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Environmental Component of Latitudinal Clutch-size Variation in House Sparrows (*Passer domesticus*)

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Many species of birds (Cody 1966) and mammals (Lord 1960, McNab 1980) show positive correlations of clutch or litter size with latitude. In birds, clutch-size gradients are also correlated with longitude (Lack 1968) and, in some species, altitude (Cody 1971). It is assumed that geographical clutch-size gradients are maintained by natural selection on additive genetic variance for clutch size. One mechanism may be increased predation acting to restrict clutch size at lower latitudes, but any factor that affects the fitness of different clutch sizes could be involved. It would represent a major advance if researchers could determine the proximate causes of clutch-size variation.

There have been at least six studies of clutch size heritability, all evaluating within-population variation (Perrins and Jones 1974, Flux and Flux 1981, van Noordwijk et al. 1981, Gustaffson 1986, Findlay and Cooke 1987, Gibbs 1988). Five of the six have shown a significant heritable component to clutch size, with h^2 ranging from 0.23 in Snow Geese (*Chen caerulescens*) to 0.5 in Great Tits (*Parus major*). Only one study, by Gibbs (1988) on *Geospiza fortis* (a Darwin's finch), found a heritability not significantly different from 0. In an artificial-selection study on a wild population of European Starlings (*Sturnis Vulgaris*), selection for clutches of five eggs or greater raised the F_1 clutch size by 0.12 eggs on average, which implied an h^2 of 0.33 (Flux and Flux 1981). Variation among populations, if it is due to genetic causes, most likely is the result of natural selection on intrapopulation heritable variation for the trait. However, as Boag and van Noordwijk (1987) pointed out, high heritability of traits within populations does not imply that among-population differences are due to genetic causes. James (1983) conducted a reciprocal-transplant experiment between two pairs of populations of Red-winged Blackbirds (*Agelaius phoeniceus*) and showed that a significant portion of the variance between populations in some morphological traits was explained by nongenetic factors.

Geographical trends for House Sparrows (*Passer domesticus*) in morphological and life-history traits have been extensively studied (Johnston and Selander 1971, 1973, Murphy 1978). Clutch size in House Sparrows varies with latitude in the New World, from over five eggs per clutch in Alberta, Canada (Murphy 1978), to

between 2.0 and 3.3 in Central America (Fleischer 1982, Thurber 1986). Clutch size in Costa Rica has been measured once (Fleischer 1982) and an average of 2.0 eggs per clutch was reported, but values for nests that may not have been complete were included. The average clutch size for House Sparrows in Ithaca, New York, has been reported as 4.7 eggs per clutch (Weaver 1943). The breeding season in Ithaca lasts from the end of March to the beginning of August (Weaver 1943, present study). In Costa Rica, breeding begins in January and continues through August (Reynolds and Stiles 1982).

House Sparrows were introduced at least 20 times in the United States using stock from England or Germany, and their spread was aided by more than 100 introductions from established populations in the United States (Barrows 1889). The sparrows have been present in the northeastern United States for 140 years, and in Costa Rica for at least 20 (Reynolds and Stiles 1982). Johnston and Selander (1971) have shown that intrapopulation variance in morphological traits for North American House Sparrows is indistinguishable from that of European populations, but that interpopulation variance is lower in North America than in Europe, possibly due to a founder effect. Morphological variation in House Sparrow populations in North America is well correlated with climatic gradients (Johnston and Selander 1971).

Given the known history of the House Sparrow in the New World, they are an especially interesting subject for the study of clutch-size evolution. The House Sparrow's relatively recent introduction in North America and its rapid differentiation suggests that variance in clutch size might be due to environmental factors. Even a low heritability, however, could easily account for a decrease of as much as 2.8 eggs per clutch in 140 years, if the variation was maintained in the face of natural selection. It is unlikely that a trait so closely tied to fitness as clutch size would not be under mostly genetic control. On the other hand, a trait subject to strong selection is more likely to be fixed genetically. I report the results of a study—using House Sparrows captured in Costa Rica and Ithaca, New York, and then bred in aviaries in Ithaca—designed to examine whether the latitudinal variation in clutch size is determined by genetic or environmental causes.

Methods.—I captured 51 Costa Rican House Sparrows using mist nets in a one-month period in July and August of 1989. These included 44 birds caught at three rice processors on the Pan American Highway

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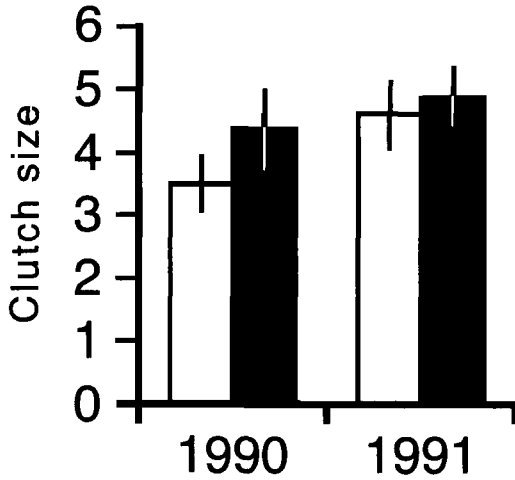


Fig. 1. Per-pair average clutch sizes (\pm SD) of House Sparrows from Costa Rica (white bars) and Ithaca (dark bars) in 1990 and 1991.

or in the northwestern towns of Santa Cruz, Canas, and Philadelphia (10° – 11° N latitude). The northwestern corner of the country is dominated by cattle ranches and rice plantations. The other seven sparrows were caught in the Central Plateau cities of San Jose and Cartago (10° latitude).

