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Rapid Temporal Reversal in Predator-Driven Natural Selection

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Because of its potentially epochal scope, evolutionary biology is often caricatured as a strictly descriptive science, but recent years have shown that evolution can be studied on short time scales and that evolutionary biology can be both experimental and predictive (1, 2). Here, we report just such an example by demonstrating the occurrence of a predicted reversal in the direction of natural selection on limb length in *Anolis sagrei*, a common Bahamian lizard often found on the ground in the absence of terrestrial predators.

Previous research showed that, when a larger and entirely terrestrial predatory lizard, *Leiocephalus carinatus*, invades, *A. sagrei* becomes more arboreal and that the extent of this habitat shift broadens through time (3). Hence, we predicted that the direction of selection operating on limb length in *A. sagrei* would change through time in the presence of *L. carinatus* (4): Initially *A. sagrei* occurs mostly on the ground, so individuals with relatively longer legs, being faster (5), would be better able to elude the predators and thereby be favored. As *A. sagrei* becomes more arboreal, however, we predicted that selection would favor the reverse because shorter limbs are better suited for movement on the narrow and irregular surfaces *A. sagrei* would use to avoid the terrestrial predator (5).

To test this hypothesis, we introduced *L. carinatus* to six small Bahamian islands that naturally contained *A. sagrei*, randomly choosing six others to serve as controls (*L. carinatus* occurs on nearby larger islands and is known to colonize smaller islands); the number of *L. carinatus* introduced (all adults) was proportional to the number of *A. sagrei* resident on the island. Before introduction of *L. carinatus*, *A. sagrei* individuals on each island were measured and individually marked. Islands were exhaustively censused after 6 and 12 months to determine survival (6).

All predictions were confirmed. *A. sagrei* on introduction islands became increasingly arboreal, whereas use of the ground remained unchanged in controls (Fig. 1A); differences in perch diameter between lizards on experimental and control islands also increased through time (Fig. 1B). These trends are the same if comparisons are restricted to only those individuals surviving to the end of the experiment, indicating that differences between treatments resulted from individual shifts in behavior, rather than selection among individuals differing in habitat use [see also (4)]. In the first 6 months, longer legs were

more strongly favored on introduction islands than on controls, but in the second 6 months, selection was reversed and more strongly favored shorter legs on introduction islands [repeated-measures analysis of covariance (ANCOVA),

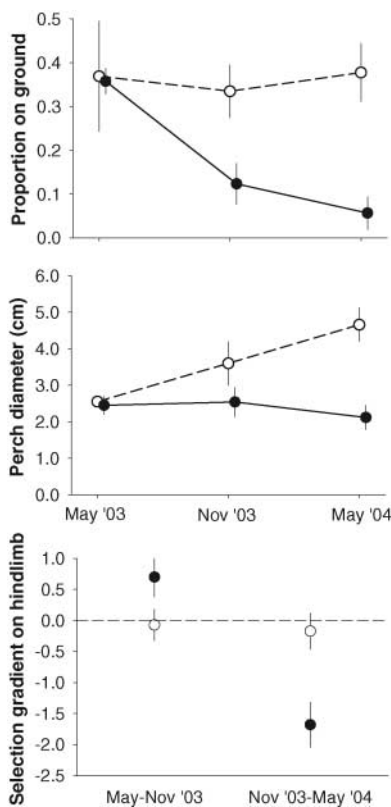


Fig. 1. Changes in habitat use and pattern of natural selection. For use of the ground (top) and perch diameter (middle), data from May 2003 represents habitat use before the initiation of the experiment. All data are for individuals initially measured and marked in May 2003. Lizards grew throughout the experiment, probably explaining the increase in perch diameter on control islands (an intraspecific relationship between body size and perch diameter is well established in *Anolis* lizards). (Bottom) Selection gradients were calculated for two time periods, May 2003 to November 2003 and November 2003 to May 2004. Selection gradients in the figure were adjusted for log-transformed island area (included in the repeated-measures analysis as a covariate) by using least squares means from the ANCOVA. Open symbols indicate control islands; filled symbols, introduction islands. Error bars are ± 1 standard error.

time*treatment interaction, $F_{1,2} = 59.04$, $P = 0.017$ (Fig. 1C)]. This reversal was accompanied by an especially great divergence in perch diameter during the second six months (repeated-measures analysis of variance, time*treatment interaction, $F_{1,10} = 11.38$, $P = 0.007$).

Thus, we showed that selection dramatically changed direction over a very short time, within a single generation, favoring first longer and then shorter hindlimbs. The behavioral shift from the ground to higher perches of smaller diameter apparently caused this remarkable reversal; behavioral flexibility, indeed, may often be the key in driving extremely rapid reversals in evolution (4). Our experiment also illustrates the complexity of measuring natural selection in the field (7). For example, had we waited 12 months to first measure selection, we could have concluded that the predator's presence had little if any effect on selection, and we certainly would have failed to detect the transitory selection for longer hindlimbs over the first 6-month period (table S1).

Nonetheless, over the much longer term, we expect that in the continued presence of *L. carinatus* the initially long-legged *A. sagrei* would remain on high, thin perches, eventually evolving substantially shorter legs. We base this expectation both on functional studies of locomotion (5) and on the observation that twig specialists have arisen four times on Caribbean islands, in each case evolving very short hind legs (8). Evolutionary biology is by its nature an historical science, but the combination of microevolutionary experimentation and macroevolutionary historical analysis can provide a rich understanding about the genesis of biological diversity.

References and Notes

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Supporting Online Material

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Materials and Methods

Fig. S1

Table S1

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