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Environmental Component of Morphological Differentiation in Birds

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very little PS, there was a high correlation ( $r = .94$ ,  $P < .001$ ) between their PS (percentage of baseline) and survival time in the experiment. Survival time did not correlate highly with other sleep variables. The result suggests a vital role for PS, but it is so at variance with previous reports (8) that we believe it needs further confirmation.

Because the only difference in the treatment of the rats was that disk rotation was linked to sleep onset in deprived but not control rats, the pathological changes and mortality in deprived rats must be attributed to the disruption of sleep or a related process. Since the observed physiological impairments were not uniform across deprived rats, the nature of the functional deficit remains unclear. Nevertheless, these results support the view that sleep does serve a vital physiological function.

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3. Dimensions: disk diameter, 45.7 cm; thickness, 1 cm; floor area for each rat, 420 cm<sup>2</sup>. Trays were 70 cm long, 20 cm wide, and 4.6 cm deep. Cages were 72 cm long, 21 cm wide, and 60 cm high. Supporting stilts raised the cages 6.4 cm above table level, permitting clearance of 2 mm between cage and disk and 6 mm between disk and water tray.
4. B. Bergmann, C. Eastman, R. Rosenberg, and A. Rechtschaffen [*Sleep Res.* 10, 24 (1981)] showed that LS (previously designated "quiet state"), which is defined by low amplitude EEG, EMG, and theta activity and which occurs mostly for short intervals between other stages, behaviorally resembles HS.
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9. Supported by NIH grants MH-4151 and MH-18428 to A.R. We thank L. Wold for the histological examination of the lungs, J. Russel for assistance with necropsies, V. E. Fang for the corticosterone assays, and R. Rosenberg, V. House, and C. Anderson for technical assistance.

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## Environmental Component of Morphological Differentiation in Birds

**Abstract.** *Geographic character variation in birds is usually attributed to natural selection for phenotypes that reflect locally adapted genetic differences. However, experimental transplants of red-winged blackbird eggs between nests in northern and southern Florida, and from Colorado to Minnesota, show that in this species a significant proportion of the regional differences in nestling development is nongenetic. If natural selection is maintaining the clines of character variation that are observed in adult phenotypes, the genetic and nongenetic components of phenotypic variation must covary.*

Many species of vertebrates exhibit parallel patterns of geographic variation in external morphology (1). In birds, regional trends of size variation change gradually in a way that may reflect topographic features (2). The mechanism that maintains such clines of character variation is traditionally assumed to be natural selection for polygenic traits that represent adaptations to local conditions (3). Inferences about the agents of selection are usually based on correlative methods and are necessarily weak. Nevertheless, the thermoregulatory arguments of Bergmann (2, 4, 5) are supported by very high correlations between size variation and climatic factors, especially when all avenues of heat exchange are considered (2, 6, 7). Other arguments proposed for mammals involve the energetics of procuring food (8), predator-prey relationships (9), and competition with related sympatric species (10). There has been little attention paid to the significance of shape variation that is allometrically associated with size variation or to the extent to which clinal variation is environmentally induced.

I report here the results of transplant experiments designed to estimate the magnitude and direction of direct environmental effects on regional morphological differentiation in the red-winged blackbird (*Agelaius phoeniceus*). In the United States the smallest adult redwings are the slender-billed population in southeastern Florida. Breeding adult males there weigh about 47 g and have a bill length of approximately 23 mm. An example of large birds is the stocky conical-billed population in central Colorado, where adult males weigh about 70 g and have a bill length of approximately 21 mm (11). These regional intraspecific differences are similar to generic differences in the blackbird family Icteridae (for example, between orioles, *Icterus*, and cowbirds, *Molothrus*), but they are smaller (12). Despite massive winter movements of red-winged blackbirds (13), relatively stable clines of character variation are reestablished across the continent every breeding season.

Regional variation in the shape of adult redwings in Florida can be detected in the development of nestlings. For example, nestlings (14) and adults (15) at a study site in the northern part of the state (Tallahassee, Leon County) have higher ratios of bill depth to tarsus, and lower ratios of bill length to tarsus and toe to tarsus than do nestlings in the southern part (Everglades, Dade County). Similarly, nestlings in Clearwater County, in northern central Minnesota, have higher ratios of wing length to tarsus and toe to tarsus than do those at Fort Collins, Larimer County, in central Colorado, and differences in small samples of adults appear to be in the same direction. The fact that the shape characters that best distinguish the populations in Florida are different from the ones that best distinguish the Colorado from the Minnesota populations is evidence of the complex nature of geographic character variation.

