

**Endurance trials**

Endurance was measured on a circular treadmill<sup>21</sup>. Lizards (warmed up and maintained at a temperature close to their field optimum) were stimulated to run at a constant speed by gently tapping the base of their tail with a soft paintbrush. Endurance capacity was measured as the time to exhaustion (to the closest second), signalled by the lack of response after 10 consecutive taps<sup>22</sup>. There was a highly significant correlation between first and second measurements ( $r = 0.78$ ) (ANOVA on 70 offspring from 14 families measured two days apart, log-transformed endurance,  $F_{69,70} = 10.18$ ,  $P < 0.001$ ).

**First analysis of natural selection**

In July 2001, all offspring were released in nine enclosures, each receiving 10 families, 21 adults (including mothers) and 16 yearlings. Two recapture sessions took place in August 2001 (average age = 33 days  $\pm$  7.7 s.d.) and June 2002 (average age = 311 days  $\pm$  9.9 s.d., all individuals were then removed to the laboratory). Capture probabilities in August 2001 were estimated by fitting probabilistic models of individual capture-recapture histories<sup>23</sup>. Estimates were very close to one, allowing us to assume that individuals not seen in August 2001 had died before that census.

**Dietary effects on ontogenic consistency and second analysis of natural selection**

In 2002, we performed a laboratory manipulation of rations during the four weeks following birth. Two food treatments were designed on the basis of our unpublished growth data (used to calibrate a realistic distribution of postnatal growth rates), and physiological data<sup>24</sup> (to translate growth rates into expected food intakes in the laboratory). Dietary restriction was set to a delivery of 15 mg day<sup>-1</sup> of house cricket larvae (*Acheta domestica*, 3–5 mm size) during the first week, and raised each subsequent week to match the pattern of individual growth (see Table S4 in Supplementary Information). The full feeding treatment followed a parallel pattern in a 1:3 ratio. Over the entire manipulation, average food provision was 20.5 mg day<sup>-1</sup> in the low-food treatment and 61.5 mg day<sup>-1</sup> in the high-food treatment. To compare siblings, we selected two males and two females from 32 families and allocated one individual of each sex to each treatment. We recorded endurance at the age of one day and at the end of the manipulation (age 33 days). Siblings were then released at random in one of two outdoor enclosures where populations of 13 adults, 30 yearlings and 10 juveniles had been established two months earlier. All individuals were removed from the enclosures in late May of the following year. The difference in annual survival probabilities between this and the first analysis of natural selection is likely to reflect costs of settlement in already populated enclosures and costs of translocation from the laboratory<sup>25</sup>. The directional prediction that dietary conditions should affect the relationship between endurance and survival probability was tested with a mixed-effects logistic regression using a one-tailed test<sup>26</sup>.

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**Predator-induced behaviour shifts and natural selection in field-experimental lizard populations**

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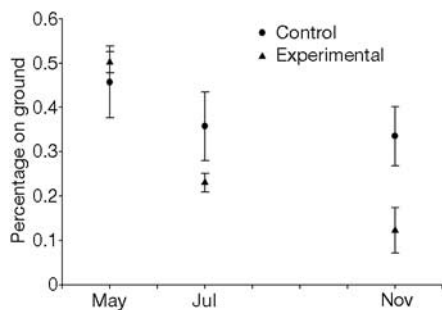
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The role of behaviour in evolutionary change has long been debated. On the one hand, behavioural changes may expose individuals to new selective pressures by altering the way that organisms interact with the environment, thus driving evolutionary divergence<sup>1–3</sup>. Alternatively, behaviour can act to retard evolutionary change<sup>4–6</sup>: by altering behavioural patterns in the face of new environmental conditions, organisms can minimize exposure to new selective pressures. This constraining influence of behaviour has been put forward as an explanation for evolutionary stasis within lineages<sup>4,7–9</sup> and niche conservatism within clades<sup>10,11</sup>. Nonetheless, the hypothesis that behavioural change prevents natural selection from operating in new environments has never been experimentally tested. We conducted a controlled and replicated experimental study of selection in entirely natural populations; we demonstrate that lizards alter their habitat use in the presence of an introduced predator, but that these behavioural shifts do not prevent patterns of natural selection from changing in experimental populations.

