavities in tree trunks, logs, or rocks, where there is sufficient moist debris to prevent desiccation (Andrews, 1982; Tokarz and Jones, 1979; Valderrama Puente and Rodriguez Schettino, 1988). The oviposition behavior of *N. polylepis* remains poorly studied in the wild. Extensive searches of all possible micro-habitats in forest plots revealed a dozen eggs and hatched shells. All eggs discovered in the field were located under ca. 1 cm of soil below the forest leaf-litter. These eggs also resembled in size, color, and texture eggs of *N. polylepis* laid in captivity (M. A. Schlaepfer, unpublished data). *Norops polylepis* is not known to exhibit parental care (Andrews, 1983). Egg production in *N. polylepis* occurs year-round, but is greater during the wet season (up to one egg per week) than in the dry periods (one egg ca. every 2 weeks) (Andrews, 1983; Andrews and Rand, 1974). The relatively high frequency of egg production of *Norops/Anolis* species makes them conducive to repeated ovipositioning trials.

We collected 17 mature female *N. polylepis* (41–51 mm SVL; mean mass: 2.15 g, SD = 0.40) from two forest fragments ("5" and "Forest Reserve" in Schlaepfer and Gavin, 2001) located at 1200–1300 m on Fila Cruces near Las Cruces Biological Field Station of the Organization for Tropical Studies (OTS) in Coto Brus, Costa Rica. The vegetation on Fila Cruces is described as pre-montane wet forest (Holdridge, 1947; in Hartshorn, 1983). The dry season, which occurs sometime during December–April, is characterized by sunny, clear skies, strong gusts of wind, and monthly rainfall 10–20% of that of the rainy season. Soil water potential in the field can range from dry (–280 kPa) to water-logged (0 kPa) depending on the micro-habitat and recent rainfall, and *N. polylepis* eggs placed under such conditions can potentially desiccate and drown, respectively (Schlaepfer, 2003).

All experiments were conducted in a covered (shaded) area behind a research laboratory, at approximately 1100 m, under natural light and temperature regimes. Temperatures at the research laboratory (mean temperature March–July: 17.2 C, mean of daily highs: 26.5 C, mean of daily lows: 13.0 C) were overall similar but more variable than the forested habitat of Fragment 5 (mean: 17.6 C, mean of daily highs: 20.0 C, mean of daily lows: 15.9 C) during a similar time period (February–August) (Schlaepfer, 2003).

Experiment I: Soil Moisture Preference

Females were held individually in cages from January to May 2000. Cages were misted daily and females readily fed upon live insects captured daily in pastures. Each female was placed periodically with a sexually mature male in a separate cage to ensure that eggs would be fertile. Due to the possibility of sperm storage (Fox, 1963), we were unable to ascertain the paternity of each egg, and we made the assumption that the paternal identity would not influence a female's oviposition choice.

Testing cages were 23 cm in diameter, approximately 50-cm high, and enclosed in plastic mesh. Each cage contained three Petri dishes (diameter: 91 mm) filled with local Andept soil (Vásquez Morera, 1983), and a wooden perch located equidistant to the three dishes (Fig. 1a). We intentionally chose moisture levels that we believed, a priori, would have significant fitness consequences for the eggs. Specifically, soil samples were oven-dried for 24 h and then re-hydrated to 10% (10 g of H_2O and 90 g of dry soil), 42%, and 70% water content, respectively. The position of each soil treatment within the cage was randomized at the beginning of each new trial. We maintained soil samples within 5% of their target moisture by adding water every second day to correct for evaporative losses. Each female was housed in her own cage and was given fresh soil at the beginning of a trial. Petri dishes were replaced with new soil every two weeks to reduce the risk of fungal growth. We checked cages daily for eggs, and recorded the soil treatment of the dish in which each egg was found. Eggs were removed from the cages and randomly assigned to incubation in one of the three soil moisture treatments (see Experiment II).

Experiment II: Egg Incubation

To determine the probability of egg survival in each of the different soil treatments in Experiment I, we randomly assigned 81 eggs (63 from Experiment I, supplemented with 18 eggs from females not used in Experiment I) laid between 8 March and 7 May 2000 to a dry, moist, or saturated soil treatment (10%, 42%, and 70% water content, respectively). Eggs were placed under ca. 1 cm of the same soil type as that used in Experiment I. We discontinued placing eggs in the dry soil once it became apparent that they were not viable in that treatment. We maintained soil moistures in each dish to account for evaporative water losses. Fungal growth occasionally appeared on the soil and eggs, particularly in the saturated soil treatment. In such cases we gently removed visible fungal growth. Eggs were monitored until they hatched or died by desiccation or rot, and the incubation time (in days) was recorded for all eggs that hatched. We performed a G-test of independence with Yates correction for continuity (Sokal and Rohlf, 1981) to test for differential survival of eggs in the different soil moisture treatments (Experiment II).

