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Martin A. Schlaepfer

## Successful lizard eggs in a human-disturbed habitat

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**Abstract** As humans extend their influence to an increasingly large portion of the globe, it becomes of both theoretical and practical interest to understand the consequences of our activities on wildlife populations. *Norops polylepis* is a small anoline lizard native to rainforest of southern Costa Rica. It is also found and known to lay eggs in cattle pastures immediately adjacent to forest. I predicted that *N. polylepis* eggs would fare poorly in pastures because of the important abiotic and biotic differences with their native forest habitat. I obtained eggs from captive females and estimated an egg's probability of hatching, daily survival rate, and incubation time at various distances along a forest-to-pasture gradient. Contrary to expectation, egg survival rates were higher in pastures than in forest areas. Furthermore, egg incubation times were significantly shorter in pastures than in their native forest. As a result, eggs were at least as likely to hatch in pastures as in forested areas. Thus, pastures may represent a benign or even beneficial habitat for the eggs of some reptile species. High survival of eggs will facilitate range expansion into human-altered habitats such as pastures, but does not guarantee it. Indeed, pastures could represent an ecological trap and a population sink if adults are drawn there (e.g., in search of favorable ovipositioning sites) yet suffer higher mortality than in forests.

**Keywords** Anthropogenic · Edge effects · Life-history · *Norops polylepis* · Ovipositioning

### Introduction

An overarching question in ecology and conservation biology is how human activities alter the distribution and population dynamics of other species. As a result of habitat fragmentation many organisms are confronted with evolutionarily novel habitats (e.g., pastures in formerly forested tropical landscapes) and the edge effects that arise from the juxtaposition of different habitat types (Murcia 1995; Laurance and Bierregaard 1997). The response of species to environmental change will depend on their biotic and abiotic requirements for growth, reproduction, and survival. At worst, suitable conditions for some species will persist only in the core of large habitat fragments, thereby reducing overall population numbers and limiting genetic exchanges between sub-populations (Doak et al. 1992; Laurance and Bierregaard 1997; Bender et al. 1998; Laurance et al. 1998). Other species will benefit from human 'disturbances' if the novel habitat 'matrix' and associated edge effects enhance their growth, survival, or reproduction (Laurance et al. 2002).

The relative contribution of each life-stage to the population growth ( $\lambda$ ) can differ across habitats and populations might not be self-sustaining in a habitat that is unsuitable to one or more life-stages. In particular, the egg-stage can play a crucial role in determining the distribution of oviparous reptiles. For example, the geographic distribution of the desert iguana *Dipsosaurus dorsalis* is limited by soil moisture and temperature conditions necessary for proper egg development (Muth 1980). Likewise, the northern distribution of the snapping turtle *Chelydra serpentina* appears to be limited by incubation conditions for the egg-stage (Bobyn and Brooks 1994). However, the importance of the egg-stage in determining the geographical distribution of oviparous reptiles in human-altered landscapes remains largely unexplored.

Here, I test the effects of forest-to-pasture conversion on the egg-stage of a Neotropical forest lizard, *Norops polylepis*. I predicted that eggs would fare poorly in

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M. A. Schlaepfer (✉)  
Field of Ecology and Evolutionary Biology  
and Department of Natural Resources, Cornell University,  
Ithaca, NY 14853, USA  
e-mail: mas50@cornell.edu  
Fax: +1-607-2544308

*Present address:*

M. A. Schlaepfer, Department of Neurobiology and Behavior,  
Cornell University, Mudd Hall, Ithaca, NY 14853–2702, USA

pastures because of the many abiotic and biotic differences with the forest habitat in which they evolved. I addressed three questions: (1) does the probability of egg hatching vary along a pasture-to-forest-interior gradient? And (2) how do egg incubation times, and (3) egg predation rates vary along this gradient? The first question addresses the pattern of egg survival in this human-altered landscape; the second and third question address possible mechanisms underlying the observed pattern.