In 1980 and 1981, eggs were transported between study sites by car. Clutches of eggs were carried in an incubator connected through an inverter to the car battery and then placed in foster nests (16). For comparison control eggs were held in an incubator for 2 days and then placed in other local nests. The results are presented as (i) differences between the control and transplanted nestlings (Table 1) and (ii) differences between these groups plotted along the axis that best separates the normal (unmanipulated) nestling populations (Fig. 1) (17). In a reciprocal transplant of eggs between northern and southern Florida, and in a transplant from Colorado to Minnesota, the transplanted nestlings demonstrated a shift from the phenotype of the controls toward the phenotype of nestlings in normal unmanipulated nests of the foster population (18). Discriminant analyses and univariate *F* tests between the control and transplant groups (Table 1) show which characters have the largest component of environmental plasticity. In the reciprocal transplant across Florida the ratio of bill length to tarsus shifted most and was in the direction

predicted by differences among adults. In the transplant from Colorado to Minnesota the ratio of wing to tarsus shifted most and again was in the direction predicted by differences among adults (19). These environmentally plastic characters (bill shape in Florida, ratio of wing to tarsus in Colorado) are also the same characters that discriminated best between the respective pairs of normal nestling populations (Fig. 1).

Apparently, the extent to which shape differences among the redwing populations are genetically based is geographically variable. For example, although discriminant analysis shows that there are highly significant environmentally induced shape changes between each of the three pairs of control and transplant groups (Table 1), the relatively low magnitude of the shift in Tallahassee birds when differences are plotted along the axis that best separates normal nestlings (Fig. 1A) suggests that the genetic component of variation may be higher in Tallahassee than in the Everglades. The ratio of bill length to tarsus is very plastic in both populations, and therefore the difference in Fig. 1A is probably attributable to differences in other characteristics. Taken together, the results presented in Table 1 and Fig. 1 show that (i) clinal character variation contains important directional environmentally induced effects and (ii) individual characters have geographic variation in levels of phenotypic stability. These findings are particularly interesting in light of research on genotype-environment interactions in plants whereby the environment can induce changes in some varieties that are similar to those that are genetically fixed in other varieties (20).

Calculations of local heritability of individual characters of birds have been accumulating along with recent improvements in the methodology of field experimentation. Regressions of measurements of offspring on those of their parents, after the young have been reared by foster parents in other local nests, provide estimates of the proportion of local variation that is attributable to genetic differences. Such estimates are relevant to whether natural selection is operating on the character of interest in the classical microevolutionary sense (21), but they are not sufficient evidence to establish that this is the case. If natural selection is maintaining the between-locality clinal variation in redwings, in which there is evidently also directional environmentally induced variation, then regional genetic variation must covary positively with the environmentally induced variation. This relationship is

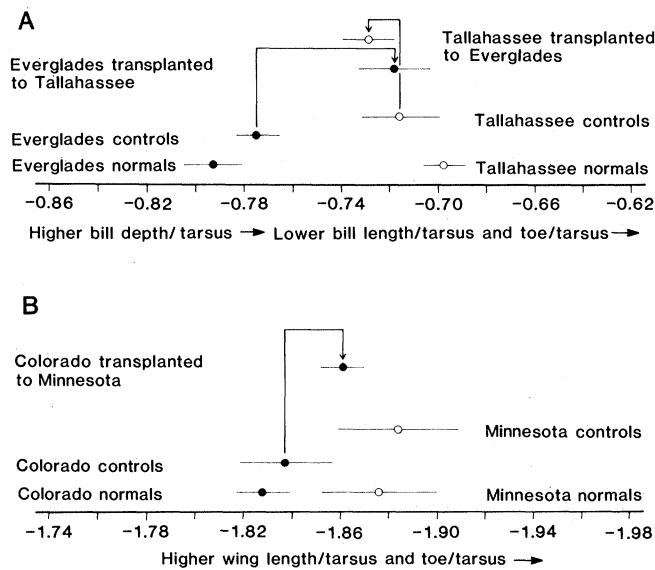


Fig. 1. Two highly significant canonical discriminant function analyses of shape characters of normal nestlings in unmanipulated nests. The axes maximize the differences between (A) normal Everglades ( $N = 13$ ) and Tallahassee ( $N = 30$ ) nestlings and (B) Colorado ( $N = 17$ ) and Minnesota ( $N = 9$ ) nestlings. Numbers give units of discrimination. Means and 95 percent confidence intervals are given for scores along these axes for control and transplant groups as well as for normal groups. In each case the shape of transplanted birds shifted toward that of normal nestlings in the foster population (16, 17).