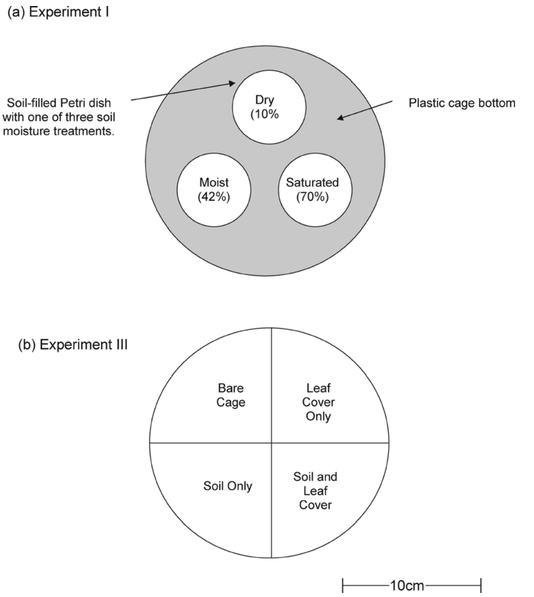

FIG. 1.—Cage designs for (a) Soil Moisture Preference (Experiment I) and (b) Soil versus Leaf Cover Preference (Experiment II). Percent soil water content is indicated next to each treatment in (a). The location of soil samples was randomized in each trial.

Experiment III: Soil versus Leaf Cover Preference

From May to June 2000, the same 17 female *N. polylepis* as in Experiment I were held individually in cages with four equal quadrat substrate treatments (Fig. 1b): (1) soil and leaf cover, (2) soil only, (3) leaf cover only, and (4) bare cage (plastic). The soil and leaf treatments each covered half of a cage bottom, offset by 90°. As a result, the bare cage treatment was opposite the "soil-and-leaf-litter" treatment, although we randomized the sidedness of "soil-only" and "leaf-litter-only" treatments. All soil used in this experiment was maintained at a moisture that we judged to be adequate for survival of a developing egg, approximately that of the moist soil treatment from Experiment I (42% water content), and a fresh soil sample was used for each trial. We checked cages daily for eggs and recorded the substrate in which they were laid. We removed the eggs from the cages so that a female's subsequent oviposition choices would not be influenced by their presence. We released all adult and hatchling lizards at their original point of capture upon completion of our experiments.

Statistical Analysis

Most females laid multiple eggs (see Appendices 1 and 2). As a result, our experimental units (eggs) may not have been independent. To address the possible bias of individual preferences combined with uneven egg production across females, we used a randomization test to obtain a distribution and confidence intervals (CI) for the test statistic of each null hypothesis (H_0^{1A} through H_0^{2C}; see below) (Sokal and Rohlf, 1981). This randomization approach assumes that the variation in oviposition preferences in the experimental females accurately represents the population in the wild. Each iteration of the randomization process consisted of a randomly drawn sample, with replacement, of 16 females from the corresponding data set (Appendix 1 or 2). The number of eggs laid by the sample of females in each treatment was summed and test statistics were calculated. Each data set was bootstrapped (i.e., iterated) 2000 times in this manner. The resulting distribution of each test-statistic could then be tested for significant deviations from zero (i.e., the null hypothesis). All tests were two-tailed, and the standard α-level (0.05) was adjusted for (three) multiple comparisons using a Bonferroni correction. As a result, we present $(1.00 - [0.05/2 \times 3]) = 99.2\%$ CIs for all of our test statistics.