## Materials and methods

### Site description

This research took place along the southern edge of a medium-sized forest fragment (ca. 25 ha) located at 82°59.670'W., 8°47.105'N. (elevation: 1,300 m) near San Vito de Java, Puntarenas, in southern Costa Rica (Fragment 5, in Schlaepfer and Gavin 2001). The forest fragment consisted of primary rain forest and has been surrounded by pastures for approximately 30 years (Daily and Ehrlich 1995). The pasture was grazed by livestock during this study and a fence prevented cattle from entering the forest. Experiments were conducted on six transects (each 25 m long) parallel to the forest-pasture edge. Data from multiple transects were pooled for categorical tests in the following manner. My first aim was to contrast pasture (+25 m and +50 m from the edge) with forest (0 m to -100 m) habitat. The 0-m transect was characterized by leaf-litter from forest trees, not pasture grasses, and was overshadowed by shrubs and overhanging tree branches. As a result, it was placed within the forest habitat category. My second goal was to look for evidence of a biological edge effect within the forest habitat. The forest transects were further divided into 'forest edge' (0 m and -25 m) and 'forest interior' (-50 m and -100 m) habitat based on evidence that various abiotic edge effects are detectable generally within 15–60 m of an edge (Laurance et al. 1997).

### Study organism

*Norops polylepis* (Polychrotidae), formerly *Anolis polylepis* (Cannatella and de Queiroz 1989; Guyer and Savage 1992), is a small lizard, with maximum adult snout-vent length (SVL) = 52 mm (Andrews 1983), found in southwestern Costa Rica (Savage 2002). Its native habitat is rainforest (Hertz 1974; Andrews 1991), although adults and juveniles were found in the pastures approximately 50 m from the forest edge at several sites near San Vito. Studies conducted near sea-level found that females lay single-egg clutches throughout the year, and as often as every 1–2 weeks during the rainy season (Andrews 1971; Andrews and Rand 1974).

Before the onset of this study, I found two live eggs and six eggshells of *N. polylepis* in the field, including four eggshells in the pastures. In the forest, the eggs and egg shells were found just below the leaf-litter, buried 1–2 cm within the decomposing organic layer. In the pastures, egg shells were found buried at similar depths in loose soil below clumps of moss or vegetation. Nest-sites were not associated with any obvious microhabitat feature. Also, in a separate study, gravid *N. polylepis* females kept in experimental enclosures buried their eggs 1–2 cm within the soil, preferably under leaf-litter cover. These eggs hatched without parental care as long as the soil remained suitably moist (Socci, Schlaepfer, and Gavin, unpublished data). Evidence from a 12-month mark-recapture study of 1,274 individuals strongly suggests that adults captured in pastures reside there permanently and do not move back and forth into the forest (Schlaepfer 2002). Thus, available evidence indicates that females reside and lay eggs just below the soil surface in both pasture and forest habitat.

### Egg experiments

The experimental units for this study consisted of eggs obtained from captive *N. polylepis* females. Twenty-seven sexually mature females (range of SVL = 40–51 mm) and ten adult males were collected from the pasture, forest edge, and forest interior of the study site. Females were given access to a male every few weeks, taking care only to pair males and females from the same habitat (as defined above) to avoid uncoupling any potential genetic adaptation to their respective environments. Females were housed in individual cages (25x25x40 cm) containing 4–5 cm of moist soil, leaf-litter, and perch sites, located in a shady outdoor location. Each cage was misted and provided with 30–50 insects every morning. The insect prey, which consisted primarily of homopterans, orthopterans, and coleopterans, were collected by sweep-netting nearby pastures, and were coated once a week with Reptocal (Tetra Sales, Blacksburg, Va., USA) lizard vitamins. Cages were checked daily for eggs by sifting gently through the soil. The length and width of the eggs were measured on the day they were discovered. Eggs were left in the cage's soil until the following Saturday, when they were placed into the field. Rubber gloves and plastic or metal utensils were used at all times to avoid contaminating the eggs with human scent.

### Abiotic variables

Air temperature was measured every 30 min at 50 cm above the ground throughout the experiment (14 February to 15 August, 2000) using Hobo dataloggers under protective housing at three locations along the gradient, one in each habitat: +25 m (pasture), -15 m (forest edge), and -60 m (forest interior). Soil temperature along the pasture-forest gradient was quantified by taking 'series' of soil temperature readings from ten different distances along the gradient (from 130 m in the forest to 45 m in the pastures) over a brief time span (20 min). Ten series were conducted on ten different days at times of day ranging from dawn (0500 hours) to late afternoon (1700 hours). Soil temperature was measured at a depth of 2–3 cm, the minimum depth to which the soil temperature probe had to be inserted. Soil temperature was also measured at the site of each nest-site for eggs used in experiment 2 (see below) on three different occasions. These nest-site measurements were then averaged and used as a predictor variable for egg incubation time.

