

# CORRELATIONAL SELECTION ON LAY DATE AND LIFE-HISTORY TRAITS: EXPERIMENTAL MANIPULATIONS OF TERRITORY AND NEST SITE QUALITY

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Abundant evidence suggests that females may engage in mate choice to gain nongenetic (material) benefits from high-quality territories; however, the selective consequences that influence those choices are not well understood. We studied the fitness effects of territory quality and incubation temperature on juvenile lizards in nature. We manipulated territory quality by redistributing rocks between pairs of neighboring home ranges. Rock manipulations set up adjacent plots that were either experimentally improved or reduced in quality. We incubated eggs from field-caught gravid females in each of three temperature treatments in the laboratory (low, medium, and high temperature). Progeny were released in either experimentally improved or reduced-quality plots upon hatching, and the following spring we measured survival as a function of egg size and laying date. We conducted concurrent studies of the thermal environment on experimental territories. Improved territories provided significantly more hours for lizards to behaviorally thermoregulate at their preferred body temperature and also provided nest sites with incubation conditions that were closer to optimal compared with reduced-quality plots. Reduced-quality plots were significantly more variable in quality. Finally, we measured significant correlational selection between egg mass and laying date on manipulated plots in two separate years. Results indicate the influence of environmental variation on correlational selection on life-history traits.

**KEY WORDS:** Correlational selection, lay date, lizards, morphs, territory quality.

Nongenetic (material) benefits of mate choice may have important influences in the evolution of mating systems (Kirkpatrick 1982; Andersson 1994; Moller and Jennions 2001); however, we still do not understand the cascading selective effects on progeny that arise due to female preferences for nongenetic benefits. Some examples of nongenetic benefits to females include parental care (Davies 1985), nuptial gifts (Gwynne and Simmons 1990), or territory quality (Alatalo et al. 1986). Although nongenetic benefits are usually thought of in terms of fitness gains to the female (see references cited above), enhanced fitness owing to female pref-

erences for nongenetic benefits may extend to progeny through increased growth and/or survival to maturity. Philopatric progeny may benefit by inheriting a parent's high-quality territory.

The most important nongenetic benefits for terrestrial ectotherms are likely to be high-quality thermal resources associated with good territories (Huey et al. 1989; Adolph and Porter 1993), especially in taxa that lack parental care. For example, studies of territory selection in reptiles have demonstrated the importance of thermal regime to progeny growth rates and survival (Christian and Tracy 1981; Huey et al. 1989; Sinervo and Adolph

1994; Calsbeek and Sinervo 2002a). Thermal properties on high- and low-quality territories may also differ below ground and can affect the quality of nest sites. Quantitative accounts of progeny success from different nests reflect the importance of variable incubation temperatures to progeny size, locomotor performance (Shine and Harlow 1996), and hatching date in reptiles (Svensson and Sinervo 2000). In this study, we investigate variation in natural selection on egg size and laying date as a function of territory quality in a natural population of side-blotched lizards, *Uta stansburiana*. Thermal characteristics of the nest sites and territories of reptiles are simple to quantify (Huey et al. 1989), and the consequences of incubation temperature on offspring fitness are likewise readily measured by studying the impacts on offspring survival.

Side-blotched lizards provide an ideal system in which to test ideas regarding the fitness consequences of territory quality. Females demonstrate strong preferences for high-quality thermal territories (Calsbeek and Sinervo 2002b), and the thermal quality can be experimentally enhanced in the wild by constructing large rock piles. Moreover, we can readily assess fitness differences among females or among their progeny by incubating eggs from field-captured females in the laboratory and performing mark-recapture studies on progeny. The importance of territory quality for adult males (Calsbeek et al. 2002; Calsbeek and Sinervo 2002a) and the importance of philopatry versus dispersal for progeny (Sinervo and Clobert 2003; Sinervo et al. 2006) are considered elsewhere.

Although we do not directly treat the color morphs in this paper, a bit of natural history background is necessary to understand the evolutionary consequences of variation in territory quality in the maintenance of alternative strategies. In California Coast Range populations, male and female side-blotched lizards exhibit one of three genetically determined throat colors that differ in behavior, physiology, and life-history strategies (Sinervo and Lively 1996; Sinervo et al. 2000). Male lizards may have orange, blue, or yellow throats and throat colors are associated with alternative territorial and reproductive behaviors. Female throat colors are associated with alternative progeny size strategies; orange- and yellow-throated females have r- and K-selected life histories, respectively (Sinervo et al. 2000). Females with blue throats exhibit a strategy that is more similar to females with yellow throats (Sinervo and Calsbeek, unpubl. ms.). Throat colors and alternative strategies appear to be controlled by a single mendelian locus with three alleles (*a*, *b*, *y*) as demonstrated by field pedigrees (Sinervo and Zamudio 2001), laboratory crosses with field release of progeny (Sinervo et al. 2001), and gene mapping studies (Sinervo et al. 2006).

Life-history tradeoffs in female side-blotched lizards lead to disruptive selection that favors alternative combinations of traits that determine life history, behavior, and physiology (Svensson and Sinervo 2000; Sinervo and Zamudio 2001). Disruptive se-

lection favoring nonrandom combinations of traits is referred to as correlational selection (Brodie et al. 1995; Blows and Brooks 2003; Blows et al. 2003; McGlothlin et al. 2005) and may be responsible for the origin or maintenance of alternative strategies (Forsman and Appelqvist 1998; Sinervo and Svensson 2002; Abbott and Svensson 2005). Previous work in this system has revealed a variety of trait combinations that are under correlational selection (e.g., clutch size, egg size, immunocompetence, and laying date [Svensson et al. 2001; Sinervo and Svensson 2002]). Based on results from these studies, we predict that when selection is associated with differences in territory quality, correlational selection should favor trait combinations that lead to ecological niche partitioning between morphs. Given the central role of thermal biology in terrestrial ectotherms (see references above), selection driven by differences in territorial quality should act on traits such as laying date, nest-site choice, egg incubation regimes, and the availability of thermal resources for behavioral thermoregulation. Moreover, territory quality manipulations that alter environmental agents of selection should mitigate the force of correlational selection on certain trait combinations. Here we develop such manipulations of thermal opportunity to test the hypothesis that correlational selection on life-history traits arises due to variation in territory quality per se.

Manipulations of the mean and variance in thermal quality are also germane for theories on the evolution of polymorphism. A classic hypothesis concerning the evolution of genetically based alternative strategies posits that environmental grain is responsible for generating the conditions favorable to genetic polymorphism (Levins 1962a, b; Lively 1986). In particular, coarse-grained environments are conducive to the formation of genetically fixed alternative strategies, whereas more fine-grained environments are conducive to plastic strategies. Given that correlational selection on quantitative life-history trait variation is thought to be important in the genesis of discrete polymorphisms (see references above), we posited that experimentally manipulating the variance in thermal quality should alter correlational selection on life-history traits such as egg size and lay date, which are central to the life-history polymorphism of side-blotched lizards. We predicted that manipulating environmental quality would result in significant differences in correlational selection on high- and low-quality territories.

We experimentally manipulated territory quality and the quality of potential nest sites by altering rock abundance between pairs of adjacent lizard home ranges. We monitored temperature regimes at potential nest sites on improved and reduced-quality territories. Because temperatures were not sampled at every possible basking site within territories, we refer to temperature measurements on improved and reduced-quality "plots" within territories. We also measured effects of temperature on lizard eggs across three incubation temperatures (26°C, 28°C, and 30°C).

