Spatial Scale and Temporal Component of Selection in Side-Blotched Lizards

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ABSTRACT: Spatial variation in selection has long been recognized as promoting population divergence and in maintaining genetic polymorphisms, but selection at a fine spatial scale is seldom measured directly. We analyzed spatial and temporal variation in selective regimes on egg size using long-term population data of the side-blotched lizard (*Uta stansburiana*). Juvenile survival rates varied between years at a small spatial scale that was reflected as a strong interaction between the local neighborhood level and year. Spatially and temporally variable selection acted jointly on egg mass, which presumably would facilitate the maintenance of high additive genetic variance for this trait. Local selection gradients calculated at the neighborhood level were significantly correlated with the annual global selection gradients calculated at the metapopulation level. However, there was substantial variance in these local selective regimes, which suggests that strong local selection could go undetected if the analysis was limited to the global level. We also investigated the degree of spatial synchronization among outcrop in local selection gradients. The degree of synchrony was higher among later-clutch hatchlings than among first-clutch hatchlings, and we suggest that more intense density- and frequency-dependent selection on egg size later in the season is responsible for this effect.

Keywords: competition, egg mass, frequency dependence, polymorphism.

Evolutionary biologists have long been aware of the importance of the spatial scale of selection in the genetic differentiation of populations. The spatial scale over which selection favors particular phenotypic traits or alleles relative to the scale at which dispersal takes place is a critical parameter in models about the evolution of clines (Slatkin 1973), multiple-niche polymorphisms (Levene 1953), species ranges (Kirkpatrick and Barton 1997), and metapopulation biology (Barton and Whitlock 1997) and in theories about the adaptive value of plastic phenotypes versus genetic morphs in coarse and fine-grained environments (Levins 1968). The strength of selection at a global scale in large panmictic populations relative to the strength of local selection at the level of demes in structured populations was one of the major controversies between R. A. Fisher and S. Wright in their different views of the evolutionary process (Fisher 1930; Wright 1932; Provine 1986; Barton and Whitlock 1997; Coyne et al. 1997; Wade and Goodnight 1998).

Most workers recognize that strong local selection, which varies in direction and magnitude between demes, is important since it can potentially both maintain genetic polymorphisms and permit the buildup of substantial levels of adaptive linkage disequilibrium between traits under selection (Levene 1953; Felsenstein 1976; Wade and Goodnight 1998; Sinervo and Svensson 2002). Indeed, one of the recent models of sympatric speciation suggests that such local selection in structured populations will, in combination with genetic drift, tip the balance between recombination and selection to facilitate speciation (Dieckmann and Doebeli 1999). Although many workers have applied the statistical framework developed by Lande and Arnold (1983) to investigate and quantify the strength of selection on phenotypic traits in nature, few have studied more than one or a few target populations simultaneously, and selection studies are thus seldom spatially or temporally replicated (Endler 1986; Kingsolver et al. 2001). Notable exceptions are long-term studies of temporal variation in selection on morphological traits of finches and flycatchers (Merilä et al. 2001; Grant and Grant 2002) and analyses of spatial variation in selection in some plant study systems (Stratton 1994, 1995; Stratton and Bennington 1998; Juenger and Bergelson 2002). The next step in selection analysis must be to extend these efforts to other study systems and analyze spatial heterogeneity in

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selective regimes (Heisler and Damuth 1987; Wade and Kalisz 1990; Barton and Whitlock 1997).

In this article, we use data from our long-term population study of side-blotched lizards (*Uta stansburiana*) to assess spatial scale and temporal (between-generation) variation in selection. Side-blotched lizards are very appropriate to address these questions because we can investigate selection and dispersal in great detail, since these lizards are easy to capture, mark, and follow throughout their life span. Recently, we have investigated how selection on egg size, an important trait for juvenile survival, is strongly affected by year-to-year variation in density- and frequency-dependent competitive interactions (Sinervo et al. 2000; Svensson and Sinervo 2000).

At our study area in Los Banos, central California, the lizards inhabit semi-isolated rock outcrops, generating a metapopulation structure in which the selective regimes and local densities vary strongly between both different neighborhoods and different years (Sinervo et al. 2000; Svensson and Sinervo 2000). We used this long-term data set, consisting of more than 2,700 individually marked female lizard hatchlings over a decade of study, to investigate variation in survival and selection in relation to year and two spatial levels: outcrop groups and neighborhoods. We also calculated spatial autocorrelations between outcrop groups to investigate the degree of spatial synchrony of selective regimes. Finally, we compared our estimates of local selection on outcrops with those of global selection from the whole population.