We used the data from the soil moisture preference experiment (Experiment I) to test whether females were more likely to lay an egg in the moist soil treatment than in any other treatment, and whether dry soil or saturated soil would be considered the next preferred choice. Eggs were sometimes laid outside of the Petri-dishes (see Results), an outcome we had not anticipated. As a result, we ran an extra test with "bare cage" as a treatment. These three tests are presented as formal null-hypotheses (labeled H_0^{1A}, H_0^{1B}, and H_0^{1C}) to illustrate the calculations underlying each test statistic: (1A) The number of eggs laid in the moist soil was equal to the number of eggs laid, on average, in the dry soil, saturated soil, or the bare cage (H_0^{1A}: moist – 1/3[dry + saturated + bare cage] = 0); (1B) The number of eggs laid in the moist soil was equal, on average, to the number of eggs laid in the dry soil and the saturated soil, excluding eggs laid on the bare cage (H_0^{1B}: moist – 1/2[dry + saturated] = 0); (1C) Eggs were equally likely to be laid in the dry and saturated soil treatment, excluding eggs laid in the moist soil treatment and the bare cage [H_0^{1C}: dry – saturated = 0].

We used the data from the soil and leaf cover experiment (Experiment III) to test three null hypotheses (H_0^{2A}, H_0^{2B}, and H_0^{2C}) analogous to those in Experiment I: (2A) The number of eggs laid in the "soil and leaf cover" substrate was equal, on average, to the number of eggs laid in the other three substrates (H_0^{2A}: soil and leaf cover – 1/3[soil only + leaf cover only + bare cage] = 0); (2B) Eggs were equally likely to be laid in "soil-and-leaf-cover" as in "soil-only" and "leaf-cover-only" substrates, excluding "bare-cage" data (H_0^{2B}: soil and leaf cover – 1/2[soil only + leaf cover only] = 0); (2C) Eggs were equally likely to be laid in "soil-only" and "leaf-cover-only" substrates (excluding all "soil-and-leaf-cover" and "bare-cage" substrates) [H_0^{2C}: soil only – leaf cover only = 0].

Results

Experiment I: Soil Moisture Preference

Sixteen females of *N. polylepis* laid a total of 63 eggs (median: 4, range: 1–7 per female) in the soil moisture preference experiment (Appendix 1). One female that did not lay any eggs in Experiment I and III was excluded from the analyses. Females laid significantly more eggs in the moist soil than in any of the other three treatments (Fig. 2; H_0^{1A}: moist – 1/3[dry + saturated + bare cage] = 17.67; 99.2% CI = [4.33, 30.33]; $P < 0.0005$). Females still showed a significant preference for the moist soil treatment when eggs laid on the bare cage were excluded (H_0^{1B}: moist – 1/2[dry + saturated] = 21; 99.2% CI = [11.0, 31.50]; $P < 0.0005$). Females showed a significant preference for the saturated soil relative to the dry soil when only these two treatments were considered (H_0^{1C}: dry – saturated = –12; 99.2% CI = [–19.0, –5.0]; $P < 0.0005$). Of the 18 eggs laid on the bare floor of the cage, three (17%) were laid immediately adjacent to a dish

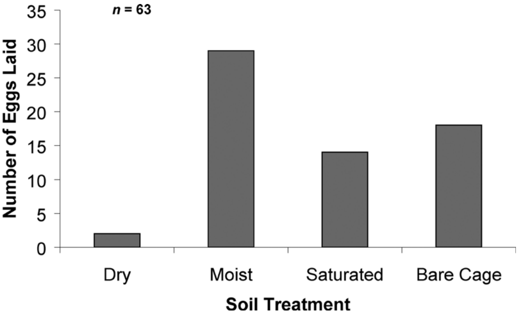

FIG. 2.—Number of *Norops polylepis* eggs laid in four substrate treatments in Experiment I. Dry, moist, and saturated soil contained a soil water content of 10%, 42%, and 70%, respectively. Significantly more eggs were laid in the moist soil than in any other treatment.

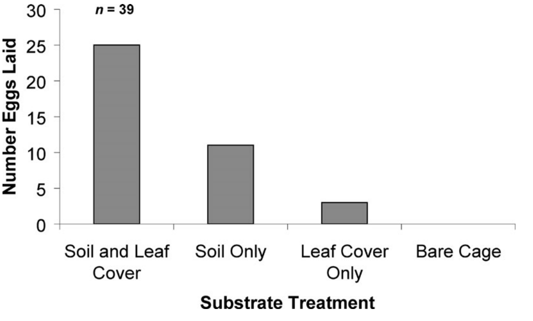

FIG. 3.—Number of *Norops polylepis* eggs laid in four substrate treatments in Experiment III. Significantly more eggs were laid in leaves + soil than in any other treatment.

and covered with soil (two covered with moist soil, one covered with dry soil).