Finally, we measured selection on both laying date and egg mass as a function of territory quality, by releasing progeny from each of the three incubation temperatures to experimentally improved or reduced-quality plots in the field. We discuss the results in the context of a genetically based polymorphism in females that determines alternative life-history (Sinervo et al. 2000) and behavioral (Sinervo and Lively 1996; Calsbeek et al. 2002) strategies in progeny. Elsewhere (Sinervo and Calsbeek, unpubl. ms.) we present results from a parallel study in natural populations of side-blotched lizards in which we present the heritability of traits under selection and discuss results of both studies in the context of female r- versus K- selection density cycles (Sinervo et al. 2000).

## Materials and Methods

The side-blotched lizard, *Uta stansburiana*, is a small annual lizard (40–60 mm snout-vent length) that matures and dies after a single reproductive season throughout much of its range. This study took place on a 300-m long sandstone rock outcropping adjacent to Billy Wright Road in Merced county California, near Los Baños Grandes. The experimental outcropping was 1.3 km from a control rock outcropping where we measured selection and trait heritabilities (Sinervo and Calsbeek, unpubl. ms.). Male and female *Uta* defend territories throughout the entire year (Svensson et al. 2001; Calsbeek and Sinervo 2002c). Females lay one to three clutches of eggs at monthly intervals beginning in April (Sinervo 1997). Most (about 80%) progeny are philopatric (Doughty et al. 1994) and begin to exhibit territorial behavior within a few days of hatching (Sinervo, unpubl. ms.).

### TERRITORY QUALITY

We measured the importance of territory quality in males and females by experimentally manipulating the available thermal resources on 30 plots (i.e., 15 pairs of home ranges) that had previously been occupied and defended as lizard territories (Calsbeek et al. 2002). We removed about 30% of the available rock habitat from half of the territories and used it to construct two to three rock additions on each of the adjacent territories. Rock additions consisted of 10–40 rocks each (mean = 15.7, SD = 11.1) and provided perch heights of about 0.5–1 m, which are similar to those available on naturally high-quality territories defended by males and females (personal observations). We used small (> 40-cm diameter), medium (40–75 cm), and large (> 75 cm) rocks to construct additions.

During 1999, we captured gravid females from the experimentally manipulated rock outcropping ( $N = 16$ ). During 2001, the spring following our manipulations, we captured an additional 18 females from a remote outcropping that had not undergone experimental territory quality manipulations. Capturing gravid females from a remote outcropping in 2001 allowed us to manipu-

late incubation temperatures for eggs in the laboratory, without the potentially confounding effects of differences in incubation temperatures that may have arisen through our manipulations of maternal territory quality. Furthermore, capturing females with recently fertilized eggs and housing them in the laboratory during the phase of the reproductive cycle in which females retain fertilized eggs in the oviduct allowed us to eliminate many of the in utero effects of territory quality on egg development that could have arisen after fertilization. Females retain eggs in the oviduct for an average of 10 days prior to laying. In both years, females were housed individually in the laboratory in plastic terraria with a damp mixture of sand and peat moss, and were provided food (*Achaeta* crickets) and water ad libitum. Terraria were kept in an environmental chamber with a 12L:12D photoperiod, and were provided with full spectrum fluorescent lamps and a 40-W bulb as a heat source. Terraria were checked daily for eggs.

### INCUBATION TEMPERATURE

During 1999, all eggs were incubated under standard laboratory conditions (28°C). Eggs were placed in individual 100-mL plastic cups filled with a 9:1 mixture of vermiculite and water, which maintained the hydric conditions (–200 kPa) that are near optimal for development (Sinervo et al. 1992). This mixture was changed weekly. Cups were placed in plastic boxes, wrapped in plastic bags and incubated until hatching. During 2001, we divided clutches of eggs from each female across three incubation temperature treatments to assess the importance of incubation temperature on timing of development. Clutches were divided into three groups of equal size (as permitted by total clutch size) and were randomly assigned to 26°C, 28°C, or 30°C incubators. Although we could have incubated eggs in variable temperature regimes more similar to incubation conditions experienced in the wild (Shine and Elphick 2001), variable incubation temperature would have made the detection of selection on other traits of interest more difficult. By varying incubation temperatures we intended to generate variation in hatching dates, the trait of interest in this study. We incubated a total of 100 eggs during 1999 and 125 eggs (44, 39, and 42 eggs at 26°C, 28°C, and 30°C, respectively) during 2001.

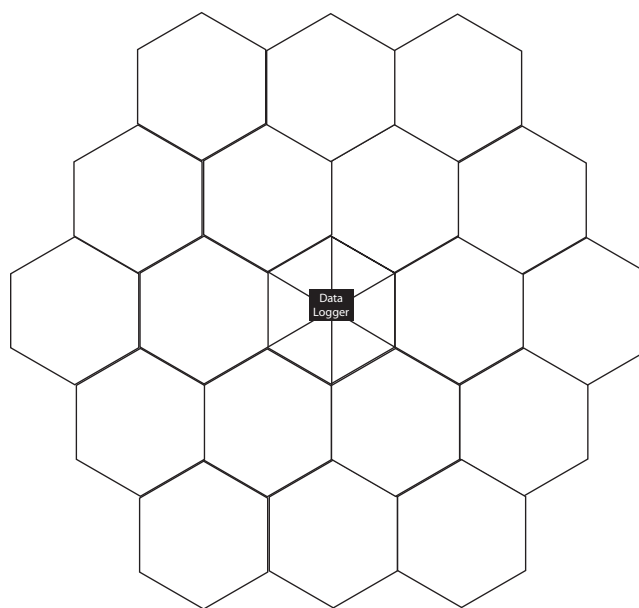
Upon hatching, all lizards were assigned a unique toe clip for permanent individual identification. Hatchlings were weighed (g), measured (snout-vent length [mm]), sexed (males have enlarged postanal scales), and released in the center of field plots. Progeny were randomized with respect to sibship (both years) and temperature treatment (2001 only), and were released in pairs to either improved (rock added) or reduced (rock removed) quality territory treatments (described above). We released a total of 75 progeny to experimental sites during 1999 (45 and 30 to improved- and reduced-quality sites, respectively), and 96 progeny to experimental sites during 2001 (55 and 41 to improved- and reduced-quality sites, respectively). Progeny were released within two days

of hatching and no more than one pair of hatchlings was released to an improved- or reduced-quality site on any given day. Total hatchling densities did not differ from densities normally experienced in nature (Svensson and Sinervo 2000). Prior to progeny releases, we removed all adult lizards from the entire experimental outcropping. Thus, hatchlings in both years were deposited on vacant home ranges.

