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# Density cycles and an offspring quantity and quality game driven by natural selection

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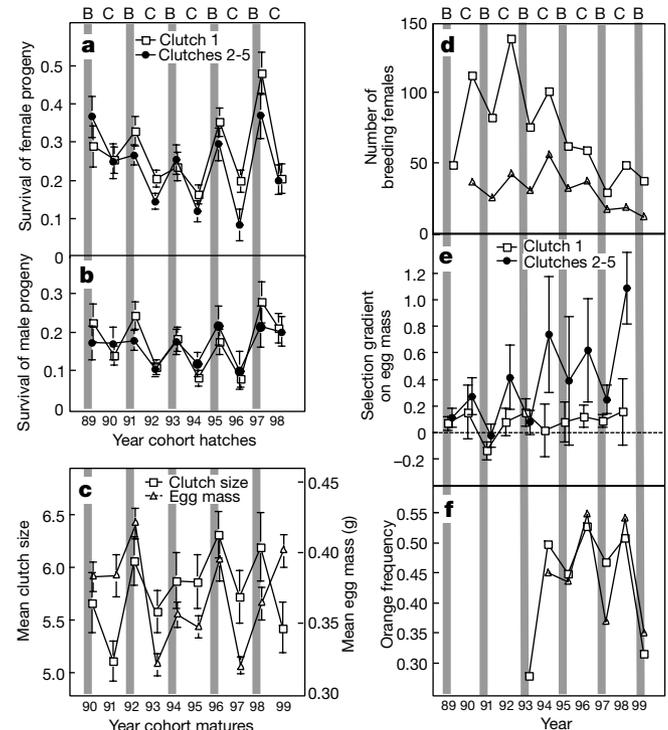
A long-standing hypothesis<sup>1,2</sup> posits that natural selection can favour two female strategies when density cycles. At low density, females producing many smaller progeny are favoured when the intrinsic rate of increase, *r*, governs population growth. At peak density, females producing fewer, high-quality, progeny are favoured when the carrying capacity, *K*, is exceeded and the population crashes. Here we report on the first example of a genetic *r* versus *K* selection<sup>3–5</sup> game that promotes stable population cycles in lizards. Decade-long fitness studies and game theory demonstrated that two throat-colour morphs were refined by selection in which the strength of natural selection varied with density. Orange-throated females, *r* strategists, produced many eggs and were favoured at low density. Conversely, yellow-throated females, *K* strategists, produced large eggs and were favoured at high density. Progeny size should also be under negative frequency-dependent selection in that large progeny will have a survival advantage when rare, but the advantage disappears when they become common. We confirmed this prediction by seeding field plots with rare and common giant hatchlings. Thus, intrinsic causes of frequency- and density-dependent selection promotes an evolutionary game with two-generation oscillations.

The side-blotched lizard (*Uta stansburiana*) has an annual life history in that it matures in one year but rarely survives more than one reproductive season. Fecundity is high and females lay up to five clutches (2–10 eggs per clutch, mean is 6 eggs) at monthly intervals from March to August at Los Baños Grandes, Merced County, California. Progeny defend territories at hatching. Density-dependent natural selection should be intense: adult density can exceed

850 per hectare and 2,600 hatchlings can be produced per hectare. From 1989 to 1999, we measured lizard density and collected eggs from females. Fitness was assessed by counting the number of progeny that reached maturity<sup>6</sup>. In 1992, we discovered two morphs of females—yellow-throated and orange-throated<sup>7</sup>. From 1993 to 1999, we studied frequency cycles, natural selection and the genetics of throat colour<sup>6</sup>.

On the basis of 5,618 individually marked progeny released during a decade of study, annual progeny survival oscillated with a two-year period, as did the mean egg mass and mean clutch size produced at maturity (Fig. 1a–c). Population density of adult females oscillated with a two-year period (Fig. 1d). Density also oscillated synchronously in an adjacent population (Fig. 1d). We designated years when progeny cohorts had low survival as ‘crash’ years, because the density of progeny as adults was reduced. Progeny cohorts that matured in crash years laid small clutches of small eggs (Fig. 1c). We designated years when progeny cohorts had high survival as ‘boom’ years, because the density of progeny as adults increased. Progeny cohorts that matured in boom years laid large clutches of large eggs (Fig. 1c). Population cycles cause density environments of parents and progeny to be diametrically opposite, which should lead to oscillatory natural selection. We observed the predicted two-year oscillation in natural selection acting on the egg mass of clutches 2–5 (Fig. 1e), which is when hatchling density is highest and selection should be most intense<sup>8</sup>. The selection gradients<sup>8,9</sup>, which measure the strength of natural selection, are among the highest reported in nature<sup>10–12</sup>. In contrast, selection was weaker on clutch 1 and did not oscillate (Fig. 1e).