Experiment II: Egg Incubation

There were significant differences in the numbers of eggs that hatched from each of the three soil moisture treatments ($G_{adj} = 15.05$, df = 2, $P < 0.001$). All 10 eggs incubated in dry soil appeared desiccated within the first 24 hours of incubation, without increasing in mass or size measured at oviposition, and eventually died. All 32 eggs incubated in the saturated soil initially gained in size and mass (probably as a result of water absorption), but eventually appeared discolored with visible fungal growth, and appeared to be dead after 3–4 weeks of incubation. Of 39 eggs incubated in moist soil, 28 (74%) hatched. The mean incubation time for the eggs hatched from the moist soil treatment was 94.1 days (SD = 3.4).

Experiment III: Soil versus Leaf Cover Preference

Sixteen females laid a total of 39 eggs (median: 2, range 2–3 per female) in experiment III (Appendix 2). Females laid significantly more eggs in the "soil-and-leaf-cover" substrate than in any of the other three substrates (Fig. 3; H_0^{2A}: soil and leaf cover − 1/3 [soil only + leaf cover only + bare cage] = 20.3; 99.2% CI = [13.3, 28.3]; $P < 0.0005$). Females still showed a significant preference for "soil-and-leaf-cover' substrate over the "leaf-only" and "soil-only" substrates when eggs laid on the bare cage were excluded from the analysis (H_0^{2B}: soil and leaf cover − 1/2[soil only + leaf cover only] = 18; 99.2% CI = [9.5, 27.0]; $P < 0.0005$). Females preferred to lay their eggs in "soil-only" substrate relative to "leaf-cover-only" substrate when only these two treatments were considered (H_0^{2C}: soil only − leaf cover only = 8; 99.2% CI = [2,15]; $P = 0.0035$).

DISCUSSION

Females laid their eggs in a nonrandom pattern in both nest choice experiments. We conclude that female lizards can discern variations in soil moisture and leaf cover in their environment and integrate this information into their ovipositioning decisions. Results from Experiment II demonstrate that the moist soil treatment was the best choice for proper egg development and that the females' preference for this treatment is most likely adaptive in the wild. Although we did not incubate eggs under the various treatments from Experiment III (leaves only, soil only, and leaves + soil), it seems reasonable to assume that eggs would be most likely to survive in the preferred 'leaves + soil' category, where they could potentially benefit from suitable hydric conditions and protective cover. Future studies of egg survivability in the wild could allow us to determine if this assumption is correct.

Our experiments were not designed to determine which factors are important for egg survival. Rather, our goal was to investigate whether *N. polylepis* females assess soil moisture and leaf-cover when seeking an ideal oviposition site. We intentionally selected dramatically different moisture content values of each soil treatment for this experiment. Egg fitness in the field may be affected by smaller differences in soil moisture content. The degree to which an organism can discern variation in a given environmental factor is expected to be related to how strongly the factor affects the fitness of the organism (Resetarits, 1996). Future studies could test how narrowly females can discriminate between different soil moistures, and how they use this information to select nest sites that maximize egg survival.

Preference for the saturated soil over the dry soil suggests that females generally seek a minimum of soil moisture for ovipositioning (Warner and Andrews, 2002). The death of all eggs in the saturated soil treatment of Experiment II may have been a product of our experimental design. Indeed, it is possible that in the field soils rarely remain saturated with water for 3–5 weeks. A female's preference for saturated soils may, in fact, be adaptive under natural conditions if such soil conditions provide insurance against desiccation during periods of low precipitation.

In Experiment I, females did not always deposit their egg in the Petri dishes. This is most likely the result of artificial soil boundaries (limited within the Petri dishes) relative to conditions found in nature. Indeed, three eggs found on the plastic were laid immediately adjacent to a dish and covered with soil. This suggests that *N. polylepis* females, after accidentally laying an egg on the plastic, attempted to create a more favorable microenvironment for the egg by covering them with soil from the adjacent Petri dish. Females in other lizard species are also known to manipulate the microenvironment of the egg after ovipositioning. For example, *Anolis carolinensis* females use their snout and forelimbs to conceal eggs under leaves, logs, or other debris as a predator-defense measure (Tokarz and Jones, 1979). Females of *Eumeces fasciatus* control nest moisture by digging moist substrate beneath the eggs, or even voiding bladder contents onto the nest (Tokarz and Jones, 1979). Our observations under semi-natural conditions suggest that females of *N. polylepis* also manipulate the microenvironment of their eggs in the wild by covering them with soil.