Material and Methods

Fieldwork

Details about the natural history of side-blotched lizards and general field methods are provided elsewhere (Sinervo et al. 2000; Svensson and Sinervo 2000). We only summarize the main points here. The side-blotched lizard is a small (6–9 g) iguaniid lizard that matures at 9 mo and rarely survives more than one reproductive season. Most adult mortality is due to snake predation, which especially affects gravid females that are yolking up their eggs (Sinervo and DeNardo 1996). The reproductive season begins in late February or early March each year, and the first clutches are laid in April. Females lay clutches of two to 10 eggs, separated by approximately 1 mo during the reproductive season, which may extend throughout August. Throat color morphs, which are not the main subject in this article, develop among adult males and females during the reproductive season (Sinervo and Lively 1996; Sinervo et al. 2000), but throat color is not expressed among the hatchlings that are the subject of the analyses in this article.

Basic fieldwork consists of regular captures, recaptures, and resightings of marked individuals in the field and territorial mappings. Near-term gravid females are collected and brought to an indoor laboratory for oviposition. Freshly obtained eggs are incubated in a common laboratory environment, which controls for maternal effects due to variation in oviposition sites among dams (Svensson et al. 2001*a*). After the incubation period, which lasts for 40–50 d, new hatchlings are marked (toe clips) and released at sites in the field that are random with respect to the dam's territory (Sinervo 1999).

Hatchlings were released at local mapped positions in our study area. The main areas at which hatchlings were released are hereafter denoted "neighborhoods." Neighborhoods are defined as isolated or semi-isolated contiguous areas of rocks, separated from other neighborhoods by areas of grassland or other unsuitable lizard habitat. A total of nine different neighborhoods were studied, and they form the lowest spatial level of analysis in this article (fig. 1). Data on selection gradients and local survival rates are not available from all neighborhoods for all years, because in low-density years, there were not enough hatchlings to calculate these parameters for every single neighborhood. Sample sizes do therefore vary between analyses. We were also interested in whether a higher spatial (regional) level could be important in explaining hatchling survival and variation in selection, and we therefore defined such a higher level, which we hereafter denote the "outcrop group." Outcrop groups are clusters (two to three) of adjacent and closely located neighborhoods, and because of their close physical affiliation, they are likely to share similar physical characteristics (e.g., temperature, sun exposure, or moisture). Four such outcrops groups (A–D) were considered in the analyses, and each of these consists of two or three neighborhoods (fig. 1): A (Monet 1 and Monet 2), B (Duet and Triplet), C (E-quartet and W-quartet), and D (Bchd, Sat, and Sqrk).

Demarcation of outcrop groups and neighborhoods was performed on the basis of considerations on habitat structure (e.g., stretches of grassy areas that are not preferred by lizards) and background knowledge about dispersal distances of lizard hatchlings (Doughty and Sinervo 1994). Demarcation of outcrop groups and neighborhoods took place before any selection analyses and without any prior knowledge about spatial variation in selective regimes, as part of our previous studies on density- and frequency-dependent selection on egg size (Sinervo et al. 2000; Svensson and Sinervo 2000). Hence, spatial demarcations are based entirely on natural history considerations, making it possible to evaluate how successful we were in choosing the appropriate spatial scale in our previous selection analyses.
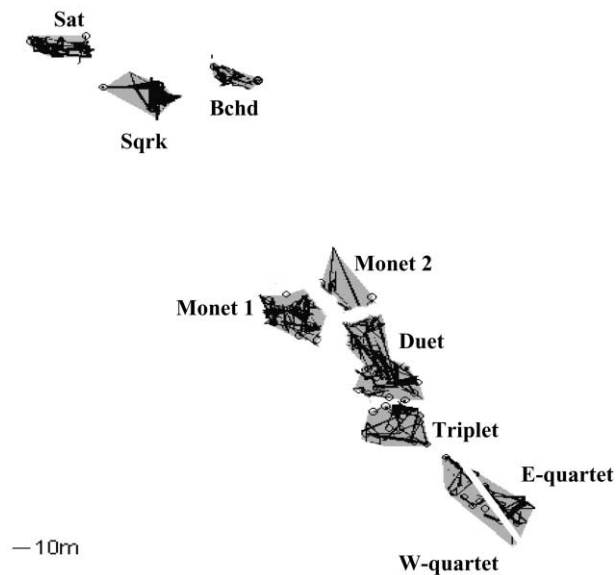
Figure 1: Map over the metapopulation of lizards and the nine neighborhoods at our main study site at Los Banos. The neighborhoods that were used in the analyses are shaded, and the white area represents areas of unsuitable lizard habitat (e.g., grassland) or physical barriers inhibiting lizard dispersal. Note that demarcation of neighborhoods is based not only on physical locations but also on topography (for the purpose of clarity, not shown in figure). For instance, the two neighborhoods E-quartet and W-quartet are physically close but are separated by a ridge of rocks (indicated in white) that inhibits extensive dispersal. Shown in figure are also some adult lizards that were observed only once (*circles*) and examples of lizard movements within neighborhoods (*dark lines*) from the 1998 breeding season. Outcrop groups (see "Material and Methods") are defined as clusters of closely located neighborhoods and were defined to investigate the importance of a higher (regional) spatial level above neighborhoods.

