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SIZE AND MORTALITY IN MALE YELLOW-HEADED BLACKBIRDS

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Non-monogamous species of icterids tend to be more sexually dimorphic in size than are monogamous species (Selander 1958), which implies that large size evolved in males because of sexual selection (Selander 1958, 1972, Orians 1961). Selander (1965) proposed that large size in male Great-tailed Grackles (Quiscalus mexicanus) is limited by increased risk of mortality, and thus selection for survival ability favoring small size opposes sexual selection favoring large size. Selander showed that male Great-tailed Grackles suffered higher winter mortality than females. Recently, Baker and Fox (1979) found that small male Common Grackles (Quiscalus quiscula) were more likely than large males to survive the stress of being sprayed with a wetting agent and water in a winter roost. Similarly, D. M. Johnson and co-workers (unpubl. data) found that large male Brown-headed Cowbirds (Molothrus ater) were more susceptible to winter mortality than small males. However, neither Johnson and his coworkers nor Searcy (1979) could find evidence that among Red-winged Blackbirds (Agelaius phoeniceus), large males were at a survival disadvantage relative to small males.

Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) are polygynous, with most male territory owners acquiring two to five mates (Willson 1966). As expected, the species is strongly dimorphic. In this paper, I examine whether there is selection against large size in male Yellow-headed Blackbirds due to lower survival of large, compared to small, males.

METHODS

This work was done at the Turnbull National Wildlife Refuge, near Spokane in eastern Washington (see Willson 1966 for description of habitat). Yellow-headed Blackbirds were captured in May and June of 1975 and April through July of 1976. All captures were made using funnel traps baited with grain. In both years the traps were placed in the same two locations, about 5 to 20 m from marshes where Yellow-headed Blackbirds were nesting.

I used length of the flattened wing, measured to the nearest 0.1 mm, as an index of size. Wing length is known to correlate closely with fat-free weight in some birds (Connell et al. 1960) and is generally considered a good measure of size (Hamilton 1961, James 1970). Wing length has the advantage, relative to weight, that it does not change greatly during a season. Using data from 1975, I calculated the regression of weight against day of measurement for 214 weighings of 87 adult male Yellow-headed Blackbirds and found that weight declined by 0.24 g per day (r = -0.440, P < 0.001). Wing length, however, did not decline during the same period (r = -0.058, P > 0.5).

RESULTS AND DISCUSSION

The average wing length for 90 males measured in 1975 was 144.6 \pm SD of 2.81 mm and for 28 females

was 115.9 ± 3.54 mm. This 24.8% longer wing length of males corresponded to an 81.6% difference in average weights (92.8 g for males versus 51.1 for females). Thus Yellow-headed Blackbirds are more size dimorphic than Brown-headed Cowbirds, Common Grackles, and Red-winged Blackbirds, but less dimorphic than Great-tailed Grackles (Selander 1958).

If large adult males experience greater mortality than small males, then the wing lengths of those males that survive from one spring to the next should average smaller than the wing lengths of the males that die during the same interval. Of the 90 adult males measured in 1975, 46 (51.1%) were recaptured in 1976 (Table 1). This rate of return closely approximates the annual survival rates found by Fankhauser (1971) for male Red-winged Blackbirds (51.1%) and Common Grackles (49.9%), giving some confidence that few males that survived escaped recapture. The average wing length of 46 returning adult males (144.6 mm) was identical to the average of 44 non-returning males (144.6 mm). Of 42 first-year males measured in 1975, only 8 (19.0%) were recaptured in 1976 so it seems likely that many which survived escaped recapture. However, the eight recaptured birds are probably an unbiased sample with respect to size of those that survived. The 8 returning and 34 non-returning first-year males had identical average wing lengths (136.0 mm). The evidence, then, is that large males do not suffer greater mortality than small males.