Population parameters also exhibited long-term trends unrelated to two-year cycles. For example, adult density rose over the period 1989–1992, but fell thereafter, reflecting a significant long-term quadratic change over a decade ( $F_{1,8} = 5.21$ ,  $P = 0.05$ , Fig. 1).

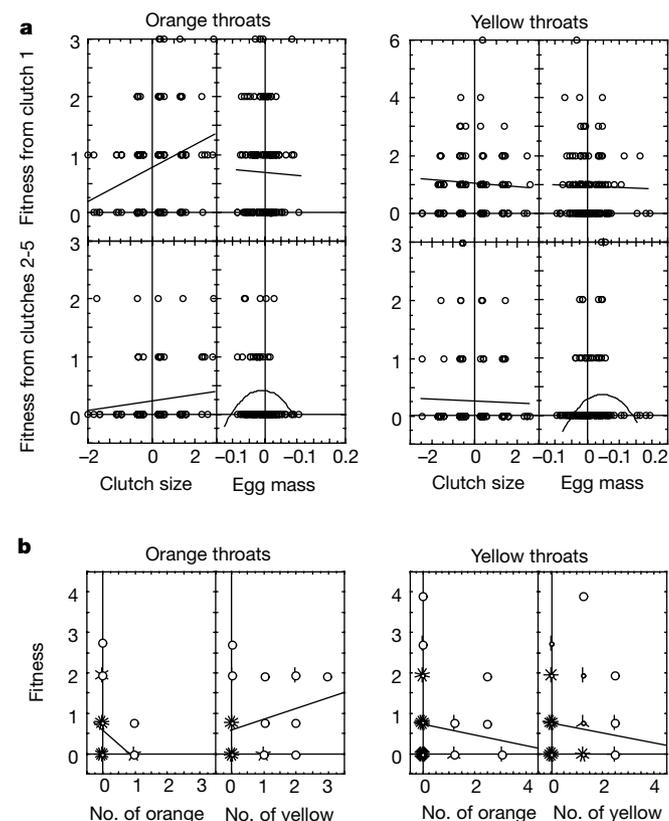


**Figure 1** Cycles of demographic parameters and natural selection on egg mass. **a–c**, We observed oscillations of survival of female progeny (**a**), survival of male progeny (**b**), egg mass (triangles), and clutch size (squares) produced by progeny at maturity (**c**). B, boom years (grey bars); C, crash years. **d**, Adult density oscillated in a population where we measured survival and fitness (squares) and in a control population where we only counted density (triangles). **e**, Selection gradients acting on egg size of clutches 2–5 oscillated, but selection gradients on clutch 1 did not oscillate. **f**, Orange frequency oscillated synchronously in two populations. Means  $\pm$  s.e.m. are shown.

