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HONEST ADVERTISEMENT IN FLIGHT DISPLAYS OF BOBOLINKS (*DOLICHONYX ORYZIVORUS*)

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ABSTRACT.—We studied the flight display of the Bobolink (*Dolichonyx oryzivorus*) to determine if it functions as a signal of male quality. We tested the hypothesis that flight display is an honest signal of male quality limited by its energetic costs. Male Bobolinks' display durations positively correlated with condition, and with the number of young fledged. To increase variation in display durations, we handicapped some males by wing clipping. Mating success, male condition, and fledging success were used as possible measures of male quality to compare clipped with unclipped birds. Males with clipped wings had shorter display durations and acquired fewer mates. The evidence supports the hypothesis that the Bobolink's flight display could be used as a reliable signal of male quality. *Received 3 October 1991, accepted 31 March 1992.*

A SEXUALLY selected character can arise or be maintained through honest advertisement if it provides information about an individual's quality as a mate (i.e. mate choice) or as a competitor (i.e. intrasexual competition). Individuals should select mates or avoid competitors by the relative expression of the character (morphological or behavioral) that demonstrates an individual's ability to fight, survive, reproduce, provision young, or maintain superior breeding sites (Zahavi 1975, 1977, Kodric-Brown and Brown 1984). The honesty of a character is maintained if it is both costly and phenotypically plastic such that the optimal expression of the character depends upon an individual's phenotypic condition (Nur and Hasson 1984). Phenotypic condition in turn should reflect the quality of the male's genome (Andersson 1982, Schantz et al. 1989). Hence, assessing quality based on the expression of an honest signal could indicate an individual with heritably superior fitness.

To determine if the evolution or maintenance of a behavioral trait is through sexual selection via honest advertisement, it is critical to know whether a link exists between the intensity or duration of the advertising trait and individual differences in quality. Thus, a superior individual could be recognized by producing the "best" (longest or strongest) advertisement of his quality. We investigate the possibility that the flight display in Bobolinks (*Dolichonyx oryzivorus*) is an honest signal of male quality.

Bobolinks are polygynous, open-habitat birds that use flight displays and complex songs to establish territories and attract mates (Martin 1974, Wittenberger 1978). The display flight consists of a series of fast wing beats alternated with short glides at heights ranging from 2 to 40 m over the territory. Wing beats are more rapid than in nondisplaying flight. One display can last from a few seconds to about a minute (pers. observ., Martin 1967).

Song flight display may impose considerable energetic costs. Flying birds consume energy at a rate of approximately 10 to 15 times their resting rate (Pennycuick 1975, Holmes et al. 1979). During the courtship period, male Bobolinks spend about 10% of the day in flight displays alone (pers. observ.). Singing, without displaying, is also energetically expensive (Payne and Payne 1977, Greig-Smith 1982, Reid 1987). Because both flight and song impose additional energy costs, we assume that the flight display is costly to male Bobolinks. Therefore, it might function as an honest signal of male quality, such that males in better condition can be identified by longer flight displays.

We tested two main predictions of the hypothesis of honest advertisement as it pertains to flight displays in Bobolinks. First, there should be natural variation in the display duration among males. Thus, conspecifics of either sex potentially could detect differences in quality based on the relative duration of the advertising display. To increase variation in display duration and to determine whether displays are important in some aspect of the mating process (female choice or male–male competition), we conducted a wing-clipping experiment. Second, males that display for longer durations should be of better quality. The three measures

of a male's quality used were: (1) the number of mates attracted; (2) body condition; and (3) the number of successfully fledged young. Evidence supporting these predictions would suggest that the Bobolink's flight display is maintained by honest advertisement and, thus, can be used as a signal by conspecifics to predict a male's quality as a mate or a competitor.

METHODS

We conducted this study in four adjacent hayfields near Queen's University Biological Station in southeastern Ontario, Canada from 1 May until early July 1988. Each field is approximately 300 m by 250 m, bordered by hedgerows or trees. In 1988, the Bobolink population consisted of 19 adult males and about 17 females. We captured, measured, weighed, and color banded 15 males upon their arrival at the field. Natural markings and favorite perches identified the other four males.

To determine the amount of time male Bobolinks spent displaying (display duration), we recorded 0.5-h time budgets (dawn to 0900 EST) from 12 May to 6 June during the courtship period. A display was defined as the activity involving both singing and flying simultaneously. Time spent displaying was continuously recorded on a portable computer (Radio Shack, Model 100). To obtain the maximum number of time budgets on all birds, we watched each individual at least once every three days. Within a 0.5-h period, a male could display up to 162 times.

We experimentally increased the variation in display duration among male Bobolinks by conducting a wing-clipping experiment. We clipped 1 cm from the tip of primaries 8, 9, and 10 on every second male captured until we had a total of 6 with clipped wing tips to compare with the 13 other control males used in the study. From calculation of the costs of flight based on the mass and wing area of passerines (Castro and Myers 1988, Goldstein 1988), this increased the cost of flight by about 15% in Bobolinks. We used a general linear model (SAS Institute 1985) for this unbalanced design and made all comparisons between controls and experimentals by using a nested ANOVA. When comparing the display duration of males that eventually mated with those that did not, we either used: (1) only those time budgets from before any male in the population had a female that had started to lay (22 May); or (2) used time budgets from each male before he had a nesting female on territory. Thus, we made all comparisons while all males were at the same prenesting stage.

We measured male mating success by counting the total number of nests on a territory, assuming the number of nests represented the number of mates the male attracted. We searched the study site daily from 18 May until 8 July to locate all females on each territory. To find nests we watched each male for at least 45 min every other day. We noted when he fed nestlings or courted a female on the territory to ensure that we later located the nest. We recorded first-egg dates, number of nestlings, and fledging dates for the 17 nests.