### THERMAL PROPERTIES (2001)

We quantified differences in thermal quality among territories by constructing thermal maps of experimental plots using two hexagonal grids of 54 lizard models each. Models were built from 7.0-cm lengths of polyvinylchloride tubing (1.5-cm diameter), painted 18% gray to mimic the heat absorbency of *Uta*, and sealed at both ends with cork stoppers (Adolph 1990). Models housed a copper-chromium thermocouple designed to measure the body temperature of a lizard model with an accuracy of 0.1°C. This method has been shown to be effective (Adolph 1990), although some authors encourage further tests (Dzialowski 2005). Thermocouples were calibrated in the laboratory against a standard mercury thermometer, and an ice bath. All models simultaneously recorded temperature to a programmable data logger (Campbell scientific model CR-10, Campbell Scientific, Inc., Logan, UT) at 1-minute intervals over the entire day. Each day, one of the grids sampled temperatures on an improved plot whereas the other grid sampled temperatures on the adjacent reduced-quality plot. This method allowed us to make pairwise comparisons between neighboring experimental plots. To avoid problems associated with spatial autocorrelation of temperature data, we measured the 15 pairs of experimentally manipulated territories in random sequence.

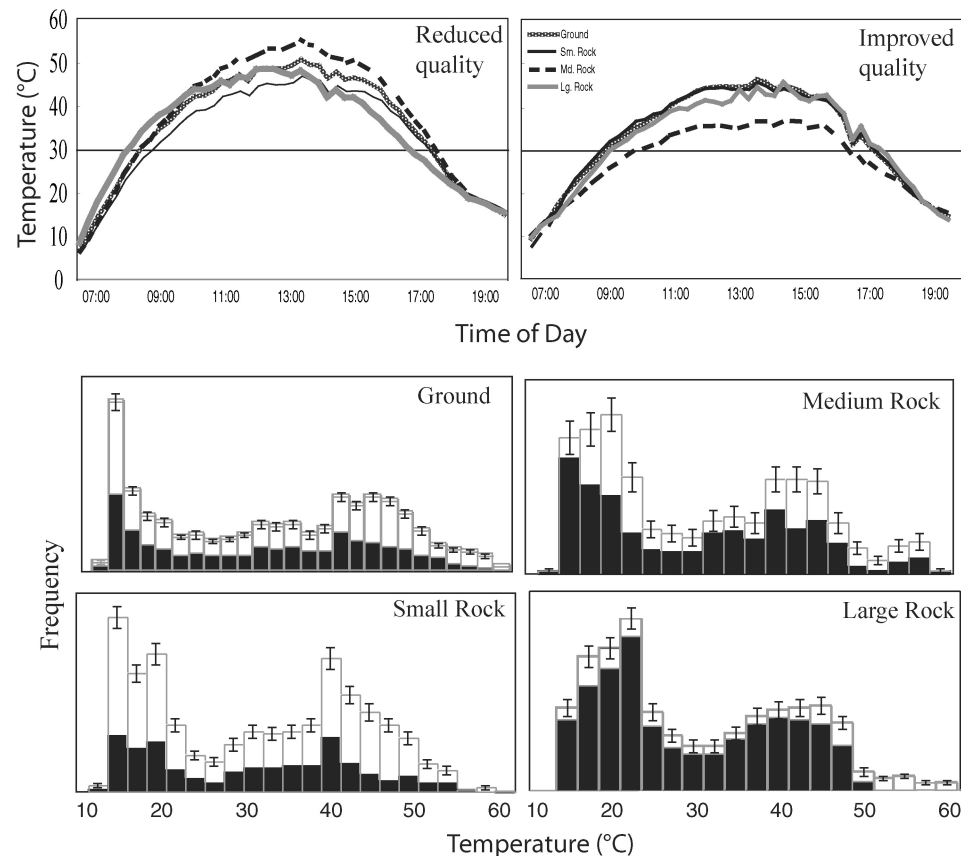
Thermal grids used to measure temperature were designed to be similar in diameter to an average male's territory. Each hexagon (with models at each vertex) measured 2 m on a side, and was tessellated with six others interior to the grid, or three others on the exterior. This pattern is extremely regular (i.e., hexagonal transect) and samples the frequency of available habitats at each site. The super-hexagon comprised of the entire array, consisted of 19 of such 2-m (sides) hexagons, thereby stretching about 10 m in diameter (Fig. 1). Thus, our grids sampled all, or most, of the available habitat on each site. The grids were always oriented to magnetic north at each site, along the vertical axis of the grid, to provide a very rigid sampling transect that reflects the relative frequency of objects on a plot. We sampled primarily terrestrial habitat near rock piles (mean models  $\pm$  SE =  $22.4 \pm 3.26$ ), small ( $5.1 \pm 1.11$ ), medium ( $1.88 \pm 0.39$ ), and large ( $3.33 \pm 0.75$ ) rocks (Fig. 2), and to a lesser extent the top surfaces of experimental rock piles, and cracks and retreat sites in rocks ( $N = 14.2 \pm 7.67$ ). We calculated the number of hours that each model registered temperatures within the range of *Uta*'s activity body temperatures (about 28–35°C; preferred body temperature 35°C, (Tinkle 1967) to esti-



**Figure 1.** Illustration showing the geometrical design of our thermal grid. We used a Campbell scientific CR10 data logger (housed in an insulated picnic cooler), which monitored model temperatures every minute, and generated an average temperature of the models every 15 min. Data were downloaded each night, when we disassembled and move the grid to the next location (always after sundown), and the move was completed in less than 30 min. Two grids were in continuous operation, one on the removal and one on the addition site for each location.

mate differences in the total number of hours available for behavioral thermoregulation for adults (Niewiarowski 2001; Dzialowski 2005). This measure is similar to the “panglossy” snake described by Huey et al. (1989) that is free to move across the territory, as sampled by models, to achieve its thermal preferendum. We calculated the variance in model temperatures at each of these specific sites as a measure of the diversity of microclimates available to individual resident lizards for basking. We also compared the overall grain of environmental variation on high- and low-quality plots by measuring the variation in number of hours of activity available for behavioral thermoregulation across each type of plot (standardized by the mean plot temperature). Coarse-grained environments, conducive to maintenance of genetically based alternatives, should have significantly higher variation in the number of hours for behavioral thermoregulation. Finally, to estimate the influence of temperature on lizard activity, we estimated the mean daily temperature (from lizard models) on our study sites and regressed this temperature value against the total numbers of lizards sighted that day. This estimate assumes that numbers of lizards seen each day is a reasonable estimate of lizard activity on the study site.

We measured differences in thermal quality at potential nest sites on lizard territories by burying thermocouples at three



**Figure 2.** Top panels show mean values of thermal profiles from adjacent low- (removal) and high (addition)-quality territories measured on the same day. The horizontal line at 30°C indicates the temperature above which side-blotched lizards are most active during the day. Lizard activity is restricted to temperatures above 30°C but below the CTMAX at about 40°C. Improved plots always provide temperatures below CTMAX but removal plots do not. Thus, experimentally improved sites had relatively more hours available for behavioral thermoregulation by side-blotched lizards compared to experimentally reduced quality sites. The lower panels show temperature distributions (+SE) from each of the four principal habitat types measured in our study (see text). Dark bars show values on improved quality sites, and light bars show values on reduced-quality sites.

different depths under rocks: 5, 10, and 15 cm under small medium and large rocks, respectively (Huey et al. 1989). High-quality territories provide all three potential nest types for females; however, low-quality territories provide only nests surrounded by small rocks (e.g., no experimentally added rock piles that are characteristic of high-quality sites in nature). We began measuring temperatures at potential nest sites when the first field-captured female laid her eggs, and continued until the last eggs hatched in the laboratory (only eggs from the first clutch). Thus, our nest-site measurements reflect differences in temperature regime on high- and low-quality territories during a biologically relevant phase of the reproductive cycle (March 17 to June 2; the range of incubation dates for the first clutch).