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Long-term trends were caused by a five fold increase of snake predators<sup>13</sup> in 1993, which reduced lizard density thereafter. We note that the two-year cycles persisted after an increase in predators, which suggests an intrinsic cause. Before testing for the statistical significance of the two-year cycles<sup>14</sup>, we computed residuals to remove the effects of significant long-term trends that were unrelated to two-year cycles (for example, the quadratic trend for survival:  $F_{1,34} = 7.44$ ,  $P = 0.01$ , the linear trend for selection on clutches 2–5:  $F_{1,8} = 6.00$ ,  $P = 0.04$ ). Temporal autocorrelations were significant for density on both study plots ( $r = -0.45$ ,  $r = -0.73$ , consensus combined  $P$ -value<sup>15</sup> = 0.005), mean density ( $r = -0.65$ ,  $P = 0.03$ ), selection gradients (clutches 2–5:  $r = -0.85$ ,  $P = 0.001$ ) and progeny survival (clutch 1 females:  $r = -0.68$ ,  $P = 0.03$ ; clutch 1 males:  $r = -0.87$ ,  $P = 0.001$ ; clutch 2–5 females:  $r = -0.95$ ,  $P = 0.00003$ ; clutch 2–5 males:  $r = -0.79$ ,  $P = 0.006$ ). Autocorrelations for clutch and egg size were not significant ( $r = -0.32$  and  $r = -0.31$ ,  $P > 0.38$ ), but the autocorrelation for total clutch mass was significant (egg mass  $\times$  clutch size:  $r = -0.65$ ,  $P = 0.03$ ). The frequency of throat-colour morphs also oscillated on both plots (Fig. 1f; long-term quadratic trend:  $F_{1,10} = 10.29$ ,  $P = 0.008$ ; autocorrelations:  $r = -0.84$ ,  $r = -0.72$ ,  $P < 0.01$ ; ref. 15).

Natural selection on female morphs  $M$  was significantly different for clutch sizes  $s$  produced on clutch 1 ( $M \times s$ :  $F_{1,257} = 5.531$ ,  $P = 0.02$ ) and for optimal egg mass  $m$  produced on clutches 2–5 ( $M \times m$ :  $F_{1,257} = 6.98$ ,  $P < 0.001$ ,  $(m_e)^2$ :  $F_{1,257} = 5.18$ ,  $P = 0.02$ , Fig. 2a). Thus, orange females laying large clutches had more



**Figure 2** Natural selection on throat-colour morphs. **a**, Natural selection on life history variation differed between morphs. For clutch 1, orange-throated females were favoured to lay larger clutches than yellow-throated females. For clutches 2–5, yellow-throated females were favoured to lay eggs that were 0.08 g heavier on average than orange-throated females. **b**, Orange female fitness was decreased by orange neighbour density but enhanced by yellow neighbour density. Yellow female fitness was not affected by density. We only show pooled data for clutches 1–5, but see Table 1 for repeated measures ANCOVA of fitness on clutch 1 versus clutches 2–5, and equations for fitness. Sample size is indicated by multiple rays on points.

progeny that survived to maturity than those laying small clutches. In contrast, yellow females laying large eggs had more progeny that survived to maturity than those laying small eggs. Throat colour was heritable between dams and daughters ( $h^2 = 0.48$ ,  $F_{1,116} = 6.92$ ,  $P = 0.001$ ). Dam's throat colour was also genetically correlated with daughter's clutch size ( $G_{ts} = 1.09$ ,  $P = 0.02$ ,  $N = 168$ ) and egg mass ( $G_{tm} = -0.84$ ,  $P = 0.05$ ). This is consistent with the action of correlational selection<sup>16</sup> (Fig. 2a). That is, orange dams produced surviving orange daughters that laid many small eggs. Yellow dams produced surviving yellow daughters that laid fewer large eggs. Morphs differed in clutch size ( $s_o = 5.92$  eggs,  $s_y = 5.60$  eggs,  $F_{1,115} = 4.99$ ,  $P = 0.03$ ) and egg mass ( $m_o = 0.371$  g,  $m_y = 0.394$  g,  $F_{1,115} = 7.07$ ,  $P = 0.009$ ) when isolated from other females (for example, no neighbours), reinforcing the view that morphs had distinct life history strategies.

The fitness of each morph in competition with alternative morphs tests for an evolutionarily stable strategy (ESS)<sup>17</sup>. The ESS receives the highest fitness pay-off when rare and common. An ESS can thereby invade and eliminate other morphs. The pay-off matrix can be computed from the significant relationship between morph fitness and density of orange and yellow neighbours<sup>7,18</sup> (Fig. 2b; analysis of covariance, Table 1). When orange females had more orange neighbours their fitness was reduced, but fitness increased with more yellow neighbours. Yellow female fitness was not affected by density of either morph. The pay-off matrix (Table 1) indicated that neither morph was an evolutionary stable state. Both morphs can invade and they may co-exist in an evolutionary stable state.