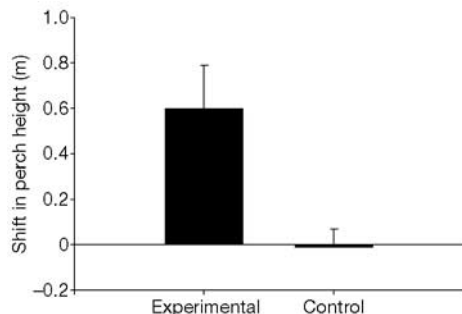
Caribbean *Anolis* lizards are ideal subjects for examining the evolutionary role of behaviour. Comparative and experimental studies indicate that populations alter their habitat use in response to the presence of competing or predatory species<sup>12–14</sup>; observations reveal that individuals change their behaviour over short periods of

time depending on the local presence of other species (reviewed in ref. 15). Previous studies on *Anolis sagrei*, a small lizard species that usually occurs on or near the ground, showed that it moved higher in the vegetation in the presence of the larger ground-dwelling curly-tailed lizard, *Leiocephalus carinatus*<sup>16,17</sup>. Because *L. carinatus* eats *A. sagrei*<sup>18</sup>, we predict that the presence of *L. carinatus* may lead to shifts in the pattern of natural selection in experimental populations. In particular, because body size and relative limb length are correlated with sprinting ability in anoles and other lizards<sup>19</sup>, we predict that the presence of *L. carinatus* may favour larger and longer-legged *A. sagrei* individuals that are better able to escape. In addition, gape-limitation of *L. carinatus*<sup>18</sup> would also favour larger *A. sagrei* individuals. On the other hand, by moving into the vegetation, *A. sagrei* may avoid predation by the more terrestrial *L. carinatus* and thus preclude selection on these traits. Previous studies comparing populations in the presence or absence of *L. carinatus* have detected differences in population size and trait distributions<sup>16,17</sup> consistent with the hypothesis of predation-driven natural selection, but selection on individual traits has never previously been investigated.

To test these hypotheses, in June 2003 we staged an introduction of curly-tailed lizards to six small islands in the Bahamas. Six other islands served as controls. Immediately before the introductions, *A. sagrei* were captured, measured and marked on each island. Before the introductions, nearly half of the *A. sagrei* observed were on the ground and experimental and control islands did not differ (Fig. 1;  $F_{1,10} = 0.39$ ,  $P = 0.54$ ).



**Figure 1** Differences in proportion of animals observed on the ground in experimental and control populations. Values are the mean and one standard error of mean values for each island. Data, from 12 islands in May and November and 4 islands in July, are for all individuals >33 mm (the size cut-off for marking individuals) in May and all marked individuals in July and November.

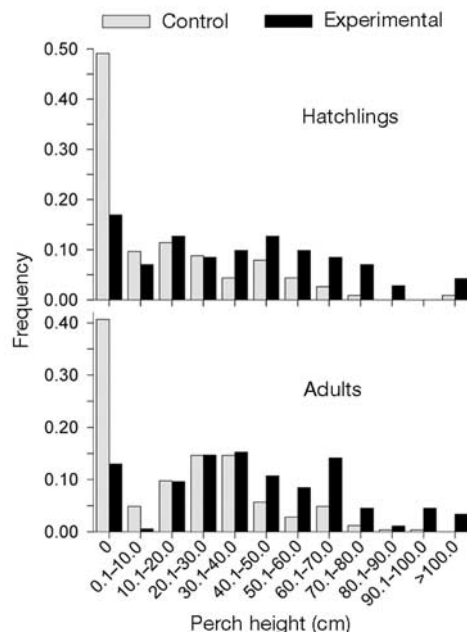


**Figure 2** Change in perch height ( $\pm 1$  s.e.) 10 min after introduction of either a live predatory lizard (experimental) or an inanimate object of the same size (control). Values are means from all individuals across four islands; statistical analyses nested individuals within islands.

When we initially introduced *L. carinatus* to the experimental islands, we released each individual predator 0.5–1.0 m in front of an adult *A. sagrei* in 10-min trials. Although *L. carinatus* almost certainly has not occurred on these islands during the lifetime of any then alive individuals, *A. sagrei* nonetheless responded to *L. carinatus* by moving higher in the vegetation (Fig. 2;  $F_{4,39} = 2.27$ ,  $P = 0.040$ ). Moreover, *A. sagrei* never moved towards *L. carinatus*, whereas on control islands, individuals frequently moved towards the control object (mean number of movements towards introduced object on control islands,  $\bar{x}$  ( $\pm 1$  s.e.) =  $1.86 \pm 0.51$ ;  $F_{4,37} = 19.71$ ,  $P < 0.001$ ).

