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GROWTH TO DEATH IN LIZARDS

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Abstract.—Negative relationships between growth rate and survival have been demonstrated in many organisms, often reflecting risks associated with increased foraging rates. More puzzling, however, are recent reports that rapid growth early in life may lower survival rates much later in life, presumably because fast-growing animals allocate resources among different body components in ways that later compromise their survival. If widespread, such delayed effects may modify our interpretation of the evolution of life histories and phenotypic plasticity. Previous reports of this phenomenon are derived mostly from laboratory studies, generally on rodents or humans. We provide the first evidence from an experimental study in the field: neonatal lizards were exposed to different thermal conditions in seminatural enclosures at two different elevations (within their natural thermal regime). This arrangement allowed relatively higher and lower levels of food intake, which modified the neonates' growth rates (because lizards at more benign thermal conditions could forage more frequently). When later released into the wild, the individuals that grew more rapidly as neonates experienced much higher mortality than did slower-growing conspecifics, regardless of the elevation at which they had been kept.

Key words.—Feeding experiment, growth rate, growth-induced mortality, survival, lizard neonates.

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There is substantial literature demonstrating that ingestion levels below what is required to sustain maximum growth rate appear to increase probability of survival under laboratory conditions (Metcalfe and Monaghan 2001). Such mechanisms could also be important factors in directing the evolution of life histories in natural populations, which has until recently been overlooked by evolutionary ecologists (Metcalfe and Monaghan 2001). The underlying physiological reason for this negative relationship between growth and survival has been suggested to be decelerated cell senescence at relatively lower levels of oxidative metabolism (Jennings et al. 1999). Furthermore, recent research demonstrates that growth rate can be increased or reduced by the individual organism depending on environmental triggers and resources allocated selectively within the soma. For example, when starvation is followed by more benign conditions, compensatory bursts in growth have been demonstrated but laboratory experiments suggest that these can be associated with a multitude of physiological costs (Metcalfe and Monaghan 2001). In this study, we test whether variation in growth rate in manipulated lizard neonates can be linked to their risk of mortality subsequent to being released into a natural population after the experimental growth period and, hence, whether juvenile growth rate may be under stabilizing selection via costs mediated at future life history stages.

MATERIALS AND METHODS

Tasmanian snow skinks (*Niveoscincus mircolepidotus*) are small (up to 6 g, 70 mm snout-vent length), viviparous, ground-dwelling lizards. Pregnant females from the summit of Mt. Wellington, Tasmania (1270 m) were caught by hand or noosing, brought into the laboratory one week before parturition, and randomly assigned to plastic cages ($30 \times 35 \times 20$ cm, or $20 \times 15 \times 5$ cm). Each cage had coarse sand as bottom substrate, an oyster shell as hiding place, and mealworms (*Tenebrio*) and water provided ad libitum. The cages were placed in a rack with a heating element at one end of the cage so that the females could thermoregulate to >30°C (their preferred body temperature) in a thermal gradient during the day (14 h). At night the heating elements were turned off and the temperature allowed to drop to ambient levels. The female cages were inspected two to three times daily for newborn offspring, which were immediately placed in separate cages. The neonates were measured (snout-vent, total length, head length, and width), and weighed (to the nearest 0.01 g), sexed (by presence/absence of hemipenises), and toe-clipped for permanent individual identification.

Rearing pens for the neonates were erected at two altitudes, 1000 m and 50 m above sea level, by using 60 cm-wide corrugated plastic sheeting pushed into the ground (diameter = 3 m). The elevations were selected to create variation in neonatal growth rate (via more thermally benign foraging conditions at the low elevation), while being within the natural summer temperature range of the lizards' natural habitat. Each pen was supplied with numerous rocks, logs, and dug-out cool, moist retreat sites to mimic the lizards' natural environment, and allow thermoregulation to the neonates' preferred body temperature (30°C) at all times when the ambient temperature was sufficiently high.

Pilot studies showed that most litters contain two young (mean = 2.7, ±0.7 SD) and we therefore released the neonates into enclosures at two elevations. For litters with more than two young, we released the surplus offspring at the high elevation (because we expected mortality to be higher in the harsher climate). At both elevations we haphazardly assigned 10–14 neonates to each pen, that is, at densities corresponding to those of free-ranging lizards at our study site (i.e., about 1.7 neonates/m^2; Olsson and Shine 1998). Thus, the only differences we could register between the two elevations were the thermal characteristics of the enclosures, which were