A relationship exists between air temperature, soil depth, and soil temperature (Campbell and Norman 1998). I used one half of all soil temperature measurements and the closest (spatially and temporally) corresponding air temperature reading to construct a non-linear model that predicted continuous soil temperature at 1–2 cm depth in each habitat (pasture, edge, interior). On average, the models (not presented) predicted the second half of soil temperature measurements within 1°C, but no better than air temperature at 50 cm. As a result, I used air temperature at 50 cm to describe mean differences in soil temperature at 1–2 cm depth across habitats.

Soil water potential was measured approximately once a week using chalk probes (model 5910A soilmoisture meter; Soilmoisture Equipment) at three to six randomly chosen locations in each of the six experimental transects. Water potential is notoriously difficult to measure with precision in the field (Packard and Packard 1988), but chalk probes yield a relative indication of the soil's water potential in dry soils (H. Van Es, personal communication). Probes (ca. 3 cm tall) were installed such that they were completely covered with 3 cm of soil (i.e., 3–6 cm deep), and allowed to settle for 1 month before recordings began. The meter reading was transformed to a pressure unit (bars) based on a conversion graph supplied by the manufacturer, and then transformed to kPa (1 bar = 100 kPa) for comparison with other studies.

### Experiment 1: egg survival

Eight to ten eggs were placed at random locations within each of the six experimental transects (+50 m, +25 m, 0 m, -25 m, -50 m,

–100 m) and monitored weekly until they hatched, died, or were preyed upon. The 56 eggs in this experiment were produced by 25 females between 27 January 2000 and 8 April 2000. To avoid any temporal, spatial, or genetic bias, a protocol was implemented whereby one egg from each batch of six consecutive eggs was placed at each of the six experimental distances, and where the habitat-of-origin of the mother was randomized with respect to the habitat-of-destination of the egg. Each egg was placed singly, approximately 1 cm below the soil surface and covered by leaf-litter (in the forest) or a tuft of grass (in the pastures).

To ensure that eggs could be relocated on subsequent weeks, a wooden toothpick was placed within a few millimeters of each egg, at the center of four stakes in a 1x1-m square formation. Every Saturday eggs laid that week were placed in the field, and all older eggs were removed from the soil using disposable plastic gloves and metal forceps, visually inspected for signs of predation, and returned to their nest site. Healthy eggs (firm and white) and hatched eggs (with apical slit) were easily distinguished from depredated eggs (with lateral irregular holes), and dead eggs (shriveled appearance, gray, fungal growth, and hardened). Egg deaths were ascribed to three different categories: unknown cause, squashed, and predation. The latter category was further subdivided into eggs that disappeared completely (presumably consumed in toto by a bird, small mammal, or reptile), and empty egg shells remaining with an irregular hole and contents cleaned out (presumably depredated in situ by an unknown predator, possibly invertebrate).

#### Experiment 2: incubation time

To obtain an accurate measure of incubation time along the pasture-to-forest gradient, six eggs were placed 1 cm below the soil surface under small metal pyramids at randomly chosen locations along each of the six experimental transects. The purpose of the pyramid was to minimize the loss of eggs to predation and to retain the juvenile on the day it hatched. The pyramid frame was made of three tetrahedrons with 15-cm sides (and with 10-cm vertical supports below the pyramid) constructed with welded rebar. The frame was covered with grid-wire (3-mm grid openings) to deter vertebrate predators. The base of each pyramid was coated with sticky-glue and sprinkled with crushed naphthalene to deter insect predators. Pyramids were visually inspected daily for hatchlings. As the expected date of birth approached, pyramids were occasionally lifted to verify that the egg was still present and healthy. In the few events in which hatchlings escaped undetected (egg shell found with apical slit), the mid-point date since the last inspection of the egg was used as the date of birth.

