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HERITABILITY OF BODY SIZE IN CROSS-FOSTERED TREE SWALLOW BROODS

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Studies of the heritability of body size have facilitated investigations of natural selection in natural populations of birds (review in Price and Boag [1987]). Many studies have documented a genetic basis to the resemblance in morphology between offspring and parents (summary in Boag and van Noordwijk [1987]). In addition, several recent experiments have shown permanent effects of the rearing environment on the size attained by Red-winged Blackbirds (*Agelaius phoenicius*) (James, 1983; James and NeSmith, 1988), Tree Swallows (*Tachycineta bicolor*) (Quinney et al., 1986), and Zebra Finches (*Poephila guttata*) (Boag, 1987). Thus, it is clear that both genetic and environmental effects may play significant roles in the determination of body size in nestling birds. However, environmental effects, such as variation in parental quality and maternal effects, may also influence the estimation of parent-offspring resemblance. One way to control for such effects is to cross-foster offspring among broods and to compare the size of offspring to both their true and foster parents (Smith and Dhondt, 1980; Dhondt, 1982; Atalato and Lundberg, 1986). I report here the results of a cross-fostering experiment in a population of Tree Swallows.

MATERIALS AND METHODS

Data were collected from late April until July in 1986 and in 1987 at the Creston Valley Wildlife Management Area in southeastern British Columbia (49°05'N, 116°35'W). Except for the repeatability estimates, the results reported here are from 1986. Swallows begin arriving in the Creston area in late March and begin laying eggs in early May. Nest boxes were erected in early March 1986 at approximately 20-m intervals around a large marsh. Nest contents were checked each morning between 8:00 A.M. and noon to determine laying dates and to number individual eggs.

To standardize the measurements of adult body mass, I captured females on the nest while they incubated eggs, 6-13 days following clutch completion. Males were captured while feeding young, 3-10 days after hatching began. Measurements taken on all birds included body mass (measured with electronic balance to the nearest 0.02 g), tarsus length (measured with dividers to the nearest 0.1 mm) from the tibiotarsal joint to the distalmost undivided scute, wing-chord length (adults) or length of ninth primary (nestlings) (both measured with a ruler to the nearest mm), and bill length from the nostril to the tip of the upper mandible (measured with dividers to the nearest 0.1 mm). Nestlings were measured at 16 days of age, about six days before fledging. At this age, body mass and tarsus, bill, and wing lengths have reached approximately 100%, 97%, 92%, and 65% of adult size, respectively.

Twenty-eight clutches were chosen opportunistically and were matched for size and laying date. Eggs from a "donor" nest, located off the study area, were placed in nests during the clutch transfers. Control clutches were removed from nests for five minutes and then replaced. Predation of females and young lowered the sample size of experimental clutches from 28 to 15 nests.

Sexual dimorphism can complicate the analysis of heritability since it may directly affect the estimate and the variation. Dimorphism was found in two traits, wing length and body mass. However, differences in body mass may simply be a seasonal effect, as females were weighed during incubation and males were weighed during feeding of nestlings. Differences in wing length cannot be corrected for as offspring cannot be sexed at day 16. Assortative mating can influence the heritability estimates, based upon regressions of offspring on one parent (Reeve, 1961). Consequently, I examined the data for four body size traits within 38 pairs of swallows for evidence of assortative mating. Parametric correlations were weak, ranging from 0.1 to 0.24, and none was significant at the $P = 0.05$ level.

Repeatabilities of adult measurements were estimated using analysis of variance (ANOVA; Lessells and Boag, 1987). Measurements from adults captured more than once in 1986 and from adults captured in both 1986 and 1987 were used in the analyses. Repeatabilities of all traits were significant and ranged from 0.28 for mass to 0.93 for wing length. I used
TABLE 1. Heritability estimates ($h^2$) from regression of offspring on midparents for body mass and tarsus length in control and cross-fostered Tree Swallow broods. Sample sizes ($N$) for body mass and tarsus length are also given.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Experimental families</th>
<th>Control families</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Foster midparent</td>
<td>True midparent</td>
</tr>
<tr>
<td></td>
<td>$N$</td>
<td>$h^2$</td>
</tr>
<tr>
<td>Body mass</td>
<td>11</td>
<td>0.01</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>15</td>
<td>0.16</td>
</tr>
</tbody>
</table>

* $P < 0.05$; ** $P < 0.01$.

ANOVA to assess phenotypic variation in mass, tarsus length, and bill length among foster, true, and control broods. ANOVA was not carried out on nestling wing lengths, as the measurement of wing length was different for adults (wing chord) and nestlings (ninth primary). Variation among broods is a prerequisite for calculation of the heritability of traits. Significant among-brood variation was found for mass and tarsus length but not for bill length. Heritability estimates ($h^2$) were obtained by regressing offspring values (brood mean) on female and male parents separately ($h^2 = \text{twice the slope}$) and on midparent values ($h^2 = \text{slope}$). Falconer’s (1981 pp. 167–168) technique was used to assign weights to families of different size.