Statistical Analyses

For each neighborhood, we calculated local survival rates and local selection gradients on egg mass. The local selection gradients were calculated by standardizing individual egg masses and hatching dates within each neighborhood to mean zero and unit variance and then regressing relative survival against these two traits (Svensson and Sinervo 2000). The slope of the partial regression coefficient in this multiple regression is the standardized selection gradient (β), and it provides information about how much relative fitness is affected as one increases egg mass by 1 SD, holding the effects of hatching date constant (Lande and Arnold 1983; Svensson and Sinervo 2000). We have previously calculated such local selection gradients for all first-clutch hatchlings (1,545 hatchlings) and all late-clutch hatchlings (1,213 hatchlings) at the local neighborhood level during 1989–1997 (Svensson and Sinervo 2000). We use this large data set in some novel analyses

in this article. We also calculated global selection gradients for all years, that is, annual mean selection gradients from the whole population, ignoring spatial variation between neighborhoods. By comparing the fit between the global and the local selection gradients, we were able to investigate whether a detailed analysis of spatial variation in selective regimes would provide any novel insights in addition to those obtained from a global selection analysis.

To investigate the role of the local (neighborhood) and the regional (outcrop group) levels, we used generalized linear models with binomial error and logit link to analyze variation in juvenile survival. We analyzed how juvenile survival was affected by clutch (first vs. later clutches), year (1989–1997), outcrop group, neighborhood, and the two-way interactions between these two spatial levels and year. This analysis was performed to identify the spatial level at which the opportunity of selection was greatest.

We proceed with a more detailed analysis of selection, in which we analyze survival of hatchlings in relation to two important traits for juvenile survival: egg mass and hatching date. In addition, we also estimate selection on the quadratic components of these traits (egg mass^2 and hatching date^2), since we know from our previous work that selection on these traits can be both stabilizing and disruptive (Sinervo et al. 1992; Svensson and Sinervo 2000). We estimated two-way interactions between egg mass, hatching date, and year, which will provide information about temporal variation (between year) in directional selection on these traits. Finally, we estimated the two and three interactions between the most important spatial level, egg mass and year. These interactions provide information about spatial and/or temporal variation in selection on egg mass. We did not estimate the interactions between spatial level and egg mass^2, hatching date, and hatching date^2, because the range of egg masses and hatching dates at the level of local neighborhoods was too narrow and resulting statistical power too low to permit meaningful estimates of these interactions. Similarly, since our main focus in this study is directional selection, we did not estimate interactions between year, egg mass^2, and hatching date^2, which would provide information about temporal variation in stabilizing or disruptive selection. However, incorporating these terms into the models does not change the major conclusions in this article.

We calculated spatial autocorrelation coefficients (cross-correlation coefficients) between outcrop groups for the local survival rates and selection gradients using the methods described by Ranta et al. (1997) and Koenig (1999; see his fig. 1). Thus, for a pairwise comparison between two outcrop groups, we compared the annual parameter values for each of these sites across all years that were available and thereby obtained estimates of the correlation coefficients. This analysis was performed at the level of the

outcrop groups rather than at the neighborhood level because the sample sizes did not permit an analysis at the latter level. The main reason was that in some years hatchling densities were not high enough to calculate a selection gradient for every single neighborhood, and hence only the correlations between outcrop group level selection gradients (closely located neighborhoods) could be calculated. Rather than not utilizing these selection gradients at all and hence reducing sample size and statistical power, we choose to calculate autocorrelation coefficients among outcrop groups instead of neighborhoods. The aim with these analyses was to investigate the degree of spatial autocorrelation, if any, in local selective regimes between the outcrop groups. In this analysis, we separated the first-clutch and the later-clutch hatchlings, since the strength of selection varies substantially over the season between the different cohorts (Sinervo et al. 2000; Svensson and Sinervo 2000).

Results

Our generalized linear model of hatchling survival revealed highly significant effects of clutch, year, and the interactions between year and the neighborhood level (table 1). The strong interaction effect between year and the neighborhood level in this model (table 1) reflects the annual cycles in juvenile survival rates that we have previously described (Sinervo et al. 2000) and indicates that there is ample opportunity for selection at the local neighborhood level. In contrast, the interaction between year and outcrop group was weaker and approached only borderline significance ($P = .07$), indicating that only slightly additional variance in hatchling survival emerged at this higher spatial level (table 1). However, the outcrop group level will still capture much of the variation in fitness when analyzed alone, since outcrop groups are defined as clusters of

neighborhoods (see "Material and Methods" and results below).