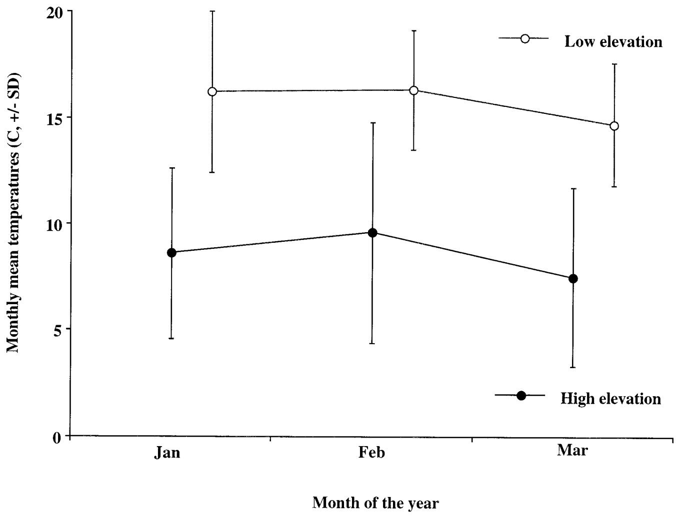

FIG. 1. Mean monthly temperatures (°C, ± SD) at the low and high elevations, respectively. The graphs have been offset to visualize the overlaps in temperature ranges.

more benign in terms of permitting activity at the lower elevation, but with overlapping ranges between the two sites (Fig. 1). Importantly, at both elevations, lizards showed the bimodal activity pattern typical of free-ranging snow skinks in summer, with periods of basking in the morning and evening, and retreat under ground during the warmer part of the day.

The offspring were then allowed to grow for three months at ad libitum food conditions, as indicated by mealworms (*Tenebrio*) and white worms (*Enchytraenus albidus*) being present at all times under logs and rocks, that is, where the lizards foraged and sheltered. In addition, naturally occurring invertebrates were often found inside the pens, thus providing an additional food source. Each lizard was weighed four times during the experiment. In order to estimate growth rate, we regressed body mass on day number, and let the slope coefficient represent growth rate (growth is approximately linear in this short interval: M. Olsson and R. Shine, unpubl. data; Andrews 1982). All neonates were then released haphazardly at our main study site (1270 m) and had survival monitored by recapture throughout the following year. Over the next four years the population was resampled twice for survivors, which allowed us to confirm our first survival estimates (Olsson and Shine 1998). We also ensured that our survival estimate was not confounded by emigration from our study area by resampling an approximately 300-m corridor around the study site with three field assistants. The width of this corridor was several times the distance any lizard was recorded traveling from its release site (or from the first site of observation for any wild-caught lizard; a maximum travel distance of approximately 100 m; M. Olsson, pers. obs.). Capture probabilities during surveys are very high for lizards on this site, and dispersal is minor. Thus, recapture offers a good index of survival (Olsson and Shine 1998).

All variables were checked for normality using Shapiro-Wilkes statistics ($P > 0.05$), before being submitted to statistical analysis. Analyses of variance were performed in Proc GLM (SAS Institute 1994), and survival was analyzed using logistic regression in Proc Logistic (SAS Institute 1994). At the end of the growth period, nine females were represented by more than one offspring in the dataset but maternal identity did not influence growth rate (single-factor ANOVA, maternal number as factor, $F = 1.12$, $P = 0.21$), or probability of survival (Exact Likelihood Ratio Test, Likelihood Ratio Statistic = 63.8, $P = 0.31$, available in StatXact 4 [Mehta and Patel 2000]). We therefore followed Leger and Didrichson (1994) in using these observations as independent data points (sample sizes in Fig. 2), rather than submitting mean growth rate and survival scores of siblings for analysis (or more likely half siblings, since 75% of clutches are sired by more than one male; M. Olsson, B. Ujvari, E. Wapstra, T. Madsen, R. Shine, and S. Bensch, unpubl. ms.).

RESULTS

In accordance with our predictions, growth rate was significantly higher at the lower elevation (one-factor ANOVA, $R^2 = 0.14$, $F_{1,54} = 8.98$, $P = 0.004$; Fig. 2; mean offspring masses at the end of the growth period at the low and high elevations were 1.04 g ± 0.13 SE, and 0.80 g ± 0.12 SE; see Fig. 2 for sample sizes). While the lizards were kept in the enclosures, there was no effect of growth rate on survival (logistic regression; growth rate as predictor variable, Wald chi-square = 0.29, $P = 0.51$). During the following year in the wild, however, a lizard's growth rate as a hatchling substantially modified its subsequent probability of survival. Lizards that were never recaptured grew at a rate that was about three times as fast as those that survived, regardless of the elevation at which they had been kept as hatchlings (Wald chi-square = 9.62, $P = 0.002$; Fig. 2). Importantly, this effect was not generated by differences in survival between lizards reared at the low versus high elevation; we confirmed that there was no difference in survival between elevations subsequent to release by including elevation in our logistic model (growth rate: Wald chi-square = 7.47, $P = 0.006$; elevation: Wald chi-square = 0.23, $P = 0.633$; Fig. 2). We also confirmed that there was no significant interaction between elevation and growth rate on probability of survival (Wald chi-square = 2.52, $P = 0.112$). However, because there were differences between the sites in growth rate, we standardized growth rate by elevation (setting mean trait value to zero, and its standard deviation to one) before we pooled the data and reanalyzed growth effects on survival. This analysis reconfirmed our initial result, now reinforced (Wald chi-square = 18.29, $P < 0.0001$, slope estimate = −4.75). In order to also control for potentially confounding effects of date of birth and mass at release on survival, we also incorporated the standardized scores of these traits. Mass at release had a marginally significant positive effect (independent of growth rate), while birth date was unrelated to probability of survival. However, with the effects of mass and birth date removed (by being included in the same model), the negative effect of growth rate on survival was even stronger (growth rate: Wald chi-square = −7.68, $P = 0.013$; mass at release: Wald chi-square = 2.18, $P = 0.052$; date of birth: Wald chi-square = −1.70, $P = 0.249$; interaction effect mass at release × date of birth: Wald chi-square = 0.013, $P = 0.910$).