This initial reaction was not permanent, as *A. sagrei* continued to use the ground, presumably when not perceiving a threat from *L. carinatus*. Over time, however, *A. sagrei* became increasingly arboreal on the experimental islands. Six weeks after the introduction, use of the ground on experimental islands was reduced by a third relative to control islands; by six months, only 12% of lizards were observed on the ground on experimental islands versus 34% on controls (Fig. 1), a difference that is statistically significant ( $F_{1,11} = 7.82$ ,  $P = 0.010$ ). Trends for perch height were the same: no difference existed between experimental and control islands in May ( $F_{1,10} = 1.39$ ,  $P = 0.27$ ), but by November, *A. sagrei* on experimental islands were perching much higher than on controls (Fig. 3; mean perch height 0.20 versus 0.10 m;  $F_{1,10} = 36.56$ ,  $P < 0.0001$ ), a difference that is also seen in hatchling lizards (Fig. 3;  $F_{1,9} = 6.45$ ,  $P = 0.016$  (no hatchlings were seen on one island)).

On each island, we measured selection gradients<sup>20,21</sup> on body size and relative limb length (the latter was measured only on males because gravidity makes this an unreliable measurement for females). As predicted, experimental and control islands differed in patterns of selection on both male hindlimb length ( $F_{1,6} = 9.05$ ,  $P = 0.012$ ) and female body size ( $F_{1,8} = 3.72$ ,  $P = 0.045$ ). These differences resulted because on all experimental islands, selection favoured (that is, positive selection gradient) larger females and males with longer legs (Fig. 4). By contrast, no consistent pattern



**Figure 3** Distribution of perch heights on experimental and control populations six months after the introduction of predatory curly-tailed lizards to experimental islands. Distributions are for all individuals on all islands (Fig. 1 presents means of proportions across islands). 'Adults' refers to animals  $\geq 36.5$  mm svl, whereas hatchlings are individuals  $\leq 30$  mm.

was apparent for male body size on experimental islands, nor for any of the traits on control islands.

Two lines of evidence indicate that differences in perch height between experimental and control islands result from individual behavioural shifts rather than selection against lizards that perch at inappropriate heights on islands with curly-tailed lizards. Four islands—two experimental and two control—were intensively studied with respect to the perching characteristics of their *A. sagrei* individuals. First, among individuals surviving to November, the shift to higher perches from the pre-introduction state was greater on experimental than on control islands ( $F_{1,2} = 36.89, P = 0.013$ ). Second, among these four islands, there was no evidence that selection favoured individuals that initially perched higher to a greater extent on experimental islands relative to controls: the highest and lowest selection gradients for initial perch height were on the two experimental islands, with the control islands being intermediate.

Our results constitute, to the best of our knowledge, the first experimental test of the hypothesis that behavioural shifts in new environments forestall natural selection. We find little support for this hypothesis. *Anolis sagrei* exhibits a marked behavioural shift in habitat use in the presence of the predatory *L. carinatus*, a shift that is as strong in hatchling lizards as it is in adults. Because *A. sagrei* on experimental islands still used the ground, albeit to an increasingly lesser extent, these habitat shifts were not enough to prevent substantial mortality of *A. sagrei* on experimental islands (mean number of marked individuals that failed to survive ( $\bar{x}$ ) = 0.66, range: 0.47–0.94; by contrast, mortality was variable and sometimes quite low on control islands,  $\bar{x} = 0.45$ , range = 0.09–0.79). This high rate of mortality provided the opportunity for selection to operate, and indeed it did in the direction predicted: the presence of the predatory *L. carinatus* favoured longer-legged male lizards, which can run faster, and favoured larger females, which are both

faster and harder to subdue and ingest. Although no selection on size in males was detected, this was not entirely unexpected: larger males may be more difficult to subdue and ingest, but this advantage is probably countered by the greater vulnerability of larger males resulting from their conspicuous territorial behaviour<sup>22</sup>.