We analyzed spatial and temporal variation in selection on egg mass, hatching date, and their squared components for first- and late-clutch hatchlings (table 2). In these analyses, we only analyzed spatial variation at the local neighborhood level, since we have already shown (see above) that this level is most important in affecting juvenile survival, whereas the effect of outcrop group was less pronounced (table 1). For both first- and late-clutch hatchlings, there was evidence for significant spatiotemporal variation in selection on egg mass, as revealed by the significant three-way interaction year × neighborhood × egg mass (table 2). We interpret this as evidence for spatial variation between neighborhoods in selection egg mass in a given year but also that the pattern of spatial selection changes between years in different ways for different neighborhoods. In other words, spatial and temporal variation in selection on egg mass are acting jointly in this system. For both first- and late-clutch hatchlings, there was evidence for temporal variation in directional selection on hatching date (cf. the year × hatching date terms in table 2). For late-clutch hatchlings, there was also evidence for both directional and quadratic selection egg mass (stabilizing) and hatching date (disruptive; see table 2).

The spatial autocorrelation analyses for selection gradients on egg mass showed that the average cross-correlation in selective regimes was low among first-clutch hatchlings but high among later-clutch hatchlings (fig. 2). Statistical tests of significance are problematic when it comes to autocorrelation coefficients, since each spatial unit is involved in several pairwise comparisons and hence these comparisons are not statistically independent (Koenig 1999). To obtain reasonably reliable confidence limits around the correlation coefficients, it has been recommended to use resampling statistics (Koenig 1999). Accordingly, we calculated confidence limits (CLs) around

Table 1: Spatial and temporal variation in survival rates

Variable	df	Log likelihood	χ^2	P
Clutch	1	−1,475.70	8.156	.0043**
Year	8	−1,434.01	83.379	<.001***
Outcrop group	3	−1,431.38	5.266	.15
Neighborhood	5	−1,430.25	2.264	.81
Year × outcrop group	20	−1,415.34	29.813	.0729
Year × neighborhood	32	−1,381.52	67.629	.000236***

Note: Data show results from a generalized linear model (binomial error, logit link) of lizard hatchling survival in relation to clutch (first vs. late clutch), year, outcrop group, and neighborhood. The highly significant interaction term between year and neighborhood reveals that opportunity for selection is greatest at this spatial level (cf. the marginally significant interaction between year and outcrop group).

** $P < .01$.

*** $P < .001$.

the correlation coefficients using a standard bootstrapping procedure (sampling with replacement 1,000 times) in Resampling Stats (Simon 2000). In addition, we tested whether the difference in means between the autocorrelation coefficients of first- and later-clutch hatchlings was significant also using a bootstrapping procedure. It turned out that the difference in means was indeed significant ($P = .02$), which is visually confirmed by the nonoverlapping 95% CLs around the means of the correlation coefficients (fig. 2). Thus, late-clutch hatchlings will, in a given year, encounter very similar selective regimes across the main study area, whereas the selective regimes between outcrops are more diverse among first-clutch hatchlings.

Finally, the mean autocorrelation coefficients for local survival rates were low and nonsignificant among both first-clutch hatchlings ($r = 0.182$; 95% CL $= -0.056$ to 0.435) and later-clutch hatchlings ($r = 0.168$; 95% CL $= -0.232$ to 0.438). This was also the case for the correlation coefficients of survival rates within outcrops between first and later clutches ($r = 0.108$; 95% CL $= -0.207$ to 0.413) and for selection gradients ($r = 0.045$; 95% CL $= -0.245$ to 0.335).

The annual global selection gradients were significantly correlated with the annual means for the local selection gradients, although there was considerable scatter around the regression line (fig. 3). We used a regression analysis in which we forced the regression line through the origin (i.e., no intercept), and we thus assumed that the annual global selection gradient arises entirely from the averaging of local selective regimes. However, the relationship between global and local selection gradients remains significant even if this assumption is relaxed (i.e., a regression with intercept). The significant fit of the regression strongly suggests that a global analysis and a local analysis give concordant results, at least in this study system. The slope of the regression line (0.693) was slightly less than unity, although this difference only approached statistical significance ($t = -1.883$, df $= 16$, $.05 < P < .10$).