#### Statistical analyses

A chi-square analysis was used to test for differences in the number of eggs that hatched between habitats (Sokal and Rohlf 1981). The Cox *F*-test was used to compare the survival functions between habitats (Tabachnick and Fidell 2001) during the first 11 weeks of egg development (i.e., the time it took for the first egg to hatch). This analysis was conducted twice: once using the actual staggered entry of eggs over time (which assumes that the egg survival rate is independent of egg age; Pollock et al. 1989), and once as if all the eggs had been placed in the field simultaneously (which assumes that the egg survival rate is independent of time of year; non-parametric product limit method, Lee 1980). An ANOVA and Tukey's pair-wise tests were used to compare incubation times among the six transects along the pasture-forest gradient. A step-wise regression ( $F=4$  in,  $F=4$  out) was used to determine the best predictors of egg incubation time from the following factors: average soil temperature at egg location, distance (m) from the edge, mother's SVL, mother's identity, mother's habitat (pasture, edge, interior), Julian date, and egg volume [estimated as  $\pi \times (\text{length})^2 \times (\text{width}) / 6$  (Maritz and Douglas 1994)]. All tests were two-tailed and a significance of  $\alpha=0.05$  is assumed throughout. Power of statistical tests was estimated following Cohen (1988).

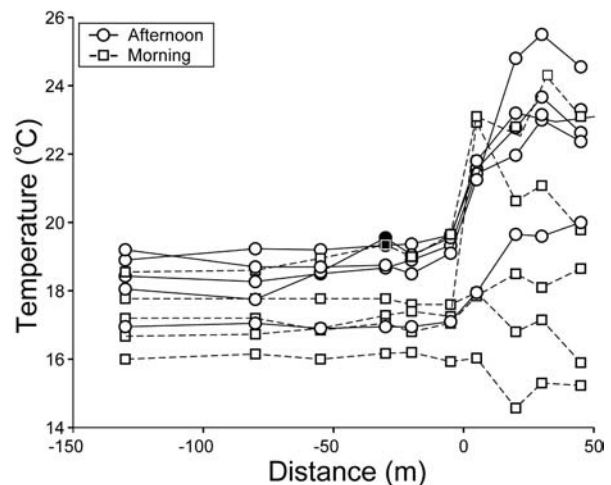
## Results

### Abiotic measurements

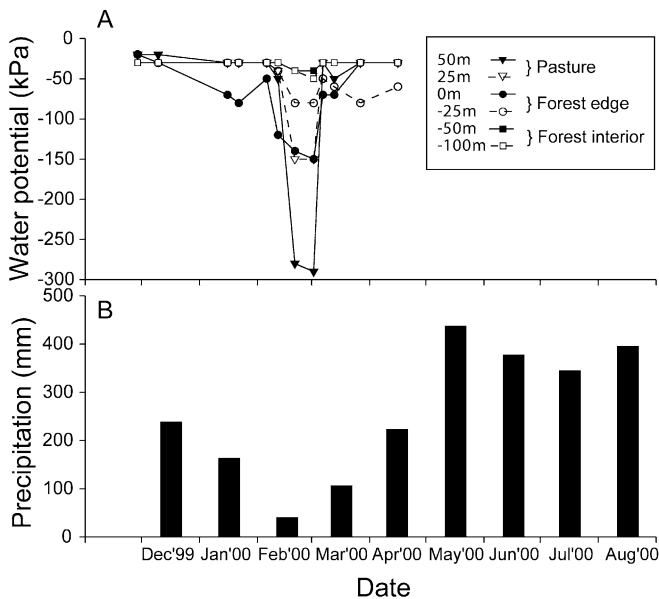
Air temperature at 50 cm above the ground, averaged over the entire sampling period ( $n=8,784$  measurements during 183 consecutive days), was warmest in the pasture (18.80°C), followed by the forest edge (17.86°C) and the forest interior (17.61°C). Pasture air temperatures were the most variable, with temperatures generally 1°C cooler at night and 5–6°C warmer during the day than the adjacent forest. Mean daily minima and maxima for the entire sampling period were: 14.80 and 25.89°C in the pasture; 15.94 and 20.71°C in the forest edge; and 15.86 and 19.95°C in the forest interior.

Soil temperature was spatially homogeneous within the forest, varying by no more than 1–2°C at any given time (Fig. 1). As with air temperatures, pasture soil was generally 1–2°C cooler than forests in the early morning and approximately 5°C warmer during sunny afternoons (Fig. 1). Soil temperatures peaked between +20 and +30 m in the pastures, and generally decreased slightly at +45 m. This occurred because of topographical differences within the south-facing pasture, where the 0–30 m segment was more inclined than the 30–50 m segment.