Although the habitat shift exhibited by *A. sagrei* did not prevent selective mortality, it does set the stage for future, behaviour-driven evolutionary change. In contrast to its potentially constraining role, behavioural change also may promote evolutionary change—by changing the way organisms interact with the environment, behaviour may alter selective pressures<sup>1–3</sup>. Such a pattern eventually may apply on our islands as *A. sagrei* becomes increasingly arboreal, a process that previous work suggests will continue for at least several years<sup>17</sup>. By shifting higher into the vegetation, *A. sagrei* uses narrower perches<sup>14,17</sup>. Comparisons of species diverging for millions of years and of populations diverging for thousands of years reveal a consistent pattern: anoles adapt to using narrower surfaces by evolving shorter limbs<sup>15,23</sup>. Functional studies illuminate the underlying cause: on broad surfaces, long limbs provide maximal sprinting and jumping capabilities, whereas on narrow surfaces, short limbs permit agile movement on narrow and irregular surfaces<sup>24</sup>. Therefore, we predict that in future generations, the pattern of selective differences that we have observed will reverse; by moving higher into the vegetation, *A. sagrei* on experimental islands may almost completely escape predation by curly-tailed lizards, but will be forced to use narrower substrates that will favour individuals with shorter, rather than longer, limbs.

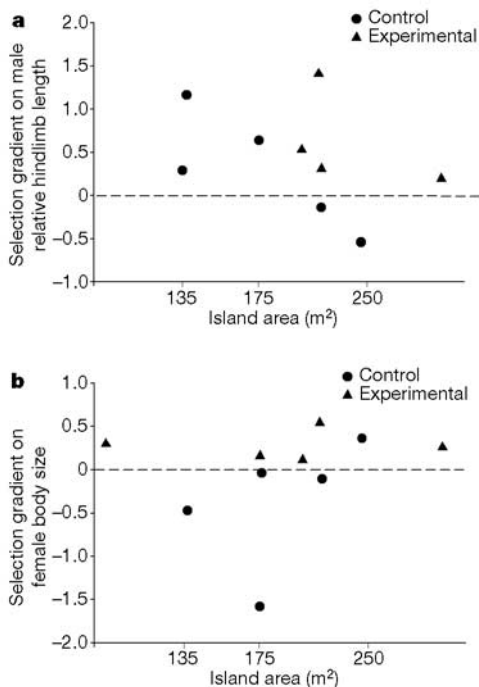
The role of behaviour in evolution is thus potentially not simple. Organisms may often alter their behaviour to avoid new selective agents such as an introduced predator, but such shifts can only forestall selection if they succeed in removing individuals from the new selective agent quickly enough. In our study, it is certainly possible that in the absence of the behavioural shift in habitat, mortality and perhaps selection would have been higher. Nonetheless, even with the habitat shift, mortality rates in populations exposed to the predator were high and provided substantial opportunity for selection to operate. As this behavioural shift continues to habitats increasingly inaccessible to the predator, selection may well change direction: even when behaviour fails to preclude selection of one kind in the short run, it can lead to another kind of selection in the long run. □

Methods

We located 12 small islands (vegetated area: 104–324 m<sup>2</sup>) lacking curly-tailed lizards in creeks near Snake Cay and Buckaroon Bay, Abaco, Bahamas. Curly-tailed lizards occur on larger islands within these creeks and occasionally colonize islands of the size studied. To ensure that the islands in the two treatments exhibited a similar range of characteristics<sup>25</sup>, we paired islands mainly on the basis of vegetated area, while also considering *A. sagrei* population size, per cent vegetation cover and location (Snake Cay versus Buckaroon Bay), and randomly selected one island from each pair to receive curly-tailed lizards. Adult curly-tailed lizards were collected from nearby areas and introduced on 1–7 June 2003, in proportion to the number of *A. sagrei* on each island (which is highly correlated with island area,  $r = 0.77$ ), which was estimated using mark-recapture methods<sup>13</sup> (estimated prereproductive-season population sizes: 22–103; approximately one curly-tailed lizard introduced per seven *A. sagrei*).

On four of the experimental islands, we conducted focal animal observations on individual *A. sagrei* to investigate their immediate reaction to the introduction of curly-tailed lizards. Lizards were approached and an experimental object—either a live curly-tailed lizard ( $n = 24$ ) or, as a control, an inanimate object of approximately the same size ( $n = 23$ )—was placed 0.5–1.0 m from the lizard on the ground and clearly in its visual field. Trials in which the lizard immediately ran away as the object was being delivered were eliminated, as were those in which the introduced curly-tailed lizard immediately fled. Experimental and control trials were alternated, and we tried to arrange trials in pairs in which the second trial involved an *A. sagrei* of the same sex as the previous one and in a similar initial position. Whether the first trial was experimental or control was randomly decided. Lizards were watched for 10 min after introduction of the object. We recorded the change in height off the ground from the beginning of the trial to the end and the number of movements the lizard made in the direction of the introduced object (this measurement was not recorded in several of the early trials). Data were square root transformed before analysis to equalize variances and were analysed with a two-way nested analysis of variance with individuals nested within islands.

