

sure for each ecotype). The authors note that their study is a long-term experiment. Without alteration of the experimental design, future results may be suspect.

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SIR — Malhotra and Thorpe² provide no evidence for a rapid evolutionary response in natural lizard populations. Their experiment, which is conceptually ingenious and potentially important, was based on the translocation of four populations of *Anolis oculatus* from different ecosystems to four neighbouring arenas. The authors claim that there was rapid selective mortality in the translocated populations, and that this is evidence for the action of natural selection.

There are three problems with their experiment. (1) The design is what statisticians call confounded and ecologists pseudoreplicated. Because each population is in only one arena it is impossible to tell whether the claimed effect is due to differences between arenas or between populations.

(2) The correlation coefficient quoted in Fig. 2 is not statistically significant. There are not six degrees of freedom (as the authors appear to assume) but only two (there being four arenas). However, the figure does show a large response in one deviant population. As this montane population was from the ecologically most distinct site it could still support the authors' conclusion that the differential mortality is evidence of rapid evolutionary change due to natural selection.

(3) Unfortunately, even if we accept that the effect is due to the montane population responding differently to translocation, this does not necessarily imply natural selection. Using the values in Table 1 of ref. 2 we can calculate the average weight of the lizards placed in the different arenas: control 3.76 g, S. Caribbean 4.6 g, Atlantic 5.26 g, Montane 8.46 g. Lizards from the montane population were, on average, more than twice the weight of the controls when they were translocated. Because the morphological measurements taken have

not been corrected for body size or age, there is the strong possibility that it was the larger or older animals that died. No evidence is presented that the difference in body size between the populations is genetically based. We therefore reluctantly conclude that no reliable evidence of a rapid evolutionary response has been presented.

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THORPE AND MALHOTRA REPLY — Our study² shows clear evidence of rapid evolutionary response in lizards and Katti's and Lawton and McArdle's claims to the contrary are based on flawed logic and misunderstanding of the statistics used.

In particular, they reach their erroneous conclusions because they fail adequately to differentiate between the within-enclosure study of morphology, which supplied the critical evidence, and the between-enclosure study of 'fitness', which supplied only supplementary information. Their point that the difference between ecotypes could be due to chance differences between enclosures cannot pertain to the difference in the morphology of survivors and non-survivors within an enclosure, but only to the between enclosure analysis of 'fitness'.

Katti's claim that the "differential survival" of ecotypes could be due to density, average body size, or chance might have been true if we had measured differential survival as the relative number of survivors in each ecotype, but we did not do this. We measured the difference in morphology between survivors and non-survivors, and the fact that the most foreign ecotype exhibited a significant difference within an enclosure has to be due to differential selection, irrespective of any differences between enclosures, be they chance, average body size or density. Even so, biomass was constant between enclosures and density was lowest in the enclosure with greatest selection effects. Lawton and

McArdle's first point is rejected for the morphology on the same basis. The point regarding replication is valid for the fitness variables, but we are dealing here not with a small plot of ground in a suburban research station, but with about 100,000 m³ of remote natural forest per set of enclosures, requiring constant management. For several replications, the time required is prohibitive and the environmental perturbation caused is unacceptable, given the entirely supplementary and non-critical role of these fitness data. Moreover, a replicate in the Atlantic habitat supports our earlier results in showing a significant difference in morphology between survivors and non-survivors of foreign ecotypes and their lower fitness (growth rate, condition and weight change).

The average specimen size differs among ecotypes because size varies racially and not because of sample bias. There is no trend for preferential survival of a given size within an enclosure. There is no basis for excluding a single measure of size as it tends to be as highly heritable as other characteristics³⁻⁶. 'Size' has to be taken into account because of its intercorrelating effect, and this we do properly by using Mahalanobis D^2 (refs 7,8) as Lawton and McArdle should have realized. Consequently, the significant difference between montane-type survivors/non-survivors is unaltered by the exclusion of snout-vent length and/or size-adjusting the few linear measurements. This is the most important point because, as Lawton and McArdle admit, this significant difference is sufficient to prove our case.

With regard to the correlation between the dissimilarity in ecology and morphological dissimilarity between survivors/non-survivors, Lawton and McArdle do not appear to regard the D^2 for sexes as varying independently, even though it clearly does so. Random permutation techniques⁸⁻¹⁰ which give the probability of association when the data points are not independent, indicate a significant association ($P < 0.01$, 10,000 permutations). Moreover, if one accepts Lawton and McArdle's point, the morphological dissimilarity can be averaged across sex (giving four points) and the relationship linearized. This gives a correlation of $r = 1.0000$ which is significant whatever degrees of freedom are used.

Our morphological analysis provides sound evidence of rapid evolution in *Anolis oculatus* and our analysis of fitness, although non-critical, provides interesting information on the interface between evolution and ecology.

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