Even when co-existence is possible, stability must be assessed with population genetic and population dynamic models. We assumed random mating, and that throat colour is due to one locus in which the orange allele is dominant to the yellow allele in females, which is consistent with dam-progeny (above) and sire-progeny pedigrees (B.S. *et al.*, unpublished data). Transmission of morphs across generations is further determined by the frequency dependence of female fitness<sup>7,18</sup>. Fitness of the  $i$ th strategy,  $W_i(t)$ , is given by the fitness when solitary,  $W_{i,sol}$ , adjusted by gain or loss in fitness of the  $i$ th strategy,  $G_{ij}$ , when playing against the  $j$ th neighbouring strategy that is found at density,  $N_{ij}(t)$ :

$$W_i(t) = W_{i,sol} + \sum_j G_{ij} N_{ij}(t) \quad (1)$$

Equation (1) is parameterized by the same relationships used to construct the pay-off matrix (Table 1). We further assumed that progeny survival is density dependent, which was confirmed by a decade of field experiments (regression of survival on density:  $F_{1,69} = 7.80$ ,  $P = 0.007$ , Fig. 3a). The carrying capacity of orange-throated females ( $K_o = 0.70$ ), which vigorously defended territories, was lower than that of yellow-throated females ( $K_y = 1.18$ ), which were more density tolerant. Recruitment rate of the  $i$ th morph at time  $t$  was modelled with two coupled logistic equations:

$$\frac{dN_i(t)}{dt} = N_i(t) \times F_i \times \frac{W_i(t)}{W} \times \frac{(K_i - N_i(t))}{K_i} \quad (2)$$

**Table 1** Fitness pay-offs for rare throat-colour morphs when competing against each common morph

	Population state	
	Orange common	Yellow common
Fitness of rare orange strategy	1	1.61
Fitness of rare yellow strategy	1.60	1

We calculated fitness of rare and common morphs by inserting mean density of each morph, which were observed in boom and crash years, into equation (1)<sup>18</sup>.  $W_o = 0.98 - 0.84 \times N_{oo} + 0.27 \times N_{oy}$  and  $W_y = 1.04 + 0.02 \times N_{yo} - 0.35 \times N_{yy}$  on clutch 1;  $W_o = 0.18 - 0.38 \times N_{oo} - 0.14 \times N_{oy}$  and  $W_y = 0.22 - 0.03 \times N_{yo} - 0.35 \times N_{yy}$  on clutches 2–5. (Repeated measures ANCOVA of fitness on clutch 1 ( $C_1$ ) versus clutches 2–5 ( $C_{2-5}$ ) indicated that fitness response of morphs to density was significantly different:  $C \times M \times N_o$ :  $F_{1,115} = 3.96$ ,  $P = 0.05$ ,  $C_{2-5} \times M \times N_y$ :  $F_{1,115} = 3.97$ ,  $P = 0.04$ .)

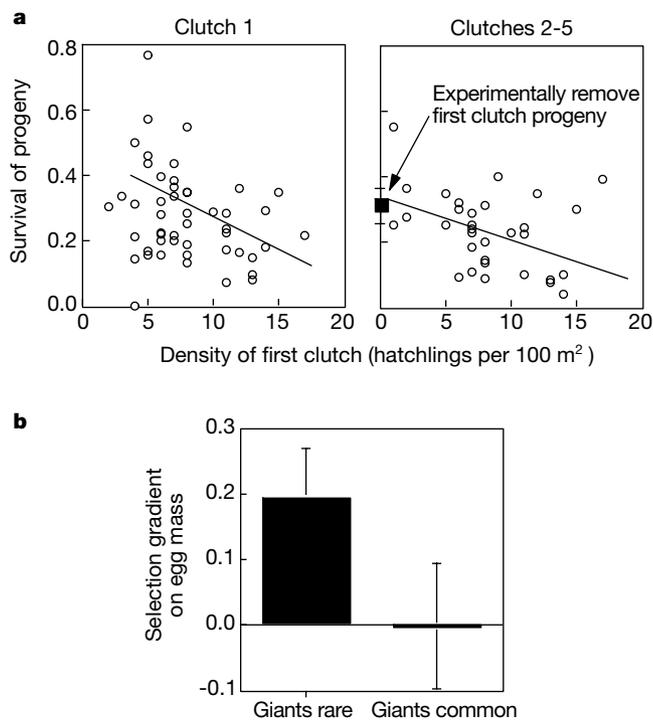
Morphs are coupled through genetics and the frequency dependence of fitness. The intrinsic rate of increase,  $r$ , in the standard logistic equation is replaced by  $F_i$ , fecundity of  $i$ th strategy adjusted by: (1) frequency-dependent fitness (such as equation (1) standardized by mean fitness,  $W_i(t)/\bar{W}$ ), and (2) density-dependent progeny survival of the  $i$ th strategy (such as  $K_i - N_i(t)/K_i$ ). Numerical simulations of a discrete logistic ESS model (equation (2)), appropriate for annual side-blotched lizards, confirmed that morph frequency oscillates with a two-year period (Fig. 4). Juvenile survival (for example,  $N_i(t+1)/F_i(t)$ ) also oscillates in the logistic ESS model. Frequency-dependent selection maintains both morphs in an evolutionary stable state, whereas time lags in density-dependent regulation promote stable oscillations. Time lags occur because the evolutionary change in morph frequency (Fig. 1f) is necessarily one generation removed from the action of selection. Thus, the evolutionary lags in our model are analogous to time lags in ecological models that also promote stable cycles<sup>19</sup>.