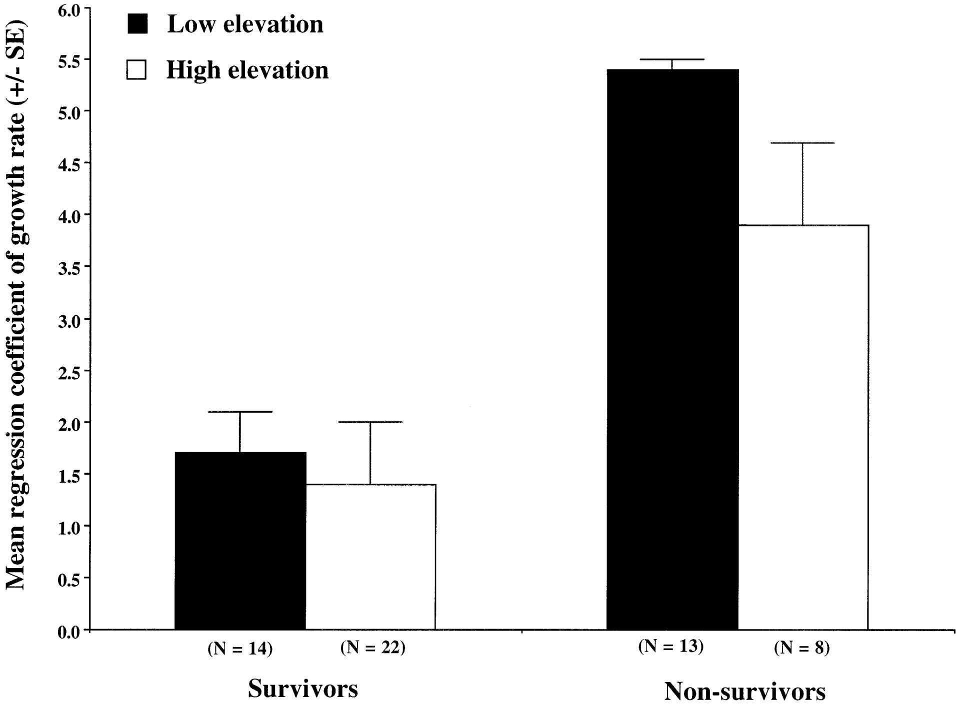

FIG. 2. Mean growth rates (slope coefficients ± SE) for surviving versus nonsurviving snow skink young from 46 females (see text for details). Note that slow-growing lizards have approximately the same survival advantage regardless of the elevation at which they were raised.

DISCUSSION

These are the first field-based data to show that rapid growth early in life may confer a subsequent penalty in survivorship. The implications for microevolutionary analyses are strong: we cannot assume that traits manifested at early ages are independent of those expressed later in life. Studies on many organisms have assumed that faster-growing neonates have higher lifetime reproductive success (because reproductive success increases with adult body size in many species; Andersson 1994), leading Grafen to coin the term ''silver spoon effects'' in analysis of lifetime reproductive success (1988). However, here we demonstrate that ''silver spoons'' may sometimes be tarnished in natural populations, in agreement with observations on laboratory animals (reviewed in Arendt 1997).

To what degree do our data reflect selection in unmanipulated systems, and what may constitute the negative link between growth and survival? The present study was instigated by our observation in a previous year that six surviving lizards in a cohort grew 25% slower than those 58 that died (0.06 mm/day ± 0.018, and 0.08 mm/day ± 0.006, respectively). Our experimental work indeed seems to support this observation, although our thermal manipulation was not strong enough to induce a direct effect of elevation on risk of mortality. However, the underlying mechanism explaining our results is less clear. High growth rate may lead to reduced immune capacity and reduced capacity to respond to environmental stress (Arendt 1997). In rats, fast growers show a reduced lifespan, in part because of greater tumor production, and higher susceptibility to external parasites (Eklund and Bradford 1977; Kajiura and Rollo 1994). Similar phenomena have been described for salmon (*Salmo salar*), with high growth rates being associated with increased incidence of coronary lesions unrelated to age, diet, and maturation (Saunders et al. 1992). In the present study, we have no evidence that growth-induced mortality is due to immunodeficiency or compromised maintenance of tissue, but published data suggest that such costs could stabilize evolution of high growth rate in natural populations.

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