probable but it has not been confirmed. Another possibility is that genetic differences between populations are independent of the environmentally induced differences (22), but the latter are associated with differences in reproductive rate. For instance, if environmentally induced differences in morphology covary with environmentally induced differences in clutch size, the latter may drive directional gene flow between localities. In such a case the environmental component of phenotypic variation would be causing changes in gene frequencies and thereby affecting evolution. A third possibility is that intraspecific patterns of geographic variation may not be adap-

tive in any sense. The biological significance of morphological and associated developmental or physiological differences that vary clinally on a continental scale, but are barely detectable within and between adjacent localities, is very difficult to determine. Berven *et al.* (23) showed that clinal variation in the morphology and development of the green frog (*Rana clamitans*) is primarily induced by the environment and that between-locality genetic differences in growth rate are actually counter to the observed pattern of clinal variation. Future studies of character variation should be designed to estimate not just the proportion of local variance that is genetic

Table 1. Five shape variables ordered by decreasing power of discrimination in three highly significant canonical discriminant function analyses of differences between nestlings in control and transplant groups for a reciprocal transplant experiment within Florida and a transplant from Colorado to Minnesota (each with  $P < .005$ ). Sample sizes are in parentheses. Analyses were performed on logs (14, 15).

Place of origin	Shape variable	Significance of		Average ratio at predicted tarsal length of 20 mm		
		Stepwise contributions to discrimination	Univariate $F$ tests	Control	Transplant	
Tallahassee	Control ( $N = 19$ ) versus transplanted to Everglades ( $N = 16$ )					
	Bill length/tarsus	0.0008	0.001	0.468	0.492	
	Toe/tarsus	0.0009	0.093	0.718	0.694	
Everglades	Control ( $N = 13$ ) versus transplanted to Tallahassee ( $N = 11$ )					
	Bill length/tarsus	0.01	0.01	0.502	0.476	
	Bill depth/tarsus	0.0001	0.07	0.208	0.217	
	Toe/tarsus	0.0001	0.14	0.702	0.681	
	Bill width/tarsus	0.0001	0.39	0.191	0.194	
Colorado	Control ( $N = 8$ ) versus transplanted to Minnesota ( $N = 22$ )					
	Wing length/tarsus	0.007	0.005	1.423	1.546	
	Bill length/tarsus	0.001	0.82	0.513	0.496	
	Bill depth/tarsus	0.001	0.22	0.236	0.232	
	Bill width/tarsus	0.002	0.20	0.213	0.210	

but also geographic variation in the genetic and environmental contribution to patterns of phenotypic variation.