RESULTS

There were no significant resemblances between parents and true or foster offspring in body mass (Tables 1, 2). Scatterplots of true and foster offspring tarsus lengths on midparent values are presented in Figure 1. Significant resemblances were found between true midparents and their offspring in both control and experimental treatments (Table 1); offspring did not resemble their foster parents. Regressions of offspring on single parents yielded significant effects on tarsus length due to true parents but not due to foster parents (Table 2). Although there was a weak resemblance in tarsus length between offspring and foster mothers (Table 2), maternal effects appeared to be minimal, as the mother–offspring heritability estimates were similar to those for fathers and offspring. In addition, the correlation between female tarsus length and egg size was low and nonsignificant ($r = 0.17$, $N = 57$, $P > 0.05$).

DISCUSSION

None of the heritability estimates for body mass was significantly different from zero. Most other estimates of the heritability of body mass have been comparatively high (Prince et al., 1970; Grant, 1981, 1983; Lessells, 1982; Moss and Watson, 1982; Boag, 1983; van Noordwijk, 1984; but see Smith and Zach [1979]). Several factors may have contributed to these low estimates. First, the repeatability of Tree Swallow body mass was relatively low. Second, variation within broods was high, as Tree Swallows often hatch asynchronously (Zach, 1982; pers. observ.). Finally, I measured the mass of 16-day-old young. Tree Swallow young often go through a period of mass recession late in the nestling period, and measurement at day 16 may not have provided a reliable estimate of adult body mass.

The results show that offspring tarsus length resembles that of true parents and not foster parents. Thus, much of the observed resemblance between parents and offspring in tarsus length is due to the effect of shared genes. Similar results have been found in several other experimental studies on wild populations of birds (Smith and Dhondt, 1980; Dhondt, 1982; Alatalo and Lundberg, 1986; Alatalo and Gustafsson, 1988). Although all of the body-size correlations between mates were positive, none was significant, and thus, assortative mating likely had a negligible effect on the her-
iability estimate. In addition, maternal effects did not play a role, as the mother–offspring estimates were either similar to or less than the father–offspring estimates. Although nearly half of the variation in tarsus length was attributable to unknown environmental factors, my results indicate that this population would be responsive to natural selection on tarsus length.

ACKNOWLEDGMENTS

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**APEMATISM EVOLVES BY INDIVIDUAL SELECTION: EVIDENCE FROM MARINE GASTROPODS WITH PELAGIC LARVAE**

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Kin selection has been widely accepted as an explanation for the evolution of aposematism because of the observed correlation between gregariousness and aposematism in insects (Fisher, 1930; Hamilton, 1964; Harvey et al., 1982). Some authors, however, have argued that selection on individuals is sufficient to explain how aposematism evolves (Huheey, 1961; Wiklund and Järvi, 1982; Engen et al., 1986). Sillén-Tullberg (1988) performed a phylogenetic analysis showing that the evolution of aposematism preceded the evolution of gregariousness in many lineages of butterflies and, thus, that the predominant mode of evolution of aposematism in lepidopterans is by individual selection, not kin selection.

Most of the literature on the relative importance of kin selection and individual selection in the evolution of aposematism has focused on terrestrial insects, particularly lepidopterans. However, several authors have stated that kin selection cannot explain the evolution of aposematism in marine organisms that, because of dispersal of their pelagic larvae, do not occur in family groups (Faulkner and Ghiselin, 1983; Gerhart, 1986 p. 261; Edmunds, 1987 p. 190).

I have reviewed the literature on marine gastropods, and have found seven species for which developmental type is known, and for which there is experimental evidence that they have warning coloration. These are listed in Table 1. The experimental evidence consists of feeding experiments with fish in which the gastropods are rejected or avoided as prey items. As most fish are visual predators, these experiments suggest that the gastropods have warning coloration. All seven species listed in Table 1 have pelagic larvae and so cannot have evolved warning coloration by kin selection. I discuss the evidence for *Cyphoma gibbosum* in detail, as it is the best-known species.

*Cyphoma gibbosum* is an ovulid prosobranch gastropod endoparasitic on gorgonians in shallow water in the tropical Western Atlantic. The animal has a bright white, orange, and black pattern on the mantle folds that cover the shell; this coloration makes the animal conspicuous on the monochromatic host gorgonians. *Cyphoma gibbosum* is diurnally active and spends more than 99% of its time on its host (Birkeland and Gregory, 1975 [see color photograph p. 58]) and so is almost always conspicuous. Gerhart (1986) showed experimentally that mantle tissue of *C. gibbosum* is distasteful to bluehead wrasses, *Thalassoma bifasciatum*, whereas foot tissue is palatable. Steudler et al. (1977) demonstrated that *C. gibbosum* harbors steroids and prostaglandins ingested from host gorgonians, which might account for its distastefulness. Unlike most gastropods, which immediately retract into their shells when handled, *Cyphoma gibbosum* keeps its mantle extended, thereby ensuring that predators encounter distasteful tissues (Gerhart, 1986). Three other species of *Cyphoma* (*C. signatum* Pilsbry and McGinty, *C. megintyi* Pilsbry, and *C. emarginatum* Sowerby) are known to have conspicuous coloration and habits, but nothing is known about their palatability to predators. Aposematic species often have adaptations such as toughness of integument or flexibility of body and ap-