Every other generation, the cycle alternately favours large progeny (crash year) or large clutches of small progeny (boom years). Thus, our model requires that progeny size is under negative frequency-dependent selection. That is, large hatchlings should be selectively advantageous when rare, but disadvantageous when common. We tested this prediction by manipulating the size–frequency distribution of progeny on statistically independent plots. We used experimental variation in egg size, rather than natural variation. A selection study of natural variation in egg size, which differ between morphs, could be confounded with selection on throat-colour alleles or some other correlated trait. However, experimental variation in egg size tests for causes arising from egg size itself<sup>20</sup>. The progeny size distribution was adjusted by seeding plots with either

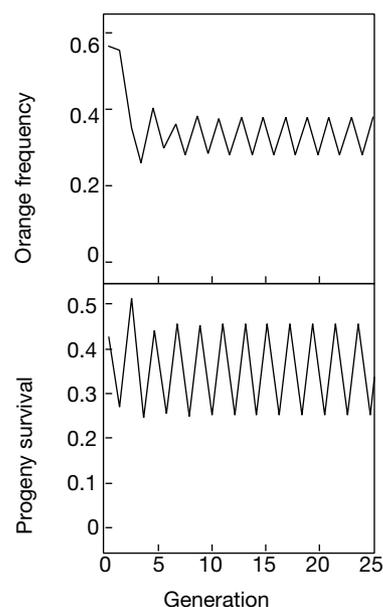
20% giant progeny (common giants,  $n = 10$  plots) or 10% giant progeny (rare giants,  $n = 17$  plots). The remaining frequencies were split between normal-sized and miniaturized progeny. Manipulated progeny are not abnormally large or small<sup>21</sup>. The size range and density of experimental progeny was carefully calibrated to explore the range of variation found in nature<sup>8,21</sup>. As predicted, strong selection favouring large progeny was observed on plots where giants were rare, and no selection was observed on plots where giants were common (treatment:  $F_{1,23} = 4.19$ ,  $P = 0.05$ ; clutch effect:  $F_{1,23} = 2.64$ ,  $P = 0.12$ ; year:  $F_{1,23} = 2.46$ ,  $P = 0.13$ , Fig. 3b).

When selection pressure on progeny size is relaxed as on common giant plots, laying more eggs maximizes female fitness. However, females laying more eggs must lay smaller eggs because of the clutch size and egg mass trade-off (that is, genetic correlation,  $G_{sm} = -0.91$ ,  $P < 0.01$ )<sup>22</sup>. Orange females lay many small eggs and are only favoured in low-density boom years. In these years, their small offspring are not a fitness liability. Conversely, yellow females are favoured in crash years. In these years, their rare large progeny survive better than small orange progeny.