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14. Nestlings were measured in the field on a minimum of 4 days. All variables were transformed to logs before analysis. For each individual, separate regressions of the logs of bill length, bill depth, bill width, wing length, and central toe length on log tarsal length were calculated. For each measurement the predicted log value at log tarsus = log 20 was obtained. Univariate *F* tests of data for unmanipulated nestling populations in the Everglades and Tallahassee showed that at a tarsal length of 20 mm the ratio of bill depth to tarsus (Everglades 0.201, Tallahassee 0.220), a ratio of bill length to tarsus (0.492, 0.463), and a ratio of toe to tarsus (0.741, 0.693) were different at  $P = .005$ . The ratio of wing to tarsus in Minnesota nestlings (1.501) was higher than in Colorado nestlings (1.378),  $P = .005$ , as was the ratio of toe to tarsus (0.745, 0.693),  $P = .01$ . Numbers in parentheses above are the antilogs of the mean predicted log value at log tarsus = log 20.
15. The methods of analysis proposed (11) permit tests of the differences in shape. Shape variables are ratios or proportions. If the original data follow a lognormal distribution, their logs follow a normal distribution, and parametric statistics can be used. Tests of shape differences can be performed on ratios transformed to differences between logs. In measurements of study skins of adults from the Everglades (66 males, 70 females) and Tallahassee (18 males, 12 females), the most highly significant univariate shape differences ( $P < .01$ ) were higher ratios of bill depth to tarsus for Tallahassee females and lower ratios of bill length to tarsus and toe to tarsus for Tallahassee males ( $P < .001$ ). For adults from Minnesota (18 males, 5 females) and Colorado (13 males, 10 females) there were higher sample ratios for wing to tarsus in Minnesota, but the differences were not significant ( $P = .07$  for males and  $P = .13$  for females). Within localities adult females weigh only about 65 percent of the weight of males. Sexual size differences are also apparent in nestlings, but when nestling measurements were standardized to a tarsus of 20 mm, within-locality nestling shape did not differ between the sexes.
16. Clutches of three eggs each were transported intact during the last half of incubation. After eggs in foster nests were removed and replaced with equivalent-sized clutches of transplanted eggs, foster mothers accepted and incubated the new eggs.
17. Log-transformed variables at log tarsus = log 20 (14) for normal nestling populations were entered into two separate canonical discriminant function analyses, one for the Florida comparison and one for the Colorado-Minnesota comparison. This log shape procedure computed equations for axes (Fig. 1) that maximized differences between groups. These axes are better discriminants than are any of the shape variables taken singly. The most important correlations between the axis in Fig. 1A and the original shape variables are ratios of bill depth to tarsus (.45) and bill length to tarsus (-.24); for Fig. 1B, the ratio of wing length to tarsus was -.78, and that of toe to tarsus was -.64. The Colorado-Minnesota axis is plotted in increasingly negative units of discrimination.
18. Apparent differences in Fig. 1 between scores along the discriminant axes for normal groups and control groups are more a result of the fact that the CDF axes are determined by the normal groups than a result of experimental error. When the control groups were used to differentiate the populations, and normals were plotted on those axes, the normals were less well differentiated than the controls. The biological result of the experiment is expressed in the differences between the scores for control and transplant groups.
19. All changes reported in Table 1 are in the direction predicted by differences among adults except ratios of toe to tarsus in Tallahassee. Even differences that are not significant at the univariate level make significant contributions to the canonical discrimination.
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## Recognition of H-2 Types in Relation to the Blocking of Pregnancy in Mice

**Abstract.** *Inbred BALB/c females were mated and subsequently exposed in a divided cage to "stimulus" males or females whose H-2 type was similar or dissimilar to the stud male's. The incidence of pregnancy blocking was considerably higher when stud and stimulus males differed in H-2 type than when they did not. Similar results were obtained with urine samples of H-2 identical and nonidentical males. Females exposed after mating to other females whose H-2 type differed from the stud male, under the same experimental conditions, also showed an appreciable incidence of pregnancy block. It is therefore concluded that chemosensory recognition of H-2 types affects the reproductive hormonal status of the pregnant female.*

Genes of the major histocompatibility complex (MHC), best known for their importance in transplantation and the immunologic handling of chemical information, also participate in a variety of other biological features (1), including chemosensory recognition.

Mice have been found to show natural mating preferences according to their H-2 (MHC) haplotypes, generally with a bias in favor of matings between H-2 dissimilar rather than H-2 identical pairs (2). The inference that H-2 haplotypes determine individual odor phenotypes that mice can sense has been confirmed by use of a Y maze in which mice were trained to distinguish the scents of congenic mice (3), or their urine (4), that differed genetically only at the H-2 region of chromosome 17, or parts of this region.

In the mouse and other species, constituents of urine and glandular secretions, acting through neuroendocrine channels, have striking effects on such reproductive phenomena as the timing of reproductive maturity and the estrous cycle (5). Another instance of olfactory induction of a reproductive hormonal

response, and one in which recognition of individual identity appears to be involved, is "pregnancy block" (the Bruce effect). Pregnancy block refers to termination of pregnancy before implantation of the embryo (before day 6 of gestation in the mouse) after exposure of the female to an unfamiliar male, particularly of a strain different from the stud male; soiled bedding or urine of a strange male has the same effect (6). Administration of prolactin or progesterone can forestall blocking (7), which is therefore viewed as the result of a neuroendocrine imbalance inimical to implantation.

The female's recognition of a strain difference between the stud and unfamiliar males implies that pregnancy block is a means of genotype selection, at least under laboratory conditions (8, 9). The particular question addressed in the work reported here is whether sensory distinction of H-2 haplotypes by the female is an appreciable factor in the blocking of pregnancy.

These studies were conducted under uniform conditions of isolation to reduce interference from extraneous airborne odors (10). Virgin BALB/c females