#### SURVIVAL

We measured the effects of hatching date, incubation temperature and territory quality on progeny survival. During the last weeks of September in 1999 and 2001, we recaptured all hatchlings from

our experimental plots. Side-blotched lizards are active throughout the entire day (Parker and Pianka 1975; Fox 1978) and it is unlikely that any lizards were missed during our censuses. The probability of capturing lizards is 0.97 during a given capture episode (Sinervo et al. 2006). Lizards that were not captured during this period were considered to have died. In addition, we monitored all rock outcroppings surrounding our experimental plots to a distance of 1 km. Surrounding plots were under investigation by other researchers and so were monitored with the same intensity as our experimental plots. This allowed us to record dispersal that may have occurred as a result of territory manipulations. None was recorded.

#### STATISTICAL ANALYSES

Parametric statistics were appropriate for all of our analyses unless otherwise noted. We used analyses of covariance to measure the effects of incubation temperature on progeny attributes (e.g., mass, size). We performed mixed model analyses including “dam



id" as a random factor to account for potential family effects. However, because family sizes were small and because progeny were released randomly with respect to sibship, family level effects were not significant and we report results only from the reduced models. We compared differences in the mean and variance in temperature on adjacent high- and low-quality plots and nest sites using paired *t*-tests. Linear ( $\beta$ ) and nonlinear ( $\gamma_{ii}$  and  $\gamma_{ij}$ ) selection gradients were estimated using standard parametric statistics (Lande and Arnold 1983; Phillips and Arnold 1989) on relative fitness and trait distributions were standardized to mean 0 and unit variance prior to analysis. Because survival data are binomial (live/die) and may violate the assumptions of parametric statistics (e.g., survival data tend to be heteroscedastic), we computed the significance of our analyses of survival using logistic regression (Janzen and Stern 1998). Fitness surfaces for progeny survival as a function of egg mass and laying date were fitted with multivariate cubic-spline regression (Schluter and Nychka 1994) and using parametric techniques. All data in the surface analyses were standardized to a mean of zero with unit variance (Lande and Arnold 1983). The cubic spline is a nonparametric method for estimating the form of selection on multiple variables and is useful for visualizing the form of selection in multivariate space. The best-fit cubic spline is found by searching over a range of  $\lambda$ -values and applying the  $\lambda$  that minimizes the generalized cross validation (GCV) score (a method analogous to minimizing the sum of squared error terms in a linear regression model).

Results from the selection analyses were similar in both years and we plotted nonparametric fitness surfaces from the pooled data set. However, smaller sample sizes in analyses conducted separately by plot and year made nonparametric spline fitting impractical (e.g., surfaces became too rough to be instructive). We therefore plotted parametric fitness surfaces for individual high- and low-quality territory treatments in individual years, using the nonparametric surfaces to inform interpretation of these surfaces following McGlothlin et al. (2005).

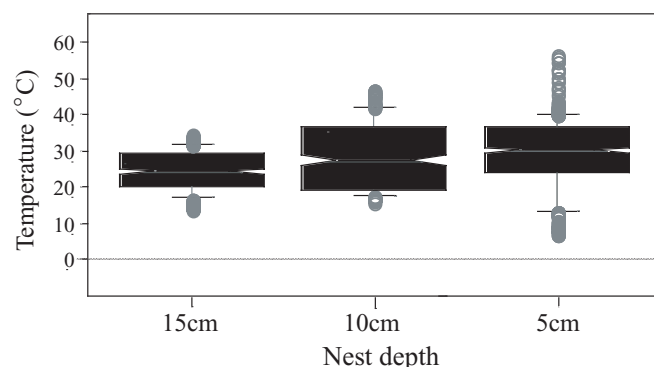
## Results

### THERMAL DIFFERENCES

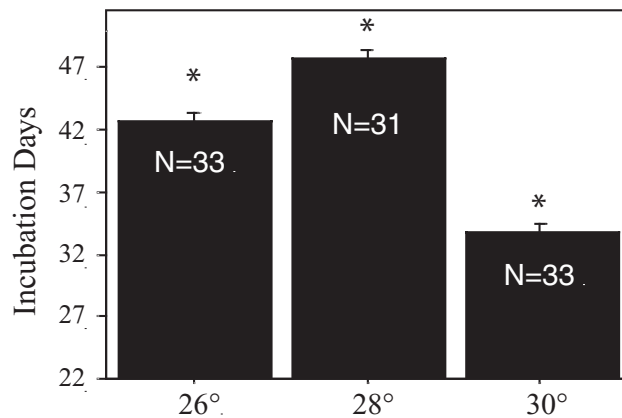
Rock manipulations had significant effects on territory quality. Experimentally improved territories had significantly more hours available each day for thermoregulation (the 73,500 temperatures recorded on the data logger were distilled to 15 pairs of means representing the average number of hours available on high versus low plots; paired *t*-test *t*-value = 3.37, *df* = 14, *P* < 0.005). Differences in experimentally improved and reduced-quality territories were most evident around rock manipulations (e.g., Fig. 2), where increased structural heterogeneity provided a wide range of microclimates available for thermoregulation. The range of microclimates at potential basking sites measured as the variance in

available basking temperatures (i.e., temperatures on rock habitat), was significantly higher on experimentally improved sites (paired *t*-test *t*-value = 3.46, *df* = 13, *P* = 0.004) (Fig. 2). However, environmental variation measured over entire plots was more coarse-grained on reduced-quality plots compared with improved plots (paired *t*-test of the difference in the coefficients of variation in temperature *t*-value = -2.50, *df* = 13, *P* = 0.01). We also found support for the hypothesis that differences in temperature should have effects on lizard energy budgets; the correlation between lizard activity (sightings/day) and average daily model temperature was significant ( $r^2 = 0.32$ , *df* = 13, *P* = 0.03).

We scored 19 potential nest sites over the course of our study. We measured differences in the mean and variance in temperature at all three nest-site depths (5, 10, 15 cm). Nest temperatures differed with nest depth (Fig. 3), but the difference in mean temperature was not significant (analysis of variance [ANOVA]  $F_{2,16} = 2.02$ , *P* = 0.1). However, the variance in temperature was significantly different among potential nest sites (ANOVA  $F_{2,16} = 15.36$ , *P* < 0.0002). Shallow nests (about 5-cm depth) under small rocks were exposed to higher and more variable temperatures than were nests at depths of either 10 or 15 cm covered by larger rocks or rock piles. Thermocouples buried at 10 cm under medium size rocks (about 0.75 m<sup>3</sup>) recorded temperatures at or near the thermal optima for egg incubation (i.e., the temperature at which hatching success is highest in the laboratory, about 28°C; Sinervo et al. 1992) and had considerably lower variance in temperature than did 5-cm nests. Finally, 15-cm nests had the lowest variance in



**Figure 3.** Nest quality varied significantly among the three different types of sites. Eggs incubated in deep (15 cm) and shallow (5 cm) nests would experience incubation temperatures different from those that optimize hatching success in the laboratory (about 28°C). In addition, thermal variation experienced by eggs incubated in shallow nests would be far too high to produce viable progeny. By contrast, eggs incubated at 10 cm under medium-sized rocks experienced thermal conditions near the optimum as measured in the laboratory. Box and whisker plots indicate the mean and associated variance for each treatment. Horizontal lines within box plots indicate the median.