The relationship in figure 3 could possibly be confounded by measurement error in the estimation of the local selection gradients. More specifically, the estimation error may be greater in neighborhoods with a low number of hatchlings, which would result in an increased scatter around the regression line for these neighborhoods. To

Table 2: Spatial and temporal (between-year) variation in selection on egg mass and hatching date for first-clutch hatchings ($N = 1,545$) and late-clutch hatchlings ($N = 1,213$)

Variable	df	Log likelihood	χ^2	P
First-clutch hatchlings:				
Year	8	−836.992	58.483	<.001***
Neighborhood	8	−834.095	5.793	.67
Egg mass	1	−833.108	1.976	.16
Egg mass²	1	−832.512	1.191	.28
Hatching date	1	−831.885	1.255	.26
Hatching date²	1	−831.099	1.571	.21
Year × egg mass	8	−828.344	5.511	.70
Year × hatching date	8	−814.308	28.072	.00047***
Neighborhood × egg mass	8	−807.834	12.948	.11
Year × neighborhood × egg mass	43	−775.124	65.418	.015*
Late-clutch hatchlings:				
Year	8	−593.173	32.587	<.001***
Neighborhood	8	−587.330	11.685	.17
Egg mass	1	−585.073	4.514	.034*
Egg mass²	1	−582.462	5.224	.022*
Hatching date	1	−579.620	5.684	.017*
Hatching date²	1	−573.108	13.024	.00031***
Year × egg mass	8	−567.442	11.332	.18
Year × hatching date	8	−558.809	17.265	.027*
Neighborhood × egg mass	8	−554.786	8.046	.43
Year × neighborhood × egg mass	40	−522.880	63.812	.0097**

Note: Included temporal and spatial factors are year and local neighborhood (the spatial level with most opportunity for selection; see table 1).

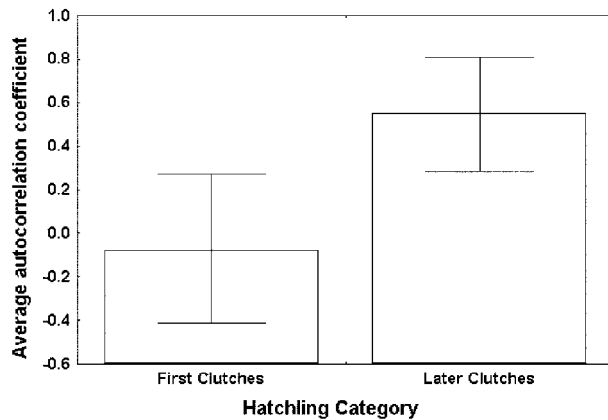* $P < .05$.

** $P < .01$.

*** $P < .001$.

Figure 2: Mean spatial autocorrelation coefficients and 95% confidence limits for selective regimes on egg size for hatchlings from first clutches (*left*) and later clutches (*right*). The spatial autocorrelation is higher among later-clutch hatchlings than among first-clutch hatchlings. See text for significance tests.

investigate this, we reanalyzed the relationship in figure 3 by a weighted regression analysis, in which each neighborhood was weighted according to the number of hatchlings that contributed to the estimation of that particular local selection gradient. The relationship between global and local selection was still highly significant ($F = 550.964$, df $= 1, 493$, $P < .001$), indicating that any potential bias of the local selection gradients did not confound the relationship in figure 3. In addition, we analyzed whether the residuals (unsigned deviations from the regression line in fig. 3) were related to the number of hatchlings in the neighborhood, since estimation bias is expected to increase with decreased number of hatchlings. However, no significant relationship between these residuals and the number of hatchlings was found ($F = 2.413$, df $= 1, 16$, $P = .14$), indicating that measurement error caused by different-sized neighborhoods was slight or nonexistent. Instead, we found that the scatter around the regression line in figure 3 was partly explained by clutch category: the variance in selection gradients was significantly greater among later-clutch hatchlings than among first-clutch hatchlings (Levene's test: $F = 5.542$, df $= 1, 16$, $P = .03$), which is consistent with the more pronounced annual cycles in selection gradients among the former group (Sinervo et al. 2000; their fig. 1).

Finally, we found a significant effect of clutch category (first- vs. later-clutch hatchlings) on the magnitude of local selection gradients, but there was no effect of the number of hatchlings in the local neighborhood (clutch category: $F = 6.621$, df $= 1, 100$, $P = .012$; number of hatchlings: $F = 0.446$, df $= 1, 100$, $P = .51$). The significant effect of clutch category is consistent with our previous studies that

have demonstrated stronger selection on egg mass among later-clutch hatchlings than among first-clutch hatchlings (Sinervo et al. 2000; Svensson and Sinervo 2000). The absence of any significant effect of the number of hatchlings contributing to the local selection gradient suggests that these gradients are not biased in magnitude because of different size of neighborhoods.