The soil at a depth of 3–6 cm remained moist (defined here as greater than –1,500 kPa, the point at which plants begin to wilt; Packard and Packard 1988) throughout the dry season in all forest and pasture locations (Fig. 2A). At the farthest distances into the forest (–50 m and –100 m), there was no detectable decrease in soil water potential even during February and March, the driest months of the year (Fig. 2B). Soil water potential in the pasture (50 m



**Fig. 1** Soil temperature readings at 2–3 cm depth, from –130 m (in the forest) to +45 m (in the pasture). Measurements connected by a line ('series') were taken within 20 min of one another. Series were collected on different days (between Sept 1999 and March 2000) in the morning (between 0500 hours and 1200 hours; dashed line) or afternoon (between 1200 hours and 1700 hours; solid lines). A small gap in the forest canopy between –20 and –30 m resulted in some locally higher temperatures (full symbols). Soil temperatures were less variable in the forest than in the pastures



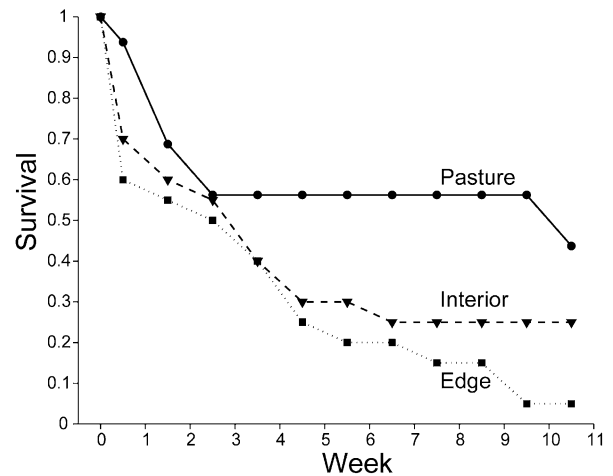
**Fig. 2** **A** Soil water potential at 3–6 cm depth along the pasture-to-forest-interior gradient collected 1–3 times per month from Dec 1999 to Apr 2000. **B** Precipitation (mm) in the pasture of the study site collected 1–4 times per month from Dec 1999 to Aug 2000

transect) was near  $-300$  kPa for approximately a week during the end of February.

### Experiment 1: egg survival

#### Probability of hatching

Unprotected eggs experienced variable hatching probabilities depending on their location along the pasture-forest gradient, ranging from 38% (3 of 8 eggs) at 50 m within the pastures, to 0% (0 of 10 eggs) at the 0 m and  $-100$  m transects (Table 1). When egg survival was compared between habitats, significant differences were detected between ‘pastures’ (31%) and ‘forest’ habitat, edge and interior habitats combined (10%;  $\chi^2=3.83$ ,  $df=1$ ,  $P=0.05$ ). I found no significant differences between the probability of eggs hatching in ‘forest edge’ (5%) and



**Fig. 3** Survival curves for *Norops polylepis* eggs placed in pastures (+50 m and +25 m from forest edge), forest edges (0 m and  $-25$  m) and forest interiors ( $-50$  m and  $-100$  m). The start date of all eggs was synchronized in this graph, and the survival curves were estimated for the first 11 weeks of development. Eggs in the pasture had a significantly higher survival function relative to eggs in the forested habitats

‘forest interior’ (15%,  $\chi^2=1.11$ ,  $df=1$ ,  $P=0.29$ ). Statistical power for all contingency table tests was relatively low (0.22–0.24, with effect size  $w=0.2$ ).

#### Egg survival rate

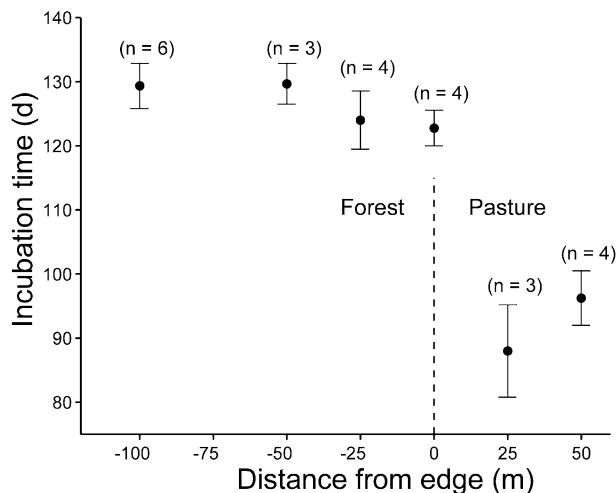
Using the staggered-entry data, the survival function was significantly higher in the pastures than in forested areas, edge and interior combined ( $\chi^2=5.16$ ,  $df=1$ ,  $P=0.02$ ). I could not detect any significant difference in survival functions between forest edge and forest interior eggs ( $\chi^2=1.15$ ,  $df=1$ ,  $P=0.28$ ). Likewise, using the temporally-aligned data, the survival function was significantly higher in the pasture relative to the forested areas, edge and interior combined ( $F_{18,68}=2.22$ ,  $P=0.01$ ; Fig. 3). As with the staggered-entry data, I could not detect any significant difference in survival functions between forest edge and forest interior eggs ( $F_{38,30}=0.65$ ,  $P=0.90$ ; Fig. 3).