**Figure 4.** Incubation times differed significantly among incubation temperature treatments. Eggs incubated at 26°C and 30°C required significantly fewer days for incubation compared with eggs incubated at 28°C. Histogram bars represent the mean (+1 SE). Numbers within histogram bars indicate sample sizes for each treatment. Following correction for three pairwise comparisons, all differences remained statistically significant (\*).

temperature; however, the mean nest temperature (24°C) of these nests was lower than the thermal optima for egg incubation (Sexton and Marion 1974) (Fig. 3).

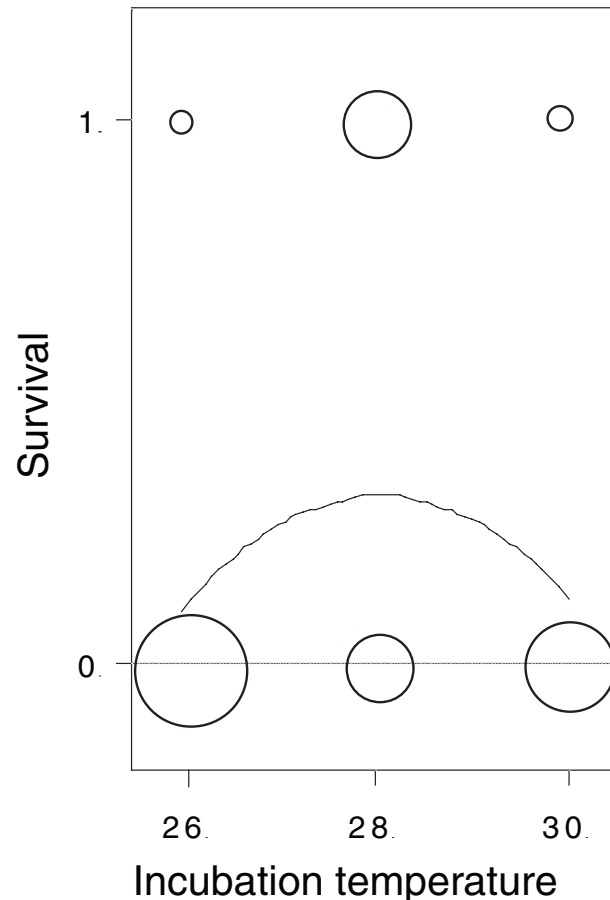
Hatching success did not differ among incubation treatments (75%, 79%, and 79% from 26°C, 28°C, and 30°C, respectively; logistic regression Wald  $\chi^2 = 0.21$ ,  $P = 0.65$ ). However, incubation times differed across all temperature treatments. Eggs from the 26°C and 30°C treatments required significantly fewer incubation days than did eggs from the 28°C treatment, and eggs from the 26°C treatment were intermediate in incubation time between the other treatments (ANOVA  $F_{2,94} = 134.74$ ,  $P < 0.0001$ ; all pairwise comparisons remained significant following Bonferroni adjustment for multiple comparisons, Fig. 4).

#### DIFFERENCES IN SURVIVAL

Incubation temperature affected hatchling survival. We detected strong and significant stabilizing selection (Fig. 5) on incubation temperature favoring eggs incubated at 28°C (ANOVA  $F_{11,21} = 8.04$ ,  $P < 0.005$ ). Although progeny from intermediate incubation temperatures had a survival advantage, we also measured linear selection that tended to favor progeny from larger eggs ( $\beta = 0.351$ ,  $P = 0.003$ ) that hatched earlier in the season ( $\beta = -0.302$ ,  $P = 0.01$ ; Table 1), a result that is consistent with classical predictions based on life-history theory (Darwin 1859; Price et al. 1988). However, multivariate selection revealed that results were more complicated and depended on variation both between years and between high- and low-quality sites.

#### CORRELATIONAL SELECTION

We measured significant correlational selection on laying date and egg mass. Averaging the combined effects of selection across



**Figure 5.** We measured strong stabilizing selection on egg incubation temperature. Progeny were significantly more likely to survive in our fall censuses when incubated at 28°C than were progeny incubated at 26°C or 30°C. Relative size of datapoints indicates the relative numbers of individuals that either lived or died in each treatment.

both years of our study (Fig. 6E, F; Fig. 7A, B), it was found that selection on low-quality territories (Fig. 6F, 6B) was very strong and included two optima, one favoring large progeny early and another favoring small progeny late in the summer (correlational selection gradient for both years:  $\gamma_{1,2} = -0.634$ ,  $P < 0.008$ ; see Table 1 for detailed results by plot and year). By contrast, the pattern of selection on high-quality territories (Fig. 6A, E) was weak and nearly flat ( $\gamma_{1,2} = -0.052$ ,  $P = 0.77$ ), the converse of the pattern observed on low-quality territories. The difference in correlational selection between high- and low-quality territories was significant in both years of our study (Table 1), suggesting that variation in thermal properties on territories influenced the strength and curvature of selection on life-history traits.

Results (i.e., three-way interactions) were significantly different by territory treatment during both 1999 (Fig. 6A, B) and

**Table 1.** Selection on egg mass and laying date during (A) both years of our study combined and broken down by plot, (B) 1999 alone and by plot, and (C) 2001 alone and by plot. Correlational selection differed as a function of territory quality (experimentally improved vs. reduced-quality territories). The dependent variable is survival (live/die). Significance values are from a nominal logistic regression with binomial errors. Significant terms are highlighted in gray, the interaction between egg mass and laying date indicates correlational selection. Abbreviations are as follows: EM, egg mass; LD, laying date; TQ, territory quality. All traits were standardized to have mean zero with unit variance. Linear and quadratic terms come from separate regressions.