Birds were matched for sex and age (15 adult males, 14 adult females, and 21 juveniles) with Ithaca-area (42° N latitude) birds. Following one month's quarantine at the U.S. Department of Agriculture facility in Newburg, New York, the Costa Rican sparrows were placed in two aviaries next to the two aviaries already occupied by Ithaca sparrows. The aviaries measured 7 m long \times 3.3 m wide \times 5-7 m high. Each aviary had three solid walls and one hardware-cloth wall open to the outside, as well as a partially translucent roof. Each aviary had 10 nest boxes of 13 cm \times 13 cm \times 26 cm internal dimensions. The birds were fed a mixture of millet, canary seeds, and mealworms during the breeding season. Nests were checked daily in 1990, but less often in 1991 after clutches were completed in order to minimize disturbance and reduce nestling mortality. In 1991, clutch size in aviary and wild sparrows was compared during the second half of the breeding season. Active nests in the Ithaca area were identified starting in May. Aviary and wild-bird clutch sizes were compared from clutches laid after 10 June in order not to bias the wild-bird clutch size towards later, smaller clutches. No new wild nests found after 10 June were included. Twenty-nine completed clutches were recorded from 33 active wild-bird nests after 10 June. In 1991, all aviary eggs were measured using dial caliper to the nearest 0.1 mm. Volume was approximated by treating eggs as cylinders.

Results.—In 1990, 16 pairs of Ithaca birds and 14 pairs of Costa Rican birds laid 43 and 52 clutches, respectively. The first egg in each group was laid one day apart, with the first egg laid on 6 April. This is in agreement with the normal start of the breeding season for Ithaca (Weaver 1943) and is in contrast with the breeding season in Costa Rica, which starts in January and continues until August. The difference in number of clutches laid was due to the Ithaca birds' broods living slightly longer. The per pair clutch-size average was used for comparison in order to avoid biasing clutch-size averages to those birds that laid more clutches (Fig. 1). The Ithaca birds averaged $4.38 \pm$ SD of 0.64 eggs per clutch, and the Costa Rican birds averaged 3.50 ± 0.46 ($P < 0.001$).

In 1991, both the Ithaca and Costa Rica birds commenced laying two weeks earlier than the previous year, with the first egg laid on 23 March. The clutch-size results changed significantly from the previous year, even though the same individuals were involved. Of the Ithaca birds, 14 pairs laid 40 clutches, while 14 pairs of Costa Rica sparrows laid 36 clutches. The average clutch size of the Ithaca birds rose, possibly influenced by the fact that all the birds were adults, by some climatic factor in 1991, or by some acclimatization to aviary conditions. The clutch size of Costa Rica birds rose dramatically from the previous year (Fig. 1). The Ithaca birds averaged 4.89 of 0.48 eggs per clutch and the Costa Rican birds 4.62 ± 0.55 , again, using per-pair clutch size. The difference in clutch size between the two groups was not significant in 1991 ($P < 0.18$). Although survival of fledglings was too low in the first year to examine clutch size in Ithaca-born Costa Rican sparrows, three hand-reared Costa Rican females nested. One had the only two dump nests of the two years, with 'clutches' of 12 and 14 eggs, and then had an incomplete clutch of 2 eggs. The other two birds laid three clutches between them of five eggs each.

Clutch size in the surrounding area was investigated in 1991. Nests were identified starting in May, and 29 completed clutches were counted from 33 active nests after 10 June. During that period, the Ithaca aviary birds averaged 4.69 ± 0.14 eggs per clutch and the Ithaca wild birds 4.72 ± 0.14 . The similarity between their clutch sizes agrees with the results of Mitchell and Hayes (1973) in Hale County, Texas, where mean values for wild and aviary clutch sizes were only 0.1 eggs apart, at 4.3 and 4.4 eggs per clutch, respectively.

Egg size was examined within the aviary populations. The per-clutch egg size of Costa Rica and Ithaca aviary populations were nearly identical ($P > 0.92$), so I pooled clutches to look at potential relationships of clutch size and egg size (Fig. 2). A quadratic regression of egg size on clutch size significantly explained a small portion of the variance in egg size ($r^2 = 0.17$, $P < 0.02$). There does not appear to be a trade-off between egg size and clutch size in House Spar-

rows. Rather, it appears that, if a bird is in sufficient condition or of sufficient quality to lay a larger clutch of five or six eggs, it is in sufficient condition or of sufficient quality to lay larger eggs as well.