Discussion

Results in this article reveal the importance of both the spatial scale and temporal variation in selective regimes and strongly suggest that analyses of global (population level) selection gradients should be complemented by local analyses to gain a better understanding of evolutionary dynamics. Our study system has allowed us to compare the merits of combining both global and local selection analyses, and although they give qualitatively similar results, there are some interesting quantitative differences. Further empirical studies in which global and local selection gradients are compared are clearly warranted.

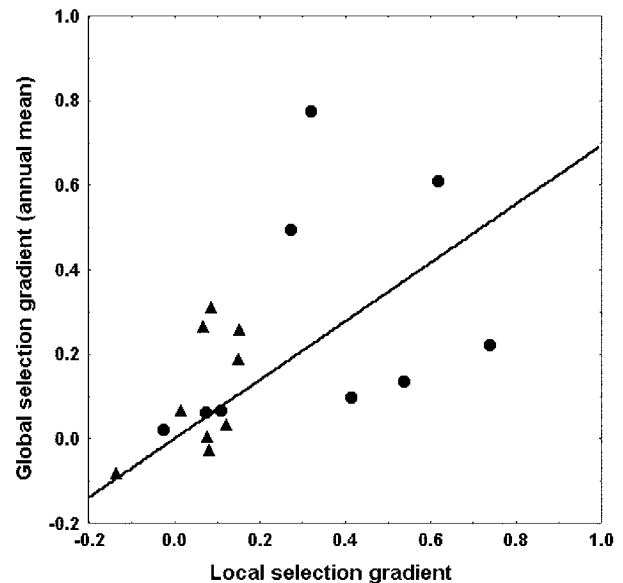Our previous work revealed that the strength of selec-

Figure 3: Global versus local selection gradients (annual means). Local selection gradients calculated on a per neighborhood basis, holding the effects of hatching date constant in multiple regression analysis. Global selection gradients calculated at the population level, ignoring spatial structure. The regression line was obtained from a model with no intercept (i.e., forcing the regression through the origin), and the equation is $y = 0.693x$ (SE $= 0.163$; $P = .0005$; $R^2 = 0.154$). The relationship is also significant using a regression model with intercept (statistics not shown). *Solid triangles*, first-clutch hatchlings. *Solid circles*, second-clutch hatchlings.

tion on egg mass in this population fluctuates markedly between generations (Sinervo et al. 2000). In high-density years, the strength of selection on egg mass is among the highest observed in natural populations, which is comparable in strength to selection on beak characteristics in Galápagos finches during drought years (Sinervo et al. 2000; Grant and Grant 2002). The highly variable local selection we have detected, reflected as scatter around the regression line in figure 3, may have gone unnoticed by us if we had not performed our local selection gradient analyses and restricted ourselves to a global analysis.

Global selection analysis averages the selective regimes across all the neighborhoods within a population. If selection differs in strength and direction in the different neighborhoods, as found in this and other studies of our population, a selection analysis ignoring spatial structure would represent an average in which the largest, densest neighborhoods would contribute more to the global selection gradient than the smaller, less dense neighborhoods. Furthermore, if there is strong local selection that varies in direction and magnitude between demes, a global selection analysis from the whole population would then result in a pattern of relatively weak stabilizing selection, as we have indeed found in our previous studies (Sinervo et al. 1992; Svensson and Sinervo 2000). However, such weak stabilizing selection at the global level would in reality be a result of strong and opposing (or conflicting) selection pressures at the local level as opposed to "true" stabilizing selection (Travis 1989; Schluter et al. 1991).

Although year-specific variation in selective regimes is clearly important in this lizard system (Sinervo et al. 2000; table 2), the interaction between temporal (year) and spatial (neighborhood level) accounts for a significant part of the variation in local survival rates (note the interaction effects year × neighborhood × egg mass in table 2). Thus, spatial variation may act jointly with temporal (between-generation) variation in selective regimes. Theoretical models for the maintenance of genetic polymorphisms indicate that spatial variation in selective regimes is more powerful in maintaining polymorphisms than is purely temporal variation, although conditions for maintenance are broader when temporal and spatial variation act in concert (Haldane and Jayakar 1963; Gillespie 1973; Felsenstein 1976). Between-neighborhood variation in selective regimes in combination with annually fluctuating selection on egg size are important in maintaining the heritable female throat color morphs, which lay eggs of different size as part of their alternative reproductive strategies (Sinervo et al. 2000).

We suggest, on the basis of the results from these analyses and the predictions from the classical population genetic models, that both temporal and spatial variation in selection at the neighborhood level play an important role

in maintaining the substantial additive genetic variance of fitness-related traits in this population (Sinervo et al. 2000; Svensson et al. 2001*b*). It would be interesting to see similar analyses performed on other study systems, both monomorphic and polymorphic ones.