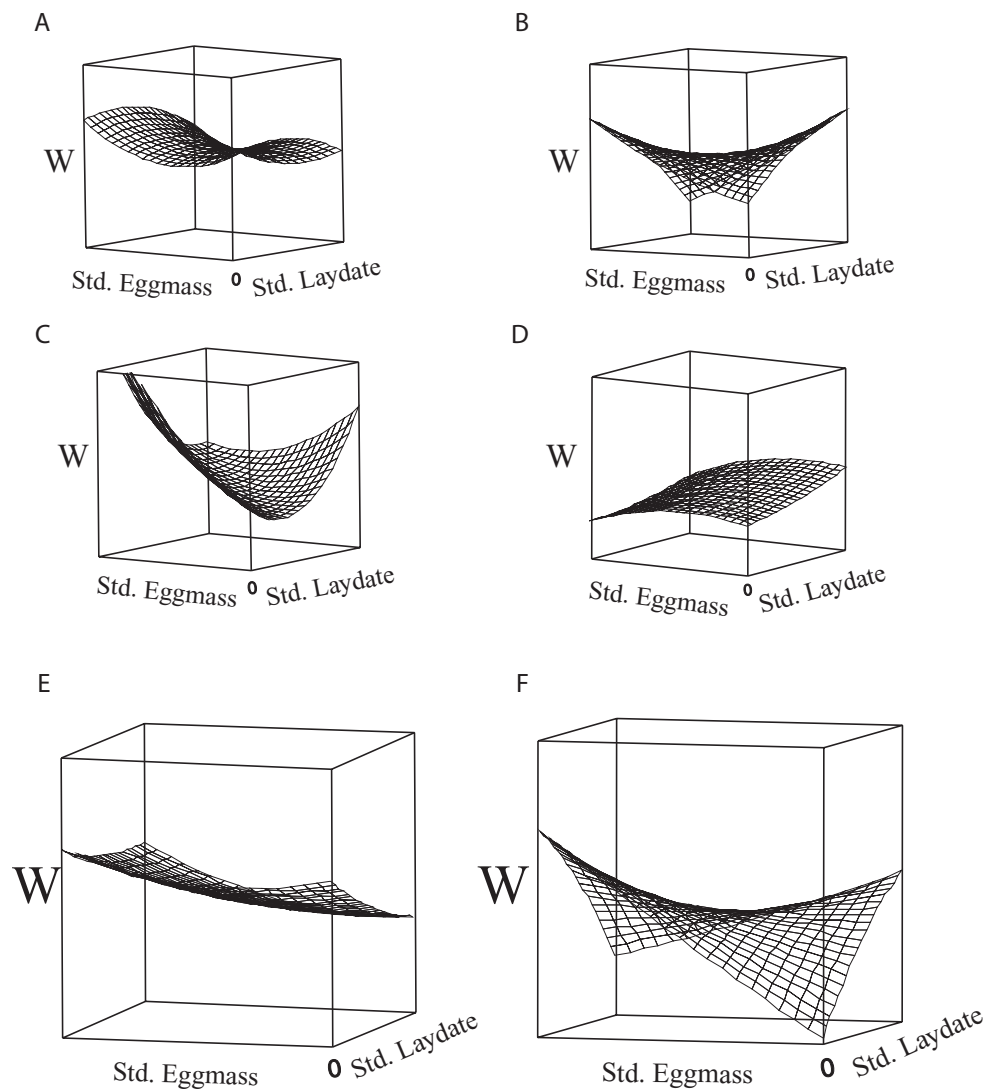
A				
	$\beta/\gamma$	SE	<i>t</i> -ratio	<i>P</i>
Source for W (both years)				
Intercept	0.843	0.221	3.82	0.0002
EM	0.351	0.117	3.00	<b>0.0031</b>
EM <sup>2</sup>	0.017	0.168	0.10	0.9174
LD	-0.302	0.117	-2.58	<b>0.0109</b>
LD <sup>2</sup>	0.039	0.159	0.25	0.8048
EM×LD	-0.269	0.173	-1.55	0.1222
TQ	-0.171	0.219	-0.78	0.4375
EM×TQ	0.143	0.159	0.90	0.3709
EM <sup>2</sup> ×TQ	-0.127	0.168	-0.76	0.4486
LD×TQ	0.355	0.185	1.91	<b>0.0574</b>
LD <sup>2</sup> ×TQ	-0.054	0.159	-0.34	0.7367
EM×LD×TQ	-0.364	0.173	-2.10	<b>0.0373</b>
Source for W (both Hi)				
Intercept	1.134	0.256	4.43	<.0001
EM	0.419	0.184	2.28	<b>0.0250</b>
EM <sup>2</sup>	0.0729	0.180	0.41	0.6863
LD	-0.331	0.198	-1.68	0.0972
LD <sup>2</sup>	-0.118	0.138	-0.85	0.3949
EM×LD	-0.052	0.179	-0.29	0.7702
Source for W (both Lo)				
Intercept	0.688	0.309	2.23	0.0296
EM	0.409	0.184	2.22	<b>0.0302</b>
EM <sup>2</sup>	-0.110	0.253	-0.43	0.6657
LD	-0.081	0.191	-0.43	0.6701
LD <sup>2</sup>	-0.014241	0.154168	-0.09	0.9267
EM×LD	-0.633914	0.230697	-2.75	<b>0.0078</b>
B				
Source for W 1999				
Intercept	0.874	0.217	4.03	0.0002
Sex	0.098	0.061	1.62	0.13
EM	0.055	0.127	0.44	0.6642
EM <sup>2</sup>	0.210	0.1278	1.65	0.1052
EM×sex	0.186	0.143	1.30	0.2003
LD	-0.278	0.127	-2.19	<b>0.0318</b>
LD <sup>2</sup>	0.054	0.186	0.29	0.7739
LD×sex	-0.377	0.176	-2.15	<b>0.0363</b>
LD×EM	-0.456	0.215	-2.13	<b>0.0379</b>
TQ	-0.032	0.141	-0.23	0.8209
EM×TQ	0.002	0.163	0.01	0.9926
LD×TQ	0.252	0.187733	1.34	0.1851
EM×LD×TQ	-0.445711	0.228571	-1.95	<b>0.0563</b>

Continued

**Table 1.** Continued

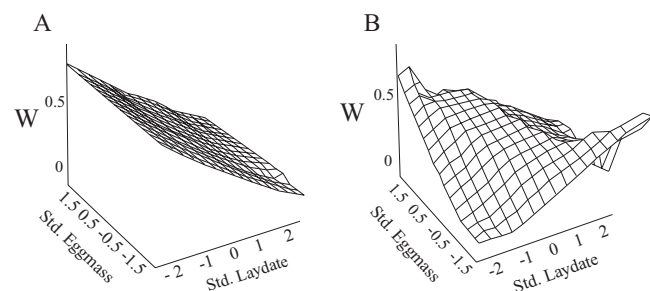
	$\beta/\gamma$	SE	<i>t</i> -ratio	<i>P</i>
Source for W (1999 Hi)				
Intercept	1.096	0.286	3.83	0.0005
Sex	0.058	0.083	0.69	0.4947
EM	0.039	0.147	0.26	0.7947
EM <sup>2</sup>	0.151	0.135	1.12	0.2681
EM×sex	0.110	0.159	0.69	0.4928
LD	-0.295	0.155	-1.90	0.0649
LD <sup>2</sup>	-0.210	0.187	-1.12	0.2682
LD×sex	-0.191	0.161	-1.19	0.2431
EM×LD	-0.064	0.178	-0.36	0.7218
Source for W (1999 Lo)				
Intercept	0.8368445	0.282265	2.96	0.0083
Sex	0.11	0.092	1.20	0.243
EM	0.0899097	0.267393	0.34	0.7397
EM <sup>2</sup>	-0.048272	0.280326	-0.17	0.8652
EM×sex	0.6874277	0.264902	2.60	<b>0.0183</b>
LD	-0.25535	0.237422	-1.08	0.2933
LD <sup>2</sup>	0.1774676	0.211347	0.84	0.4121
LD×sex	-0.664442	0.263614	-2.52	<b>0.0214</b>
EM×LD	-0.700596	0.495447	-1.41	0.1744
C				
Source for W (2001)				
Intercept	0.191	0.345	0.55	0.5812
Sex	-0.009	0.038	-0.26	0.7957
EM	0.153	0.213	0.72	0.4736
EM <sup>2</sup>	0.007	0.138	0.05	0.9611
EM×sex	-0.539	0.229	-2.34	<b>0.0215</b>
LD	0.342	0.237	1.45	0.1513
LD <sup>2</sup>	0.951	0.269	3.53	<b>0.0007</b>
LD×sex	0.256	0.276	0.93	0.3558
EM×LD	-0.348	0.267	-1.30	0.1956
TQ	0.109	0.345	0.32	0.7507
EM×TQ	-0.183	0.245	-0.75	0.4559
LD×TQ	0.051	0.290	0.18	0.8600
EM <sup>2</sup> ×TQ	-0.262	0.139	-1.89	0.0620
LD <sup>2</sup> ×TQ	-0.242	0.253	-0.95	0.3426
EM×LD×TQ	0.534	0.266	2.01	<b>0.0479</b>
Source for W (2001 Hi)				
Intercept	0.008	0.482	0.02	0.9876
Sex	-0.018	0.053	-0.34	0.7333
EM	0.266	0.315	0.84	0.4026
EM <sup>2</sup>	0.286	0.169	1.70	0.0962
EM×sex	-0.704	0.304	-2.32	<b>0.0247</b>
LD	-0.039	0.354	-0.11	0.9115
LD <sup>2</sup>	1.26	0.382	3.33	<b>0.0017</b>
LD×sex	0.406	0.368	1.10	0.2755
EM×LD	-0.904	0.481	-2.17	<b>0.0666</b>
Source for W (2001 Lo)				
Intercept	0.313	0.477	0.66	0.5155
Sex	0.004	0.055	0.07	0.9461
EM	0.067	0.261	0.26	0.7987
EM <sup>2</sup>	-0.223	0.209	-1.07	0.2934
EM×sex	-0.306	0.369	-0.83	0.4135
LD	0.844	0.290	2.91	<b>0.0060</b>
LD <sup>2</sup>	0.633	0.355	1.78	0.0842
LD×sex	0.106	0.383	0.28	0.7848
EM×LD	0.122	0.316	0.39	0.7011