Results from Experiments I and II reveal that moist soil is necessary and sufficient for egg development. However, the natural environment of *N. polylepis* varies not only with respect to soil moisture content, but also in leaf-litter depth. Results from Experiment III indicate that given the choice, females will preferentially lay their eggs in microhabitat that contains both moist soil and a leaf-litter cover. Furthermore, females attribute a greater importance to moist soil than leaf-cover, because significantly more eggs were laid in the 'soil only' than in the 'leaf only' treatments.

The positions of the four treatments in Experiment III were not completely randomized, given that the bare cage was located diametrically opposite the soil and leaf-litter treatment. We do not believe, however, that the females' propensity to lay in the soil and leaf-litter treatment was a result of avoiding the bare cage. Indeed, there was no obvious spatial pattern of eggs being laid further from the bare cage in any of the other treatments (A. M. Socci, M. A. Schlaepfer, and T. A. Gavin, personal obsevations).

The lack of unanimous preference in our experiments and in other similar studies (e.g., Warner and Andrews, 2002) may be the result of maladaptive behavior under experimental conditions. Alternatively, there may be more than one adaptive strategy for nest site selection. As we refine our understanding of cues females use to select oviposition sites, we may learn that there is significant temporal and spatial variation in nest site preferences linked to, for example, seasonality, perceived predation pressure, or an individual's age or genetic makeup.

Choice experiments can be used to reveal how organisms perceive and integrate environmental cues into crucial life-history and behavioral decisions. This experimental design also provides a window into the proximate mechanisms organisms use to maximize their fitness. Our focus in this study on extreme values in a limited set of environmental cues reflects our relative ignorance of the decision-making rules animals use, and future work may reveal complex, case-specific, perceptual and cognitive abilities in a variety of organisms.

Acknowledgments.—We thank J. and R. Figueroa-Sandí., R. Quiros, and the Las Cruces Biological Field Station of the Organization for Tropical Studies for their support in the field. We are grateful for statistical counsel provided by P. Sullivan, N. Altman, and D. Winkler, and for advice given by R. Andrews. We also thank three anonymous reviewers for their critical input. Research for this study was conducted under permit 156-2000 issued by the Ministerio del Ambiente y Energía, Government of Costa Rica. This study was funded by the Guani Family Fellowship in Conservation Biology (to T.A.G.) and by the College of Agriculture and Life Sciences Honors Program, through the Department of Natural Resources, Cornell University (to A.M.S.).

Literature Cited

Andrews, R. M. 1982. Spatial variation in egg mortality of the lizard *Anolis limifrons*. Herpetologica 38: 165–171.

———. 1983. *Norops polylepis* (Lagartija, Anole, Anolis Lizard). Pp. 409–410. *In* D. H. Janzen (Ed.), Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, U.S.A.

Andrews, R. M., and A. S. Rand. 1974. Reproductive effort in anoline lizards. Ecology 55:1317–1327.

Andrews, R. M., and O. J. Sexton. 1981. Water relations of the eggs of *Anolis auratus* and *Anolis limifrons*. Ecology 62:556–562.

Brown, K. M., and O. J. Sexton. 1973. Stimulation of reproductive activity of female *Anolis sagrei* by moisture. Physiological Zoology 46:168–172.

Castilla, A. M. 1996. Temperature selection for egg incubation by the lizard *Podarcis hispanica atrata*. Herpetological Journal 6:133–136.

Cosmides, L., and J. Tooby. 1987. From evolution to behavior: evolutionary psychology as the missing link. Pp. 277–306. *In* J. Dupré (Ed.), The Latest on the Best: Essays on Evolution and Optimality. MIT Press, Cambridge, Massachusetts, U.S.A.

Elphick, M. J., and R. Shine. 1998. Longterm effects of incubation temperatures on the morphology and locomotor performance of hatchling lizards (*Bassiana duperreyi*, Scincidae). Biological Journal of the Linnean Society 63:429–447.

Fox, W. 1963. Special tubules for sperm storage in female lizards. Nature 198:500–501.

Hartshorn, G. S. 1983. Plants. Pp. 118–157. *In* D. H. Janzen (Ed.), Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, U.S.A.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367–368.

Kolbe, J. J., and F. J. Janzen. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. Ecology 83:269–281.

Overall, K. L. 1994. Lizard egg environments. Pp. 51–72. *In* L. J. Vitt and E. R. Pianka (Eds.), Lizard Ecology. Historical and Experimental Perspectives. Princeton University Press, Princeton, New Jersey, U.S.A.

Packard, G. C., C. R. Tracy, and J. J. Roth. 1977. The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. Biological Reviews 52:71–105.

