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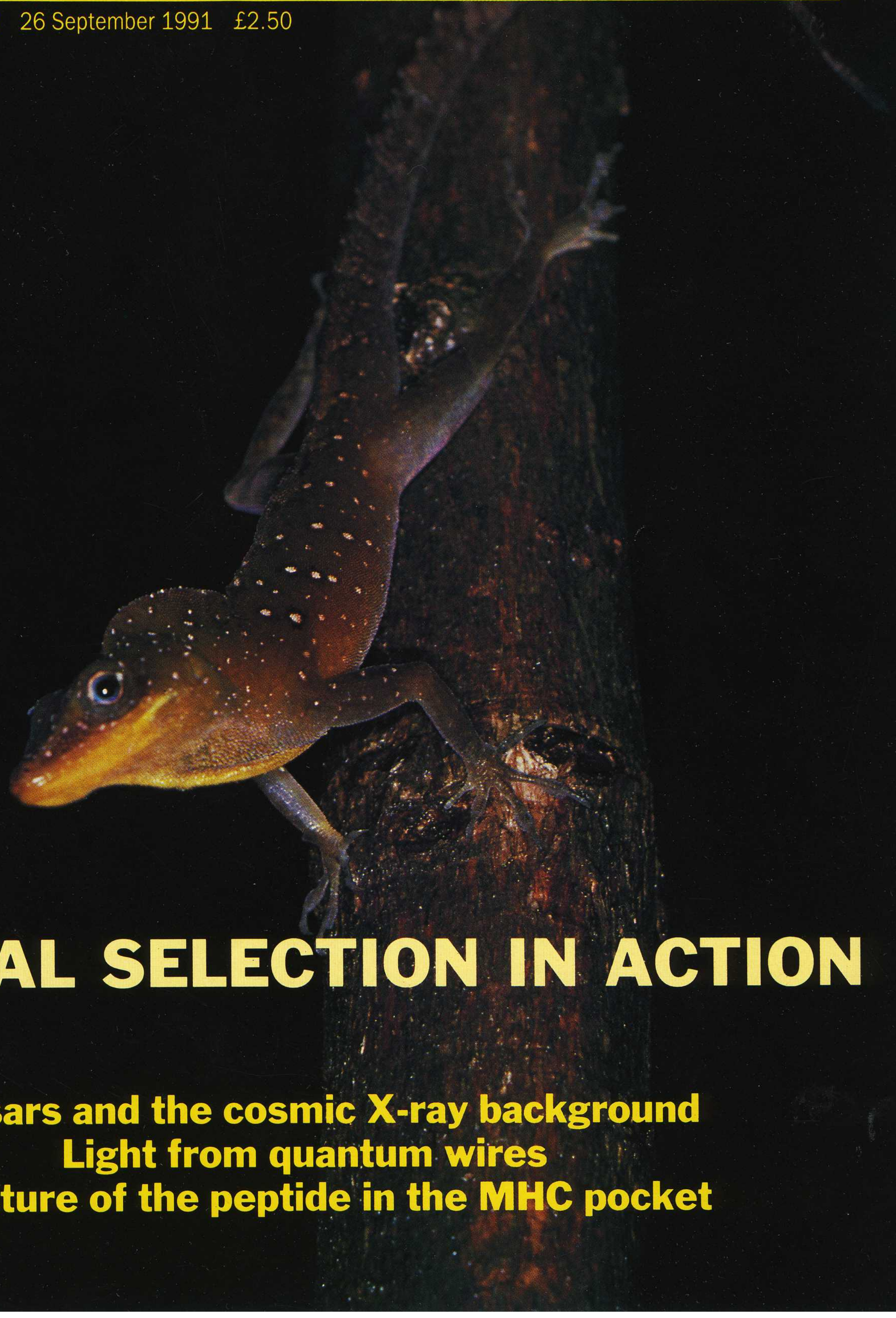

NATURAL SELECTION IN ACTION

Quasars and the cosmic X-ray background

Light from quantum wires

Structure of the peptide in the MHC pocket

Experimental detection of rapid evolutionary response in natural lizard populations

A. Malhotra & R. S. Thorpe

Department of Zoology, University of Aberdeen, Tillydrone Avenue, Scotland AB9 2TN, UK

MANY studies of geographical variation within species[1-7], including those using numerical hypothesis tests[3-10], have demonstrated a relationship between patterns of phenotypic and environmental variation. But relatively few rigorously tested direct demonstrations of current selection in natural populations exist[11-14]. Here we present evidence of a rapid response to selection from a field manipulation of the Dominican lizard, *Anolis oculatus*. There is considerable altitudinal and longitudinal variation in climate and vegetation on the island of Dominica[15]. We have recorded complex patterns of geographic variation in morphology (body size and shape, colour pattern and scalation), which we have shown to correlate (both univariately and multivariately) with these patterns of ecological variation[16] by numerical hypothesis testing[10,17,18]. Populations of several ecotypes of the species were translocated into large-scale experimental enclosures, and monitored over a period of two months. The magnitude of the difference in multivariate morphology between survivors and non-survivors within each enclosure was found to correlate with the magnitude of the difference between the ecological conditions of the enclosure site and the original habitats. Similar relationships were found for three indices of fitness of survivors.