The autocorrelation analysis showed that the selective regimes on egg mass were more strongly correlated across outcrops among later-clutch hatchlings than among first-clutch hatchlings (fig. 2). Thus, the selective environment is more "coarse grained" (Levins 1968) among later-clutch hatchlings, which should promote the maintenance of genetic polymorphisms (Kirkpatrick 1996). Consistent with this, selection on clutch size and egg mass in the two adult female throat color morphs is more pronounced for later clutches than for the first clutch, and the frequency-dependent and density-dependent oscillating selection pressures mainly arise from interactions among late-clutch hatchlings (Sinervo et al. 2000). The new results in this article suggest that similar selective regimes operate across all outcrops in a given year among later-clutch hatchlings and raise the question about the selective agents responsible for this synchronizing effect. Our previous work revealed that the degree of density-dependent natural selection on egg size is stronger among later-clutch hatchlings than among first-clutch hatchlings (Sinervo et al. 2000; Svensson and Sinervo 2000). First-clutch hatchlings are born early in the season and encounter noncrowded environments in which competitive interactions are weak and other biotic or abiotic selection pressures predominate, for example, thermal differences between outcrops. The strong density- and frequency-dependent interactions among later-clutch hatchlings that we have experimentally demonstrated to be important at the local scale in our previous studies (Sinervo et al. 2000); Svensson and Sinervo 2000) may also be responsible for the spatial autocorrelation of selective regimes among later clutches. In contrast, abiotic environmental differences between outcrops would act to weaken the autocorrelation.

Although the use of spatial autocorrelation analysis has become popular among ecologists interested in synchrony in population dynamics (Ranta et al. 1997; Koenig 1999), evolutionary biologists should also use these analytical tools to investigate spatial variation in selective regimes. There are, to our knowledge, only a few previous field ecological studies using spatial autocorrelation analysis. Stratton (1994, 1995) showed that the spatial autocorrelation for relative fitness for genotypes in the plant *Erigeron annuus* was very weak, and this was interpreted to be a result of fine-grained environmental heterogeneity and caused unpredictable genotype fitness with increasing dispersal distance (Stratton and Bennington 1998). More recently, van der Jeugd and McCleery (2002) showed that heritability estimates for laying dates in a wild bird pop-

ulation had been inflated by spatial autocorrelation of environmental effects. To our knowledge, our study is the first to use autocorrelation analysis to investigate spatial variation in selection gradients. Taken together, our analyses thus suggest that selection gradients on egg mass are, within years, more strongly synchronized over larger spatial distances than are those from first-clutch hatchlings (fig. 2), and these selection gradients are also more variable across years than among the first-clutch hatchlings (fig. 3; see also fig. 1 in Sinervo et al. 2000).

Several practical questions need to be addressed in future studies. For instance, at what spatial level should selection gradients be calculated? Should it be the global level or some lower spatial unit? Consideration of the spatial scale of dispersal relative to selection is also critical, particularly if one is interested in the maintenance of genetic polymorphisms in environments with spatial variation in selective regimes (Levene 1953; Kirkpatrick 1996). The spatial level at which most of the variation in selective regimes is found would be a natural choice, that is, the neighborhood level in this study (table 1). Should the traits and fitnesses be standardized at the global population level or at the local deme level? Should neighborhoods be weighted by the relative fraction of the population as a whole or by their contributions to the population's intrinsic increase? Intuitively, it would seem the latter, but the answers to these practical questions will be determined by the evolutionary model a particular investigator champions. In this study, we found no evidence for any bias in the estimates of local selection gradients due to different size of the different neighborhoods, which suggests that the gradients need not to be weighted by the relative size of the subpopulations. However, it is an empirical question whether this is the case in other study systems.

We encourage field evolutionary biologists interested in selection processes to critically consider whether a spatial perspective is likely to be important in their studies and analyses or whether it could be safely ignored. In our lizard system, we are convinced that a spatial perspective provides novel insights that would not have been revealed if we had used only global selection estimates. For instance, frequency-dependent (Sinervo et al. 2000) and density-dependent (Svensson and Sinervo 2000; Svensson et al. 2001*a*, 2001*b*) selection pressures are local processes, in which the phenotype fitnesses are determined by competitive interactions between neighbors. Such local competitive interactions could not be elucidated if one were to consider only the global level.

Acknowledgments

Literature Cited

Barton, N. H., and M. C. Whitlock. 1997. The evolution of metapopulations. Pages 183–210 *in* I. Hanski and M. Gilpin, eds. Metapopulation dynamics: ecology, genetics and evolution. Academic Press, San Diego, Calif.