**Table 1** Fate of 56 uncaged *Norops polylepis* eggs placed along a pasture to forest gradient (experiment 1)

Habitat	Pasture		Forest edge		Forest interior	
	+50	+25	0	$-25$	$-50$	$-100$
Unknown cause of death	0	0	0	0	1 <sup>a</sup>	0
Squashed (by horse or cattle)	1	0	1	0	0	0
Disappeared in toto	0	2	3	8	4	8
Depredated in situ	4	4	6	1	2	2
Total eggs that died	5	6	10	9	7	10
Median (range) days to death	7.0 (1–13)	2.0 (2–11)	1.0 (1–5)	5.0 (1–10)	1.5 (1–12)	3.5 (1–7)
Total eggs that hatched	3	2	0	1	3	0
Time (weeks) to hatch	12, 13, 14	13, 14	–	19	18, 18, 19	–
Total number of eggs <sup>b</sup>	8	8	10	10	10	10

<sup>a</sup> Egg was healthy looking until week 12, when it hardened and died

<sup>b</sup> Totals for each distance differ because of uneven egg production by females



**Fig. 4** Mean (SE) incubation time for eggs placed along a pasture to forest gradient (experiment 2). Sample size of eggs is indicated above each error bar. Eggs in the pastures (+25 m and +50 m from the edge) developed significantly faster than eggs in the forest

#### Source of mortality

Of the 56 eggs in experiment 1, 47 died. The median time until death did not differ across habitats (Kruskal-Wallis'  $H=1.01$ ,  $df=2$ ,  $P=0.60$ ), nor did it differ between those eggs that disappeared in toto and those depredated in situ (Mann Whitney's  $U=533.5$ ,  $P=0.49$ ; Table 1). The proportion of eggs that disappeared in toto relative to eggs that were preyed upon in situ decreased with distance from the forest interior (Table 1) and differed significantly across habitats ( $\chi^2=7.81$ ,  $df=2$ ,  $P=0.02$ ). The probability of eggs being depredated in toto was highest in the forest interior (75%, 12 of 16 depredated eggs), intermediate in the forest edge (61%, 11 of 18), and lowest in the pastures (20%, 2 of 10).

#### Experiment 2: incubation time

Incubation times of *N. polylepis* eggs differed significantly across experimental distances (ANOVA,  $F_{5,18}=16.53$ ,  $P<0.001$ ). Eggs placed in the pastures (+25 and +50 m) developed significantly (30–40 days, or approximately 30–40%) faster than eggs placed at any other distance (Tukey's pair-wise comparisons; Fig. 4). Relative to the variation within forests, the difference in incubation time between pasture and forest was astonishingly large.

Average soil temperature at egg location, Julian date, and distance (m) from the edge were all significant factors in predicting the incubation time of eggs in experiment 2 (step-wise regression analysis). Alone, average soil temperature at nest-site location explained 89% of the variation in incubation time. Julian date and distance from the edge explained an additional 7%. The mother's habitat of origin did not significantly influence egg

incubation time. The slightly shorter incubation time of eggs placed at 25 m relative to those placed at 50 m in the pastures (Fig. 4) is congruous with generally warmer soil temperatures at +25 m than at +45 m in the pastures (Fig. 1).