Packard, G. C., and M. J. Packard. 1988. The physiological ecology of reptilian eggs and embryos. Pp. 523–605. *In* C. Gans and R. B. Huey (Eds.), Biology of the Reptilia, Vol. 16. Ecology B, Defense and Life History. Alan R. Liss, New York, New York, U.S.A.

Phillips, J. A., and G. C. Packard. 1994. Influence of temperature and moisture on eggs and embryos of the white-throated savanna monitor *Varanus albigularis*: implications for conservation. Biological Conservation 69:131–136.

Resetarits, W. J., Jr. 1996. Oviposition site choice and life history evolution. American Society of Zoology 36:205–215.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica. University of Chicago Press, Chicago, Illinois, U.S.A.

Schlaepfer, M. A. 2003. Successful lizard eggs in a human-disturbed habitat. Oecologia 137:304–311.

Schlaepfer, M. A., and T. A. Gavin. 2001. Edge effects on lizards and frogs in tropical forest fragments. Conservation Biology 15:1079–1090.

Sexton, O. J., E. P. Ortleb, L. M. Hathaway, R. E. Ballinger, and P. Licht. 1971. Reproductive cycles of three species of anoline lizards from the Isthmus of Panama. Ecology 52:201–215.

Shine, R., M. J. Elphick, and P. S. Harlow. 1997. The influence of natural incubation environments on the phenotypic traits of hatchling lizards. Ecology 78:2559–2568.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, New York, U.S.A.

Stamps, J. A. 1976. Egg retention, rainfall, and egg-laying in a tropical lizard *Anolis aeneus*. Copeia 1976:759–764.

Tokarz, R. R., and R. E. Jones. 1979. A study of egg-related maternal behavior in *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology 13:283–288.

Valderrama Puente, M. J., and L. Rodriguez Schettino. 1988. Algunas características reproductivas de *Anolis lucius* (Sauria: Iguanidae). Poeyana Instituto de Zoologia Academia de Ciencias de Cuba. 358:1–15.

Van Damme, R., D. Bauwens, F. Braña, and R. F. Verheyen. 1992. Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizard *Podarcis muralis*. Herpetologica 48:220–228.

Vásquez Morera, A. 1983. Soils. Pp. 63–65. *In* D. H. Janzen (Ed.), Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, U.S.A.

Warner, D. A., and R. M. Andrews. 2002. Nest-site selection in relation to temperature and moisture by the lizard *Sceloporus undulatus*. Herpetologica 58:399–407.

Wilson, D. S. 1998. Nest site selection: microhabitat variation and its effects on the survival of turtle embryos. Ecology 79:1884–1892.

Accepted: 29 March 2005
Associate Editor: Michael Dorcas

Appendix I

Female *Norops polylepis* oviposition choices in Experiment I: *Soil Moisture Preference*, conducted 7 March–8 May 2000. Dry = 10% soil water content, Moist = 42% soil water content, Saturated = 70% soil water content, and Bare Cage = no soil, no moisture.

	Soil treatments				
Lizard #	Dry	Moist	Saturated	Bare Cage	Total eggs laid
1	0	2	2	0	4
2	0	1	0	2	3
3	0	4	2	0	6
4	0	1	0	0	1
5	0	1	0	3	4
6	0	0	1	3	4
7	0	2	1	1	4
8	2	3	1	1	7
9	0	3	1	1	5
10	0	3	1	1	5
11	0	4	2	0	6
12	0	1	1	3	5
13	0	0	0	0	0
14	0	0	1	0	1
15	0	0	0	3	3
16	0	2	1	0	3
17	0	2	0	0	2
Total	2	29	14	18	63

Appendix II

Female *Norops polylepis* oviposition choices in Experiment III: *Soil versus Leaf Cover Preference*, conducted 16 May–2 June 2000.

	Substrate types				
Lizard #	Soil and leaf cover	Soil only	Leaf cover only	Bare cage	Total eggs laid
1	1	1	0	0	2
2	2	1	0	0	3
3	2	1	0	0	3
4	0	0	0	0	0
5	1	1	0	0	2
6	1	1	1	0	3
7	1	1	1	0	3
8	2	0	0	0	2
9	3	0	0	0	3
10	1	1	0	0	2
11	2	0	0	0	2
12	1	0	1	0	2
13	2	0	0	0	2
14	1	1	0	0	2
15	1	2	0	0	3
16	2	1	0	0	3
17	2	0	0	0	2
Total	25	11	3	0	39