If survival selection does not have a directional effect on size, it may have a stabilizing effect. Fretwell (1977) found that Field Sparrows (Spizella pusilla) near the population average in wing length have higher survival than ones more extreme in wing length. I looked for stabilizing selection by dividing the adult male Yellow-headed Blackbirds measured in 1975 into groups of the 25% with the smallest wing lengths, the 25% with the largest wing lengths, and the remaining 50%. Comparing the middle group with the combined large and small group, I found exactly the same percentage of returning males in both groups (23 of 45; 51.1%). The variance in wing lengths of the returning males (7.37) was slightly smaller than the variance of the non-returning males (8.28), but the difference was not significant (F = 1.12, P > 0.5). Thus there is no evidence of stabilizing selection on size.

One complicating factor is that males increase in size

TABLE 1. Average wing lengths of male Yellowheaded Blackbirds returning or not returning after one winter.

| | N | Percent of age class | Average wing length (mm) | SD |
|------------------|----|----------------------------|-----------------------------------|------|
| Adults | | | | |
| returning | 46 | 51.1 | 144.6 | 2.74 |
| not returning | 44 | 48.9 | 144.6 | 2.91 |
| First-year males | | | | |
| returning | .8 | 19.0 | 136.0 | 2.42 |
| not returning | 34 | 81.0 | 136.0 | 2.50 |

somewhat from year to year, even as adults. First-year males, of course, grow between their first and second years; in 7 males measured both as first-year males in 1975 and as adults in 1976, the average increase was 7.0 mm, which was significantly greater than zero (t =22.15, P < 0.001). There was a high correlation between the measurements taken of individuals in their first year and again as adults (r = 0.929, P < 0.01) so the size of a first-year male is a good indicator of its future size as an adult. The 44 adult males measured both years increased an average of 1.0 mm between years, which is also significant (t = 4.48, P < 0.001). Thus, if survivorship increases with age among the adults for reasons unrelated to size, the increase in size with age among adults may prevent us from discerning a trend within age classes towards greater mortality in large birds. However, survivorship does not generally change with age among adult birds (Deevy 1947, Ricklefs 1974). The low rate of growth among adult males coupled with their high mortality rate means that only a small proportion of the variation in adult sizes could be agerelated. Furthermore, changes in survivorship with age could not explain the lack of size-related mortality in the first-year age class. Thus we can probably accept the result that selection as measured by annual survival rates exerts neither a strong stabilizing nor a strong directional effect on size.

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ADDITIONAL DATA ON BODY SIZE AS A DIFFERENCE RELATED TO NICHE

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Ecologists often assume that animals are able to coexist partly because of differences in body size (Wilson 1975). The role of body size in competition is unclear and two contradictory concepts exist in the literature: (1) differences in body size promote differences in niches (Brown and Wilson 1956, Hutchinson 1959, Schoener 1965, 1974); and (2) differences in body size form a competitive gradient such that the larger species can exclude the smaller species (Brooks and Dodson 1965, Galbraith 1967). Studies of the effects of body size on the outcome of aggressive interactions have concluded that the larger animal usually wins (e.g., Morse 1974, Kalinoski 1975, Verner 1975). Larger predators eat food unavailable to smaller competitors, but the reverse is often not true; asymmetry in resource use gives larger animals a competitive advantage (Wilson 1975).

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Most studies on resource use examine food as the limiting resource in the relationship between body size and competition. Yet animals compete for other resources, such as space for nesting. In this report, we present data on the relationship between body size and nesting space in several mixed-species colonies of herons, egrets and ibises to test the applicability of Wilson's (1975) concept to nesting space (i.e., that larger animals use a wider range of resources than smaller species).

METHODS AND RESULTS

We examined 13 colonies in the United States, Mexico, and Argentina from 1972 to 1975, containing 10 species of herons, egrets and ibises (Table 1). Colonies (75 to 2,562 nesting pairs) occurred in vegetation ranging from *Phragmites, Scirpus, Iva, Rhus,* and *Myrica* (with a maximum height of 150 cm), to *Baccharis, Tamarix,* and *Smilax* (150–300 cm in height), and to *Rhizophora, Avicennia, Languncularia* and *Prunus* (700–1,200 cm). Further descriptions of the colonies are in Burger (1978).

At each colony Burger gathered data during the first two weeks of egg-laying, including the range of vegetation heights and avian species composition. Recorded at each nest were the height of the vegetation and the height of the nest rim above the ground. We computed the mean nest height for each species and compared the standard deviations of nest height for each