Pyramids were an effective barrier to predation. The proportion of eggs that died or were lost to predation in experiment 2 (12 of 36 eggs; 33%) was significantly lower than that of the unprotected eggs in experiment 1 (47 of 56 eggs; 84%;  $\chi^2=24.38$ ,  $df=1$ ,  $P<0.001$ ). The 12 eggs in experiment 2 that died did so independently of the habitat in which they were placed ( $\chi^2=0.75$ ,  $df=2$ ,  $P=0.69$ ). They died from the following probable causes: one was probably infertile (found dead after 1 week), three died of an unknown agent (found hardened, covered with fungus, and dead after several weeks of normal growth; one in each habitat), one desiccated (placed by chance in a barren and open spot in the pasture), one drowned (placed by chance in a physical depression in the pasture), and six were preyed upon in situ despite the pyramid (four in the pasture or 0 m transects, and two in the deeper forest transects). Nine hatchlings escaped from their pyramids, but the time span between the discovery of the empty egg shell and the previous visual inspection of the egg was relatively short (median of 3; range 2–18 days). As a result, the date of birth of these renegades could generally be determined to within a few days.

## Discussion

Contrary to expectation, the temperature and hydric regimes in the pasture did not limit the normal development of *N. polylepis* eggs, even during the dry season. It appears that soil must be very dry before the development of anoline eggs is impeded. The eggs of two closely related species, *Norops auratus* and *N. limifrons*, developed normally at  $-1,480$  kPa, but eventually desiccated and died after 1–3 weeks of normal development at  $-2,130$  kPa (Andrews and Sexton 1981). Soil water potential at 3–6 cm did not descend below  $-300$  kPa in this study. Eggs placed 1 cm below the soil surface may experience drier soil conditions than those recorded at 3–6 cm. Indeed, one egg in experiment 2 desiccated as a result of being placed in a particularly barren and exposed site in the pasture. For eggs placed under protective vegetation, however, desiccation should not represent a major threat to development, at least not during years with some rain during the dry season.

Eggs in the pasture experienced a significantly reduced incubation period relative to eggs in the forest. Furthermore, the survival curve for pasture eggs was significantly higher than that for forest eggs. It appears that pasture eggs benefit from both a shorter exposure period to predation and a lower predation rate relative to eggs in the lizards' native forest.

I did not detect any statistical differences between forest edge and forest interior in the probability of egg hatching (Table 1), egg survival curves (Fig. 3) and egg

incubation times (Fig. 4), although low statistical power may have obscured biologically important differences between these two habitats. A comparison between pasture and forest interior habitats was not one of my pre-planned tests. Inspection of the egg survival data (Table 1), however, suggests that differences between pastures and forest interiors may have been biologically small or insignificant. I am hesitant, therefore, to assert that eggs are distinctly better off in pastures than in their native forest interior habitat. Instead, I conservatively suggest that lizard eggs in the pastures appeared to fare at least as well as in their original forested habitat.

#### Different predation pressures in pastures and forests

Almost all the eggs in the pasture were depredated in situ, with the empty egg shell left behind, presumably by invertebrates (Andrews 1982, 1988). I repeatedly observed small ants and invertebrate larvae emerging from a half-consumed egg in the pasture. It is not clear, however, if these were the primary predators or secondary scavengers. In contrast, most unsuccessful eggs in the forest were taken by “whole-egg” predators, such as small mammals and squamates foraging in the forest leaf-litter (Andrews 1983). Thus, eggs may be exposed to different suites of predators in each habitat: primarily invertebrates in the pastures, and primarily vertebrates in the forest. Alternatively, the same predator suites might be found in both habitats, but their efficiency of finding lizard eggs might be a function of the physical environment in each habitat (Chalcraft and Andrews 1999). Eggs at the forest-pasture edge (0 m) may have been exposed to both forest and pasture suites of predators and, as a result, particularly high predation pressure.

#### Shorter incubation times in warmer environments

The multiple regression analysis revealed that incubation time is negatively correlated with soil temperature (also compare Figs. 1 and 4). A number of laboratory and field studies have shown that warmer soil temperature results in a shorter incubation time of ectothermic, squamate eggs (e.g., Muth 1980; Burger 1991; Van Damme et al. 1992; Castilla and Swallow 1996; Shine et al. 1997; Elphick and Shine 1998; Andrews et al. 2000; Angilletta et al. 2000). In these studies, a 1°C warmer nest environment translated into a 4–10 day (7–12%) shorter incubation period. In this study, soil temperatures (using air temperature at 50 cm as a proxy for soil temperature at 1 cm depth; see Methods section) in the pasture transects were, on average, 1.0 and 1.2°C warmer than the adjacent forest edge and forest interior, respectively, and resulted in incubation periods that were, on average, 33 and 41 days (26 and 32%) shorter, the strongest response to temperature recorded to date.