**Figure 6.** Fitness surfaces showing combined fitness effects of egg mass and laying date for individual (smaller surfaces) and pooled (larger surfaces) high- and low-quality plots in 1999 and 2001; (A) 1999 high quality, (B) 1999 low quality, (C) 2001 high quality, (D) 2001 low quality, (E) average effect on high-quality plots, (F) average effect on low-quality plots. Correlational selection was significantly different between high- and low-quality plots in both years. All variables were standardized to mean 0 with unit standard deviation.

2001 (Fig. 6C, D). When we decomposed this analysis by territory quality, we found that the overall strength of correlational selection was tied primarily to low-quality territories during 1999 but to high-quality territories during 2001 (see coefficients Table 1). This between-year reversal in the effect of territory quality on correlational selection took place as population density and population frequency of the *o* allele climbed from low to high and may be explained by increased competition for high-quality sites (see Discussion). Furthermore, we detected subtle differences in the selective effects of sex between years. Differences in selection acting on males and females in the two years of our study are consistent with previous works (Sinervo et al. 1992) and, similar to the effects of territory quality are driven by changing phases of the



**Figure 7.** Fitness surfaces as in Figure 6 E and F, but plotted using the nonparametric cubic spline. (A) Pooled fitness surface on high-quality plots, (B) pooled fitness surface on low-quality plots. All variables were standardized to mean 0 with unit variance prior to visualization using the cubic spline.

population density cycle (Sinervo et al. 2001). In summary, territory quality manipulations resulted in different thermal regimes (including differences in nest-site quality) that influenced both lizard activity patterns and the multivariate selection pressures acting on life-history traits.

## Discussion

Previous work in the side-blotched lizard system has demonstrated that both males and females have a strong preference for experimentally improved territories (Calsbeek et al. 2002; Calsbeek and Sinervo 2002a), and that both males and females benefit from high-quality territories. Males benefit because high-quality sites improve growth rates and attract large numbers of females. Here we present the selective consequences of differences in territory quality and incubation temperature for females and their progeny. We measured viability selection on progeny, but because traits are influenced by maternal site choice and oviposition date, the effects of selection may be weaker than predicted here (Wolf and Wade 2001). Elsewhere we have shown that females on high-quality territories produce progeny with higher fitness than do females in low-quality territories (Calsbeek and Sinervo 2002a). Progeny fitness is the result of growth rate and survival to maturity (Calsbeek and Sinervo 2002a), traits that are optimized on high-quality territories. We have also shown that males compete vigorously over improved territories (Calsbeek et al. 2002), and that territory quality enhances male access to females (Calsbeek and Sinervo 2002b). Below, we discuss the ecological and selective consequences for lizards occupying high-quality territories in nature.

### THE ECOLOGY OF TERRITORY QUALITY

Experimental rock manipulations had significant effects on territory quality and progeny survival. We discuss thermal differences here, but point out that manipulations of territory quality could also have effected food availability, and predation regimes (Calsbeek and Sinervo 2002a), factors that might also contribute to survival differences on high- and low-quality plots. In addition, differences in egg incubation temperature had important effects on both incubation time in the laboratory and survival in the wild. Although effects on incubation time were collected in the laboratory, it is reasonable to expect that differences in incubation temperature arising due to variation in nest-site quality would have the same effects in the wild. Our measures of thermal quality at potential nest sites suggest that such differences do exist between high- and low-quality territories in nature. However, carrying out similar experiments with actual nests in the wild would be impossible given that nests are laid under rocks and are difficult to find. Once uncovered, the soil interface around the rocks would be disrupted and promote loss of soil moisture, which is essential

for the development of squamate eggs. Although we cannot directly test these effects on natural territories, other evidence from nature suggests that variation in territory and nest-site temperatures are important for females. Orange females tend to aggregate on south-facing slopes where temperatures are consistently high, in contrast yellow females are more likely to establish territories on northern parts of the rock outcropping (personal observation and Sinervo and Calsbeek, unpubl. ms.). Thus, selection appears to have shaped the ecological preferences of female morphs to maximize fitness as a function of the thermal habitat available to each type (e.g., high- vs. low-thermal quality).

Data from experimentally improved sites are consistent with lizards having more hours available for thermoregulation (Niewiarowski 2001) and having access to better nest sites (nearer optimal conditions for incubation) than lizards on reduced-quality sites. The latter conclusion is based on our observation that females on high-quality sites would have access to all three nest depths and rock-size distributions, whereas females on low-quality sites would be limited to shallow nests under small rocks (about  $0.1 \text{ m}^3$ ). Although some studies have demonstrated that higher variance in nest-site temperature may be adaptive for progeny development (Shine and Harlow 1996; Shine and Elphick 2001; Shine and Kearney 2001) this is unlikely to be the case for *Uta* living at Los Baños Grandes. Studies that show adaptive value in variable thermal regimes at potential nest sites generally exist at higher latitudes where diurnal temperature fluctuations in nests are still within the thermal tolerance of developing embryos. By contrast, highly variable nest sites associated with the small rocks (about  $0.1 \text{ m}^3$ ) in our study population experience thermal extremes (e.g.  $>60^\circ\text{C}$ ; Fig. 2) that would certainly kill lizard eggs (Angilletta Jr. et al. 2000). Even if variable incubation temperatures were somehow adaptive for *Uta* at Los Baños Grandes, experimentally improved sites provide a range of habitat suitable for females to make adaptive egg-laying decisions. Females on reduced-quality territories would have no such range of options. From Figure 3 we predict that females are likely to lay their eggs about 10–12 cm under medium-sized ( $0.3 \text{ m}^3$ ) boulders if they are adapted for oviposition site choice.