The alternative throat-colour morph in side-blotched lizards may have arisen as a mutation in an endocrine gene, given the effect of hormones on the expression of orange versus yellow throat colour of lizards<sup>23</sup>. This locus will have many pleiotropic effects on physiology<sup>6,13,22</sup> and behaviour<sup>7</sup>. However, it seems unlikely that all variation in clutch size and egg mass of morphs is due to the pleiotropic effect of a single throat-colour locus. Many loci undoubtedly affect clutch size and egg mass<sup>5</sup>. We have shown (Fig. 1e and Fig. 2a) that correlational selection<sup>16</sup> associated with density cycles is strong enough to form genetic correlations among loci for throat colour, clutch size and egg mass (such as linkage disequilibrium). Selection is disruptive in that it shapes genetic covariation to either side of the clutch and egg size trade-off<sup>22</sup>. As each strategy becomes better adapted to a different phase of the cycle, oscillations are reinforced. Adaptation of morphs as a result of correlational selection will equilibrate when segregation and recombination erode favourable linkage disequilibrium as fast as it is formed by selection. This results in a chronic selective load on morphs<sup>24</sup> that can only be reduced if life-history loci become physically linked to throat-colour loci in a tight linkage group.



**Figure 3** Density-dependent survival and frequency-dependent selection on egg mass. **a**, Survival of progeny from clutches 1 and 2–5 was lower at high density on statistically independent plots. Survival of progeny from clutches 2–5 on experimental plots where clutch 1 progeny had not been previously released (square with s.e.m.) was similar to the regression line intercept for survival of clutches 2–5 progeny on control plots. **b**, Selection acting on progeny size is dependent on frequency distribution of progeny. Positive selection gradients<sup>8,9</sup> on egg mass were measured on plots with rare giants. No selection (that is, selection gradients were zero) was measured on plots with common giants.



**Figure 4** Frequency of orange female morphs and juvenile survival. Data oscillated with a two-year period in simulations of a logistic evolutionarily stable strategy (ESS) model (equation (2)). Top, orange female morphs; bottom, survival of progeny.

The genetic consequences of density-dependent selection cause morphs to refine each other in an endless evolutionary game. The  $r$ - and  $K$ -strategy model is similar to a hypothesis proposed<sup>1,2</sup> to explain density cycles in rodents. Our study shows that  $r$ -strategists, orange females, are favoured at low density because they produce large clutches of small eggs. The  $r$ -strategists cause an overshoot of carrying capacity within a single year, which triggers a population crash. Yellow females, the  $K$ -strategists, gain a rare advantage at high density through production of fewer but larger hatchlings. Yellow progeny become larger and better adapted to survive ensuing population crashes, which concomitantly lowers post-crash density of orange. After successive crashes, orange females become better adapted by laying even more small progeny, which concomitantly enhances the overshoot of carrying capacity. Evolutionary and population density time lags ensure that selection will never reach a compromise, but will oscillate between two life-history states. Life-history theory predicts that a single egg size is optimal in a population<sup>5,21,25,26</sup>. However, it is clear that optimality models are too simplistic when selection arises from density competition. Game theory, which predicts multiple optima for egg size, is more appropriate. □

## Methods

### Population censuses

In all analyses, female fitness was assessed by tracking survival of individually marked (toe-clipped) progeny to maturity the following year<sup>6,8,22</sup>. A 500- to 1,500-m diameter area around progeny release sites was searched the following year and emigration does not confound fitness estimates<sup>22</sup>. Progeny that survived to maturity were unlikely to be missed during daily censuses (March–June)<sup>22</sup>. We collected sequential clutches from mature female progeny from March to August<sup>7,13</sup>. Adult density and throat colour<sup>7</sup> was counted in two populations that were separated by 300 m (ref. 13) of unsuitable adult habitat. Populations exchanged fewer than 5% migrants each year<sup>22</sup>. Morph frequency varied significantly among years in two populations (Fig. 1f, population where fitness was studied:  $\chi^2 = 33.87$ ,  $P < 0.0001$ ,  $n = 102, 113, 110, 108, 49, 61$  and 47; control population:  $\chi^2 = 7.13$ ,  $P < 0.01$ ,  $n = 124, 48, 44, 19, 14$  and 68).