Immediately before and six months after the introductions (22–30 November 2003),



**Figure 4** Selection gradients for male hindlimb length (a) and female snout-vent length (b). Gradients could not be calculated on all islands because on some islands all marked members of one sex either survived or died. The covariate island area was included in the statistical model for male hindlimb length (it is negative), but not for female body size (see Methods).

perch height was recorded for all observed individuals on all 12 islands; in addition, perch height was recorded for marked individuals on four islands (two experimental, two control) in July. Islands were visited multiple times but (with a few exceptions) only once per day. Data were taken for the location at which lizards were first observed; lizards that apparently were disturbed (that is, that appeared to be moving in response to our presence) when first seen were not included.

Also before the introductions, we captured lizards (>33 mm snout-vent length (svl)) on each island ( $n = 9-51$ , 342 total). Hindlimb span (length from insertion of limb in body wall to tip of claw on the fourth toe) was measured on males. Lizards were individually marked by injecting elastomer tags (Northwest Marine Technologies) subdermally in two limb segments. In November, we exhaustively sampled individuals on each island to recapture marked individuals. We estimated survival proportion as the fraction of originally marked individuals (that is, marked in May) found during the November study period, divided by the marginal recapture rate for the last complete census (see Supplementary Information for details on calculation of this rate); if this estimate was smaller than the final number actually found, we used the latter instead.

To measure the effect of curly-tailed lizards on survival selection, we treated the six-month interval as an episode of selection and calculated standardized selection gradients<sup>20,21,26</sup> separately for each sex on each island. These coefficients were then used as the data points for subsequent statistical analyses<sup>27</sup>. We also attempted to calculate selection gradient coefficients using logistic regression<sup>26</sup>, but the regression analyses failed to converge for analyses on several islands, so that estimates could not be obtained. For females, gradients were calculated only for svl, whereas for males they were calculated (in a multiple regression) for svl and relative hindlimb length (= residual of hindlimb length versus svl using the regression for individuals from all islands (analysis of covariance detects no heterogeneity of slopes among islands in the relationship between hindlimb length and svl)). Individuals not recaptured were considered to have died, with the exception that because of the loss of one of the two marks, the identity of five surviving females could not be established. On the basis of the frequency of mark loss, we estimate that one to two individuals in the study may have lost both marks and thus may have been incorrectly categorized as non-survivors. We measured selection at the intermediate time of six months, when mean survival on the islands averaged 45%, because we expected that this period was long enough for selective differences to become apparent, but not so long that marked cohorts would have mostly or entirely disappeared, thereby vitiating measurement of selection.

To test statistically the effect of *L. carinatus* on *A. sagrei* traits, we analysed selection gradient coefficients and mean perch heights from each island (one value per island) with the null hypothesis that mean values would not differ between experimental and control populations<sup>28,29</sup>. We first ran analyses of covariance on each dependent variable using island area (log transformed) as a covariate. This covariate was deleted from the model when  $P > 0.10$ ; it was retained only in the model for male relative hindlimb length. Because the variance of an estimated regression coefficient is inversely proportional to sample size, each selection coefficient for a given island was weighted by the number of individuals measured on that island; the weighting method does not change the degrees of freedom in the analysis<sup>30</sup> and statistical significance at the 0.05 level is the same in unweighted analyses. All  $P$ -values are one-tailed based on a priori hypotheses on the direction of the effect of *L. carinatus* on a given variable.

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## Magnetoreception and its trigeminal mediation in the homing pigeon

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Two conflicting hypotheses compete to explain how a homing pigeon can return to its loft over great distances. One proposes the use of atmospheric odours<sup>1</sup> and the other the Earth's magnetic field<sup>2-4</sup> in the 'map' step of the 'map and compass' hypothesis of pigeon homing<sup>5</sup>. Although magnetic effects on pigeon orientation<sup>6,7</sup> provide indirect evidence for a magnetic 'map', numerous conditioning experiments<sup>8</sup> have failed to demonstrate reproducible responses to magnetic fields by pigeons. This has led to suggestions that homing pigeons and other birds have no useful sensitivity to the Earth's magnetic field<sup>9-11</sup>. Here we demonstrate that homing pigeons (*Columba livia*) can discriminate between the presence and absence of a magnetic anomaly in a conditioned choice experiment. This discrimination is impaired by attachment of a magnet to the cere, local anaesthesia of the upper beak area, and bilateral section of the ophthalmic branch of