One possible explanation for the pronounced sensitivity of the incubation period to temperature is that this

study site was located at the upper elevational range of *N. polylepis* (Savage 2002). Temperature has the most pronounced effect on incubation time at the cooler end of a species’ developmental range (Muth 1980; Burger 1991; Castilla and Swallow 1996; Andrews et al. 2000; Angilletta et al. 2000). Forest soils at this elevation (1,300 m) might frequently experience temperatures for which the rate of embryonic growth is arrested or severely reduced. The extra latent heat available in the pasture might maintain the egg within a temperature range favorable to development for significantly longer periods of time (Shine et al. 2002), and explain the much shorter incubation period relative to forest nest sites. The long incubation periods of eggs in the forest at this elevation (1300m) also suggests that the elevational range limit (1,330 m) for this species in Costa Rica (Savage 2002) may be determined by a physiological temperature threshold for egg development. If such were the case, higher soil temperatures in open areas may allow *N. polylepis* eggs to develop at elevations that were not possible in the original forested landscape, and as a result, potentially serve as a conduit for an elevational range expansion.

Eggs laid in forest light gaps have shorter incubation periods than eggs laid in more shaded, forested areas. One egg in experiment 2 was placed, by chance, within a small light gap caused by a recent tree fall on the –25 m transect. The soil temperature of the nest-site was 1°C warmer than other nest-sites in the forest (based on three mid-day measurements), and as a result the egg had the shortest incubation time (117 days) of all eggs placed on the –25, –50, and –100 m transects. This suggests that the success of pasture eggs may be an extension of benefits accrued by eggs laid in natural forest gaps.

#### Behavioral and demographic responses to evolutionarily novel habitats

Organisms often use indirect cues in their environment to evaluate habitat quality. Habitat preferences are generally adaptive because they rely on cues that, over evolutionary time, reliably correlated with survival and reproductive success. Given the short incubation time of lizard eggs in sunny, warm micro-habitats, females may actively migrate to pastures in response to environmental cues that normally indicate good ovipositioning sites (Shine et al. 2002). However, in environments that have been suddenly altered by humans, formerly reliable cues may no longer be associated with positive outcomes. As a result, behavioral decision-making rules (or ‘Darwinian algorithms’, Cosmides and Tooby 1987) that evolved in a forest environment will not necessarily be adaptive in pasture habitat. Even though eggs fare well in open sunny habitat, pastures could possibly represent an ecological trap if post-hatching individuals experience reduced survival or reproduction there (Gates and Gysel 1978; Schlaepfer et al. 2002).

## Conclusions

Because eggs are often less tractable and less conspicuous than post-hatchlings, field studies tend to overlook this important life-stage. As a result, the mechanisms underlying a population's decline (or growth) might not be properly identified in cases in which the effects of environmental change are mediated primarily through the egg-stage. In several instances human habitat alterations have created conditions inhospitable to eggs, ultimately leading to a species' extirpation, even though the altered habitat remained suitable to adults. In anurans, for example, increased UV-radiation, fungal disease, and water contaminants reduced egg survival and contributed to some of the well-publicized population declines (Beebee et al. 1990; Blaustein et al. 1994; Lips 1999; Kiesecker et al. 2001). I initially posited that *N. polylepis* eggs would be unable to develop normally in pasture habitat. My results, however, reveal that *N. polylepis* eggs do at least as well, if not better, in the anthropogenically-altered pastures than in their native forests.

The short incubation period and high hatching rate of *N. polylepis* eggs in pastures may increase the probability of a population being self-sustaining there, but does not guarantee it. Indeed, the intrinsic growth rate ( $\lambda$ ) of populations in pastures will also depend on the survival rates of juveniles and adults, and the reproduction of mature females (Caswell 2001). Populations of *N. polylepis* will be self-sustaining in pastures if post-hatchling survival and reproduction rates are comparable to those in forest habitat. On the other hand, pastures could represent an ecological trap if adults, drawn there by formerly reliable environmental cues, suffer an unexpectedly high mortality that is not offset by high egg survival. More generally, inclusion of the egg-stage into field studies can reveal the conflicting responses of different life-stages to environmental change, and the potential importance of the egg-stage in directly or indirectly determining the viability of a population in a human-altered environment.

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