The manipulative field experiment described here was designed to test the adaptive nature of morphological variation. We constructed four large-scale lizard-proof enclosures and translocated samples of four 'source' populations, representing the four main ecotypes (Fig. 1) into these enclosures. One enclosure contained a 'resident' control, which was subjected to the same procedures as translocated 'foreign' ecotypes. Before numbering and releasing into the appropriate enclosure, 10 morphological characters (including body proportions, scalation and colour pattern characters) were recorded from each lizard. This multivariate phenotypic profile was later used to compare morphology of survivors and non-survivors (surviving lizards were not remeasured for this profile). Body weight was also recorded (to the nearest 0.01 g).

The enclosures were constructed in May 1990, stocked in June and July (at the start of the wet season), and populations were monitored in September 1990 after a period of about two months had elapsed. Monitoring consisted of one to two weeks in which all enclosures were intensively searched concurrently. Body weight and snout-vent length of each lizard was measured on capture. They were then marked near the base of the tail with

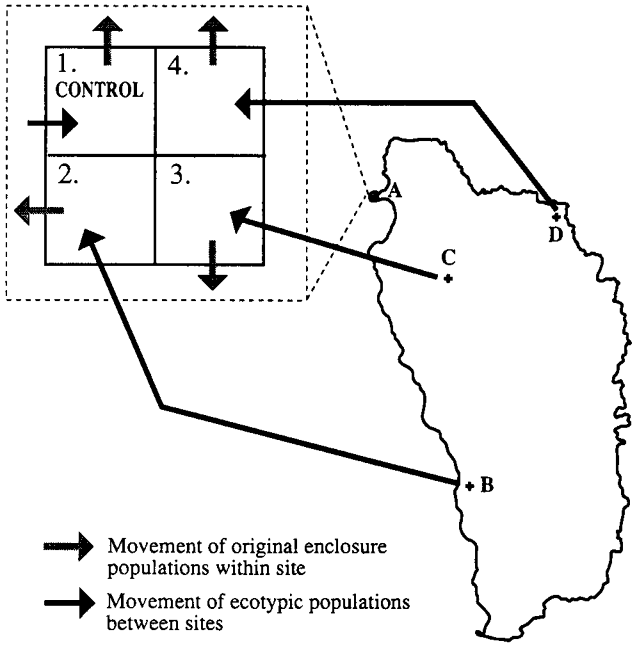

FIG. 1 Schematic representation of the experimental design. The lizard-proof enclosures were based loosely on the design described in ref. 20. The areas were enclosed by a 1-m-high fence (agricultural polyethylene netting of small mesh size), dug into the ground at the bottom and topped by a 30-cm-wide overhang of smooth plastic, with a 2-m gap to the nearest vegetation (from ground level to the canopy) on either side. Construction details will be published elsewhere. The actual dimensions of each enclosure were measured, and their area calculated. Anole biomass per unit area of habitat was determined by capturing and weighing all original inhabitants, and averaged over all enclosures. They were then stocked at the same level with animals from populations representative of the different ecotypes. Control populations were also moved from adjacent habitat into the control enclosure. The morphological characters defining the four ecotypes and their representative populations, were decided on the basis of a previous multivariate investigation of geographic variation in *Anolis oculatus* (manuscript in preparation). The North Caribbean ecotype, represented in our study by a population from the Cabrits (A; also the site of the experimental enclosures), occupies low scrub-like woodland in the most arid part of the island. The South Caribbean ecotype from the less arid southern west coast was represented by a sample from Morne Daniel (B). The Montane ecotype was represented by Syndicate Estate (C), a rainforest site at an altitude of 660 m. Lastly, the Atlantic ecotype was taken from dense, wind-blown littoral woodland at Eden Estate (D). Animals were weighed, sexed and numbered. To minimize stress, animals were anaesthetized before being processed. They were released into the enclosures as soon after capture as possible.

TABLE 1 Means of three indices of fitness of surviving individuals in each enclosure

Ecotypes in enclosures*	Enclosure area (m^2)	Biomass of site (g m^2)	*N* (start)	*N* (end)	Growth rate (mm d^{-1})	Change in condition	Rate of weight gain (g d^{-1})	D^2		*P*	
								M	F	M	F
1. N. Caribbean	131.85	2.94	103	58	0.080	24.74	0.027	1.83	0.49	NS	NS
2. S. Caribbean	100.35	2.94	63	28	0.045	−2.56	0.010	1.52	0.76	NS	NS
3. Montane	109.35	2.94	38	19	0.010	−48.20	−0.033	10.95	8.37	<0.01	<0.001
4. Atlantic	143.10	2.94	80	52	0.042	11.99	0.014	1.68	1.96	NS	NS

The difference between the means in all cases is highly significant (ANOVA, $P<0.01$). Condition is defined as SVL^3/WT, Mahalonobis distances (D^2) between survivors and non-survivors, and associated probabilities (*P*), are given for males (M) and females (F) separately. *N*, number of specimens in enclosure; NS, not significant.