### Measuring strength of natural selection

Strength of natural selection on egg mass was assessed on statistically independent plots (see below) with selection gradients<sup>9</sup>. Selection gradients are derived from regression of survival on egg mass. Large positive selection gradients reflect strong natural selection that favours large eggs (a steep slope). Standardized selection gradients<sup>9</sup> were calculated for each plot (1989–1998), while holding hatching-date effects constant<sup>8,9</sup>.

### Significance tests for two-year oscillations

We tested for statistical significance of two-year oscillations after removing the effect of long-term trends (such as decade-long trends) on the yearly means. Residuals with one-year lags (a significant negative correlation for residuals between successive years) indicate two-year oscillations<sup>14</sup> or a significant one-year temporal autocorrelation.

### Natural selection on clutch size and egg mass

We measured fitness from the number of progeny that survived to maturity (see above) as a function of female's clutch size and egg mass produced on clutch 1 and clutches 2–5. We tested for significant morph differences in selection using analysis of covariance (ANCOVA)<sup>7,9</sup> with morph  $M$  as a factor, and clutch size ( $s$ ) or egg mass ( $m$ ) as covariates. A significant difference in directional selection<sup>7,9</sup> between morphs was tested with interaction terms<sup>7,21</sup> ( $M \times s$ ). In addition, we tested for significant stabilizing selection (optimum) by including a term for  $m^2$ . In this model, an effect of  $M \times m$  indicates a significant difference in optimal egg mass between morphs<sup>7,21</sup>.

### Local density ( $N_{ij}$ ) and fitness

The number of neighbouring female morphs was calculated from home range maps<sup>7,13,17</sup>. Home ranges were computed from the minimum convex polygon circumscribing locations of adult females mapped each spring (1993–1995)<sup>7,13</sup>. We tested for differences in the fitness response of morphs to density with repeated measures ANCOVA. Fitness of females on clutch 1 versus clutches 2–5 ( $C$ ) was regressed on a factor for  $M$  and covariates for number of orange ( $N_o$ ) and yellow neighbours ( $N_y$ ). Differences in morph responses were tested with interaction terms ( $M \times C \times N_o$ ,  $M \times C \times N_y$ ).

### Heritability and genetic correlations

In our population censuses (see above), we measured clutch size and egg mass, and scored throat colour of the female parent and her individually marked progeny. We used these field pedigrees to estimate heritability of all traits<sup>22</sup>. Throat colour was scored as 0 if yellow or 1 orange<sup>7</sup>. Genetic correlations were computed from the reciprocal cross-covariance between parent and progeny traits<sup>22</sup> (for example, throat of mother and clutch size or egg

mass of progeny) and from the ordinary covariance between parent–progeny traits.

### Experiments on density-dependent survival

During 1989–1998, we released progeny from clutches 2–5 into areas that were either previously seeded with clutch 1 progeny ( $n = 35$  control pots) or not seeded with clutch 1 progeny ( $n = 18$  treatment plots). Eggs were incubated in the laboratory and progeny were individually marked at hatching; they were then randomly released with respect to dam's territory<sup>6</sup>. Each study plot<sup>8</sup> consisted of a rock outcropping separated by unsuitable lizard habitat (such as grassland). Dispersal of hatchlings largely occurs within study plots<sup>22</sup>. Area of plots varied from 311 to 953 m<sup>2</sup> (mean is 675, s.e.m. = 79). Number of progeny released per study plot varied from 8 to 61 (mean is 28, s.e.m. = 1.3).

### Manipulating progeny size–frequency distributions

During 1995–1997, we seeded progeny onto plots where giant progeny were either common (20%,  $n = 10$  plots) or rare (10%,  $n = 17$  plots) and measured selection gradients on egg size based on survival of progeny to maturity. Remaining frequencies were split between normal-sized and miniaturized progeny. Density was constant within years<sup>8</sup>. Giant eggs were obtained by ablating ovarian follicles<sup>27</sup>, which yields hatchlings 20% larger than the mean<sup>21</sup>. Miniature eggs were obtained by aspirating 20% of the yolk from freshly laid eggs with sterile syringes<sup>22,28</sup>, which yields hatchlings 20% smaller than the mean. Normal-sized eggs were poked with sterile syringes but no yolk was removed. Number of progeny released per plot varied from 10 to 41 (mean = 22; s.e.m. = 1.5).

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