Discussion.—My results suggest that environmental factors determine most of the latitudinal variation in clutch size in House Sparrows. What are those factors, and how do they act? Food may have an effect, as supplemental feeding is known to affect clutch size in European Kestrels (*Falco tinnunculus*), mostly through laying date (Meijer et al. 1988). However, food must not have had a simple effect in this case, or there would have been a difference in clutch size between the aviary and wild birds. There are areas with a higher average clutch size than Ithaca (Murphy 1978, Summers-Smith 1988), but aviary birds with unlimited food did not have larger clutches than wild birds, so some factor other than or in addition to food was working in the aviaries. It is difficult to measure the quality of food in the aviaries. Although seeds were provided *ad libitum*, the quality and quantity of insect food was most likely suboptimal for feeding House Sparrow chicks.

One cannot claim from the results of the 1991 season that none of the latitudinal variation in clutch size between Ithaca and Costa Rican House Sparrows is due to genetic causes. The power of this experiment was very low. Using per-pair clutch size, the smallest difference in clutch size distinguishable is 0.4 eggs per clutch at a probability level of 0.05. In addition, there was still variation among pairs in clutch size, despite the similar environmental conditions. However, it is unlikely that the remaining difference of 0.27 eggs per clutch is due wholly to genetic causes. The birds used originated in Costa Rica, and their clutch size may have still been influenced by maternal effects, either directly on clutch size or indirectly on some other factor that may affect clutch size.

The results of my experiment do not support an ultimate cause of latitudinal clutch-size variation, such as predation, which must operate through natural selection on heritable characters. The only mechanism in this case that could account for an indirect determinant is a highly covariant environmental feature for which a range of clutch-size responses is selected. The clutch sizes in the aviaries probably do not represent programmed responses to some cue that triggers a "correct" clutch size for a given latitude. Obviously, latitude does not set deterministic rules governing clutch size. The pattern of larger clutch sizes at higher latitudes has many exceptions, some traceable to climatic factors like altitude or longitudinal climatic patterns, or environmental factors such as predation (Cody 1971).

House Sparrows have a larger clutch size in Israel than in Great Britain (Singer and Yom Tov 1988), and a larger clutch size in Turkestan than in other continental locations higher in latitude. This is in contrast to the onset of breeding, which does have a clear

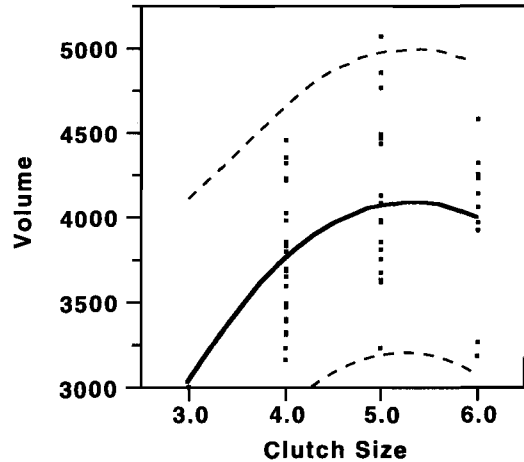


Fig. 2. Approximate egg volume in relation to clutch size for pooled sample of captive birds, fitted to quadratic regression ($r^2 = 0.17$, $P < 0.02$). Dashed lines indicate 95% confidence interval.

relationship with latitude ($r^2 = 0.88$; Summers-Smith 1988). The latitudinal variation in laying date was not evident after seven months in the aviaries, but the variation in clutch size adjusted more slowly, and may have continued to converge if the experiment had continued. This is further evidence that some physiological adjustment to the environment took place, rather than a response to an environmental signal. Any explanation of the environmental component of clutch-size variation must take reproductive physiology, and the often complex and contradictory relationships of thermoregulation, energetics, and production, into account.

In order to understand the determinants of clutch size in House Sparrows, work is needed to explore clutch size as a physiological response to environmental conditions and not simply a selective strategy triggered by external cues. While the response to the environment may be heritable and shaped by natural selection, study of that response—and not simply of the selective costs and benefits of specific clutch sizes—would be useful. One potentially fruitful course would be to evaluate the effects of temperature on the metabolic rates of wintering and breeding birds, and the effects that metabolic rate has on reproductive output. McNab (1980) observed that reproductive output in mammals increased between species with increased basal metabolic rate. He argued that mammals might not distribute a fixed amount of energy between growth and maintenance, but rather that metabolic rate determined by maintenance could affect the amount of investment in growth.

Further study is needed to see whether House Sparrows are exceptional. There is variation in the degree of clutch-size plasticity between species, as many genera and species have a single, invariant clutch size,

whereas others show differences within and among populations. Are House Sparrows more plastic than other species in clutch size, and has this contributed to their ability to expand their range? The results of my study suggest that it is a mistake to think of House Sparrows as being exceptional competitors through life-history characters, because some of these adjust phenotypically to what is typical for the area in which the birds are found, although the ability to adjust may allow them to compete where others could not.

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