* Numbers are enclosure numbers as in Fig. 1.

a permanent marker pen, and released. Searching was only abandoned when two consecutive searches failed to reveal any additional unmarked lizards.

The hypothesis that ecotypic variation is caused by natural selection for differing environmental conditions was tested in two ways. If selection is strong enough, we should detect a difference between the morphology of animals that survived and those that died within any one generation of the respective ecotypes. Furthermore, the intensity of this selection should be related to the magnitude of relative ecological differences experienced by the translocated ecotypes. Also, the surviving animals of translocated ecotypes should show detectably lower 'fitness' (the implicit assumption being that the indices of fitness used here translate into relative lifetime fitness as defined by Endler[12]) compared with the control 'resident' ecotype.

We tested for a difference in the morphology of survivors and nonsurvivors using two methods. Firstly, a 3-way multivariate analysis of variance (MANOVA) was used to examine overall differences in survival between ecotypes (Montane, North Caribbean, South Caribbean, Atlantic, as defined previously[16]). The model included interactions between sex, survival and ecotype. The interaction between survival and ecotype reveals whether the magnitude or morphological difference between survivors and non-survivors varies according to ecotype (that is, varying selection intensity), and the results show a highly significant difference does exist ($P<0.001$). A canonical variate analysis was performed on all groups (4 ecotypes × 2 sexes × survival factor = 16 groups) and the multivariate distance (Mahalonobis, D^2) between the morphology of survivors and nonsurvivors of each ecotype was obtained.

A plot of the magnitude of the morphological difference between survivors and non-survivors (D^2), against the magnitude of the difference between ecological conditions at the enclosure site and the original habitats shows a significant correlation (Fig. 2). This indicates that there has been a selective deletion of certain phenotypes over a very short time (2 months), and that the intensity of this selection is significantly related to the change in ecological conditions that the ecotypes have experienced. More extreme ecological changes (as experienced by the Montane ecotype) results in highly significant differences

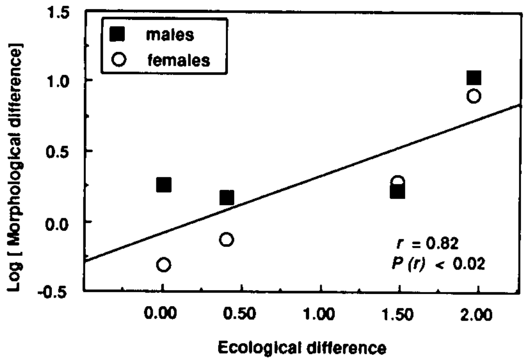

FIG. 2 The relationship between the change in ecological conditions experienced by the ecotypes, and morphological distance between survivors and non-survivors. Ecological difference is derived from a taxonomic distance matrix based on six ecological variables (namely average annual rainfall, average annual temperature, altitude and occurrence of three vegetation types). The habitats of the translocated ecotypes increasingly differ from that of the enclosure site (North Caribbean) in the following order: South Caribbean, Atlantic, Montane. The difference in morphology of survivors and non-survivors is represented by the Mahalonobis D^2 from the canonical variate analysis (see text). The morphological characters used were snout width; length of the fourth toe of the hind foot; lower leg length; the number of scale rows at mid-body; the number of scales between the supra-orbital semicircles; the degree of enlargement of lateral white scales; the number of white lateral spots covering more than 20 scales; dewlap hue and ventral hue.

(Table 1) between morphology of survivors and nonsurvivors, in spite of the low sample sizes.

Three indices of fitness of surviving individuals were also calculated; these were growth rate (mm per day), weight gain (g per day) and change in condition (where condition is defined as SVL^3/WT, SVL being the snout-vent length, and WT the body weight). These were calculated for males only, to avoid confusion arising from differences in reproductive effort in females. Table 1 shows that the fitness of the control ecotype is better than that of the translocated ecotypes for all three indices. Among translocated ecotypes, the coastal ecotypes show higher fitness than the montane ecotype.

There is much discussion of the role and mode of action of natural selection in evolution[19]. This experiment, designed to run over a long-term period, has unexpectedly demonstrated that significant mortality selection can occur over a very short timescale in perturbed populations. By showing that the intensity of selection acting on the translocated ecotypes is correlated with the magnitude of ecological change, we provide direct evidence that the high degree of morphological variation in this species is maintained by selection for different habitats, in the absence of barriers to gene flow between adjacent populations. □

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