Coyne, J. A., N. H. Barton, and M. Turelli. 1997. Perspective: a critique of Sewall Wright's shifting balance theory of evolution. Evolution 51:643–671.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. Nature 400:354–357.

Doughty, P., and B. Sinervo. 1994. The effects of habitat, time of hatching, and body-size on the dispersal of hatchling *Uta stansburiana*. Journal of Herpetology 28: 485–490.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, N.J.

Felsenstein, J. 1976. The theoretical population genetics of variable selection and migration. Annual Review of Genetics 10:253–280.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon, Oxford.

Gillespie, J. H. 1973. Polymorphism in random environments. Theoretical Population Biology 4:193–195.

Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science 296:707–711.

Haldane, J. B. S., and S. D. Jayakar. 1963. Polymorphism due to selection of varying direction. Journal of Genetics 58:237–242.

Heisler, I. L., and J. Damuth. 1987. A method for analyzing selection in hierarchically structured populations. American Naturalist 130:582–602.

Juenger, T., and J. Bergelson. 2002. The spatial scale of genotype by environment interaction (GEI) for fitness in the loose-flowered gilia, *Ipomopsis laxiflora* (Polemoniaceae). International Journal of Plant Sciences 163: 613–618.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. American Naturalist 157:245–261.

Kirkpatrick, M. 1996. Genes and adaptation: a pocket guide to the theory. Pages 125–146 *in* M. R. Rose and

G. V. Lauder, eds. Adaptation. Academic Press, San Diego, Calif.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. American Naturalist 150:1–23.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology & Evolution 14:22–26.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. American Naturalist 87:331–333.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J.

Merilä, J., B. C. Sheldon, and L. E. B. Kruuk. 2001. Explaining stasis: microevolutionary studies in natural populations. Genetica 112/113:199–222.

Provine, W. B. 1986. Sewall Wright and evolutionary biology. University of Chicago Press, Chicago.

Ranta, E., J. Lindström, H. Kokko, H. Linden, and E. Helle. 1997. Solar activity and hare dynamics: a cross-continental comparison. American Naturalist 149:765–775.

Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection pressures and life history trade-offs. Proceedings of the Royal Society of London B 246:11–17.

Simon, J. L. 2000. Resampling Stats software and user's guide, 1973–2000. Resampling Stats, Arlington, Va.

Sinervo, B. 1999. Mechanistic analysis of natural selection and a refinement of Lack's and William's principles. American Naturalist 154(suppl.):S26–S42.

Sinervo, B., and D. F. DeNardo. 1996. Costs of reproduction in the wild: path analysis of natural selection and evolutionary test of causation. Evolution 50:1299–1313.

Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380:240–243.

Sinervo, B., and E. Svensson. 2002. Correlational selection and the evolution of genomic architecture. Heredity 89:329–338.

Sinervo, B., P. Doughty, R. B. Huey, and K. Zamudio. 1992. Allometric engineering: a causal analysis of natural selection on offspring size. Science 258:1927–1930.

Sinervo, B., E. Svensson, and T. Comendant. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985–988.

Slatkin, M. 1973. Gene flow and selection in a cline. Genetics 75:787–802.

Stratton, D. A. 1994. Genotype-by-environment interactions for fitness of *Erigeron annuus* show fine-scale selective heterogeneity. Evolution 48:1607–1618.

———. 1995. Spatial scale of variation in fitness of *Erigeron annuus*. American Naturalist 146:608–624.

Stratton, D. A., and C. C. Bennington. 1998. Fine-grained spatial and temporal variation in selection does not maintain genetic variation in *Erigeron annuus*. Evolution 52:678–691.

Svensson, E., and B. Sinervo. 2000. Experimental excursions on adaptive landscapes: density-dependent selection on egg size. Evolution 54:1396–1403.

Svensson, E., B. Sinervo, and T. Comendant. 2001a. Condition, genotype-by-environment interaction and correlational selection in lizard life-history morphs. Evolution 55:2053–2069.

———. 2001b. Density-dependent competition and selection on immune function in genetic lizard morphs. Proceedings of the National Academy of Sciences of the USA 98:12561–12565.

Travis, J. 1989. The role of optimizing selection in natural populations. Annual Review of Ecology and Systematics 20:279–296.

van der Jeugd, H. P., and R. McCleery. 2002. Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. Journal of Evolutionary Biology 15:380–387.

Wade, M. J., and C. J. Goodnight. 1998. Perspective: the theories of Fisher and Wright in the context of metapopulations: when nature does many small experiments. Evolution 52:1537–1553.

Wade, M. J., and S. M. Kalisz. 1990. The causes of natural selection. Evolution 44:1947–1955.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proceedings of the Sixth International Congress of Genetics 1:356–366.