### CORRELATIONAL SELECTION, TERRITORY QUALITY, AND THE EVOLUTION OF ALTERNATIVE STRATEGIES

The fitness surfaces in Figures 6 and 7 demonstrate that egg size and laying dates are under strong correlational selection in this system, and the experimental manipulation of territory quality ties selection to the availability of good-quality territory. Correlational selection acts on the genetic architecture of morphs (Forsman and Appelqvist 1998; Abbott and Svensson 2005), favoring successful combinations of genes for egg mass and laying date in the two alternative morphs of females (Svensson and Sinervo 2000; correlation selection on a large number of female traits is reviewed in

Sinervo and Svensson 2002). Elsewhere (Sinervo and Calsbeek, unpubl. ms.) we report on the natural correlational selection gradients that shape female morphs, incubation time, laying date, and egg size. Results from the natural fitness surfaces corroborate the experimental correlational selection gradients reported here. Laying date, and territory quality both had important effects on progeny survival.

Our experimental manipulations of territory quality on field plots effectively altered environmental grain experienced by females on manipulated territories, and the availability of basking sites was significantly higher on high-quality plots compared to low-quality plots. We have previously shown that both males and females significantly prefer these improved sites (Calsbeek et al. 2002). Years in which population density and the frequency of the *o* allele are high (e.g., during 2001 on these study plots), heightened competition for improved sites appears to depress fitness for the same trait combination of laying date and egg mass that had high fitness on low-quality plots (Svensson and Sinervo 2000; Sinervo et al. 2001; Sinervo et al. 2006). However, when population density was low (e.g., 1999), competition was relaxed and females on low-quality sites suffered reduced fitness compared to females that secured a high-quality territory.

Fitness effects are also consistent with the observed ecological niche partitioning between genetically based female morphs in this system. Orange females are more likely to occupy south-facing slopes on natural plots. Hot sites lead to earlier egg-laying dates and consequently earlier hatching dates for progeny. By contrast, yellow females tend to occupy north-facing slopes and are subject to cooler temperatures. These thermal preferences may help explain why the correlational selection gradient was linked to low-quality territories in 1999 but high-quality territories in 2001. From 1999 to 2001 we measured a spike in the frequency of orange alleles (from 5.2% to 9.8% in females, and from 5.5% to 20.1% in males) that likely increased competition for high-quality sites (Calsbeek et al. 2002) and depressed fitness on these territories in 2001. In particular, the changes in correlational selection in our experimental manipulation of territory quality are entirely consistent with oscillations in the strength of correlational selection in the natural variation. In addition, statistical models from separate years (Table 1) require different use of sex terms depending on changes in the phase of female density (Sinervo et al. 2001) and male Rock-Paper-Scissors (Sinervo and Lively 1996) cycles. Among-year differences in selection acting on males and females have been demonstrated elsewhere (Sinervo et al. 1992) and are observed across all years of the RPS game (Sinervo, unpubl. data). We explore the morph-specific fitness consequences of territory quality in the context of the natural female life-history density cycle in greater detail elsewhere (Sinervo and Calsbeek, unpubl. ms.). We also present heritability estimates for laying date (Sinervo and Doughty 1996) and discuss the link between exper-

imental results presented here and selection results from natural (i.e., control) plots.

The average fitness surface for progeny from low-quality territories (Fig. 6B, F) is topologically very similar to that described by Svensson and Sinervo (2000) on natural territories in the wild. The dominant feature of both of these surfaces is a disruptive landscape indicating a fitness trough at intermediate hatching dates and egg masses with optimal strategies in opposing corners. The similarity between the surfaces from natural plots (Svensson and Sinervo 2000) and from our experimental plots suggests that most females on natural plots experience ecological conditions similar to those on experimentally reduced quality plots. Svensson and Sinervo (2000) suggested that the fitness trough resulted from density dependent competitive interactions among first and later clutch progeny, based on experimental manipulations of the presence versus absence of first clutch progeny on later clutch progeny. Evidence from the present experiment suggests that interactions between density and variation in habitat quality contribute to the complexity of the fitness surface. Fitness troughs that are shaped by physiological or developmental traits (e.g., thermal preferences) tend to be constant over time owing to the fact that certain (genetic) trait combinations (e.g., morph and temperature preference) will always have low fitness (Wright 1932, 1988). In contrast, an ecological fitness trough (e.g., density competition as demonstrated by Svensson and Sinervo 2000) would more likely respond to changes in environmental conditions (Fisher 1930). Although we could not score progeny genotypes in this study (juvenile *Uta* do not express throat color, hence we can not resolve the surface by progeny morphotypes), elsewhere we show that a very similar selective surface arises owing to the fitness differences between morphs scored as adults (Sinervo and Calsbeek, unpubl. ms.). Thus, it appears that the thermal preferences of genetically based female morphs, as well as competition among early versus late progeny, contribute to the fitness troughs observed in both studies. Given that they purposely controlled incubation temperature to 28°C to eliminate salient nest-site maternal effects, Svensson and Sinervo (2000) may have underestimated the contribution of environmental variation in shaping the fitness landscape for these lizards. Nevertheless, the selection gradients on egg mass are some of the highest reported for natural populations (Sinervo et al. 2000).

The grain of social or environmental variation is predicted to have consequences for the likelihood of evolving alternative morphs (Lively 1986; Sinervo 2001). For example, individuals in a fine-grained environment experience a wide range of environmental conditions during their lifetime. Such a variable selection regime should favor plasticity in traits governing alternative life-history or reproductive strategies (Caro and Bateson 1986; Pfennig 1992). However, individuals in a coarse-grained environment are more likely to evolve fixed genetic differences that may

lead to the evolution of alternative strategies (Shuster 1989; Sinervo 2001). Our results partially support these predictions in that the environmental variation introduced by our territory quality manipulations changed the form of correlational selection on female morphs. However, between-year differences in the effects of territory quality suggest that the role of environmental variation may be density dependent, and that coarse social environments at high density (e.g., high competition) may be responsible for the correlational selection measured in 2001.

Experimental manipulations of territory quality performed in this study reflect differences between high- and low-quality territories that exist naturally in the wild. Thus, our results underscore the importance of ecological factors such as territory quality to mate choice (Emlen and Oring 1977). Females should be under strong selection to choose high-quality territories, and males should likewise compete for high-quality territories to attract females. Indeed, results from previous studies examining the selective consequences of both intra- and intersexual conflict reveal that high-quality territories provide adaptive benefits to both males and females (Calsbeek and Sinervo 2002b). Our results reveal a potentially important factor that contributes to the density and frequency cycle of the two female morphs—thermal quality of territories. Orange females require high-quality territories such that their smaller progeny can hatch earlier and establish priority over later hatching progeny (Sinervo and Calsbeek, unpubl. ms.). However, at high density, the intense competition between orange females invariably forces many of them to establish territories on very low-quality sites that induce delayed oviposition and long incubation time, both of which are deleterious for orange female fitness. Under these conditions, any progeny produced by orange females would be very poor competitors compared to progeny from yellow-throated females that are adapted to delayed oviposition and long incubation times. Accordingly, progeny from yellow-throated females have higher survival than progeny from orange-throated females as the entire population crashes to low density. Furthermore, orange females experience a population-wide failure in progeny recruitment. Therefore, the intense competition of orange-throated females for the limited high-quality thermal territories on south-facing slopes creates low fitness in high-density years. Thus heterogeneity in thermal quality of territories, in addition to other life-history traits such as egg mass and clutch size, appears to be an important factor contributing to the density cycle of female morphs. Similar environmental heterogeneity may play a role in other population cycles, such as those found in mammals at high latitudes.

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