As an independent measure of male quality, we calculated condition using a mass/wing chord ratio (Norris and Hight 1957, Connell et al. 1960). A high ratio indicates the bird is in good physical condition. Condition as estimated by fat reserves has been shown to be an indicator of male quality in other studies (Nolan and Ketterson 1983, Thompson and Flux 1988).

RESULTS

Unclipped males and display.—For each male, display durations between observation periods did not vary significantly (ANOVA, $P > 0.05$). Thus, each timed display was counted as an independent measure of display duration regardless of the observation period. There was significant variation in mean display duration among the controls when including time budgets from the whole season (Fig. 1). We also found significant variation when comparing display durations among males using observations from time budgets from before each male had any nests with eggs (unbalanced ANOVA, $F = 2.0$, $n = 440$ from eight males, $P = 0.05$). Because some males nested earlier than others, the resulting number of time budgets per male varied from one to eight. We used the data only if at least two time budgets were done before laying. To determine if differences in displays were due to the influence of neighbors within the same field, we compared average display durations in each of the four fields. There was no significant difference in display durations among males from different fields (nested ANOVA, $P > 0.05$).

Unclipped males and quality.—To determine if display duration and mate acquisition were related, we compared the mean display duration of males before they had a nesting female with the display duration of males that never mated. The difference was not significant (males who mated, $\bar{x} = 5.8$ s; did not mate, $\bar{x} = 6.3$ s; one-tailed nested ANOVA, $n = 371$ from six males that acquired mates and 76 from two that did not; $P > 0.05$). Likewise, there was no significant difference in display duration between males that obtained mates and those that did not when no males in the population had nesting females on their territory (mates acquired,

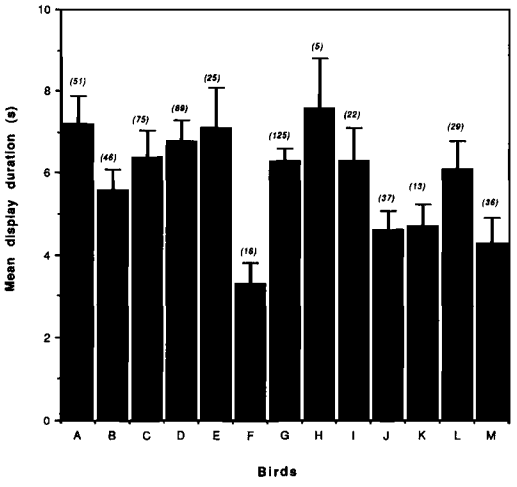

Fig. 1. Individual variation in display duration among unclipped males (unbalanced ANOVA, $F = 2.57$, $n = 278$ from 13 males, $P < 0.01$). Bracketed figures give numbers of flight displays timed for each bird and used to calculate mean display duration. Whiskers indicate standard errors.

$\bar{x} = 5.5$ s; no mates, $\bar{x} = 5.6$ s; one-tailed nested ANOVA, $n = 90$ from four mated males and 41 from two unmated males; $P > 0.05$).

The correlation between the number of mates acquired and condition shows a significant, positive relationship among the nine control males whose weights were recorded ($P < 0.05$; Fig. 2A). There also was a suggestion of a positive correlation between display duration and condition ($P = 0.08$; Fig. 2B). This correlation is not significant, although the trend is as expected from the honest-advertisement hypothesis. Among the five Bobolinks used in the previous correlation, there also was a positive correlation between the display duration and the number of young fledged ($P < 0.05$; Fig. 3).

Wing-clipping experiment.—The male Bobolinks with clipped wing tips appeared to fly much like unclipped males within the first few minutes of clipping. Throughout the courtship period they continued to display and some of them attracted mates. The mass/wing chord ratio of clipped versus unclipped males showed no significant preclipping differences between the two groups (t-test, $P = 0.91$, $n = 6$ and 9 for clipped and unclipped, respectively). Thus, we did not select different-quality males for the two treatments.

The display duration of clipped males was less than that of the unclipped (control) males

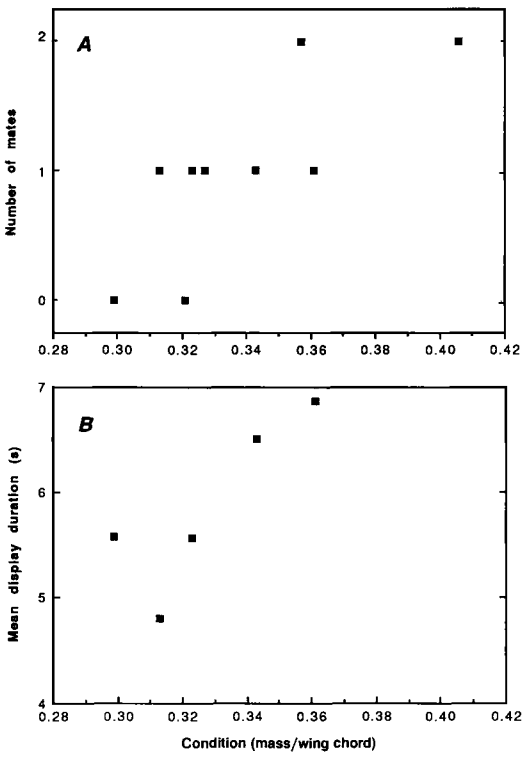

Fig. 2. Relationship of male condition (mass/wing chord) in controls to: (A) number of mates acquired; and (B) display duration (where measures of both condition and display duration were available). Males in better condition attracted more mates (Spearman rank correlation = 0.77, one-tailed, $P < 0.01$) and displayed longer (correlation = 0.71, one-tailed, $P = 0.08$).

(clipped, $\bar{x} = 3.5 \pm$ SD of 0.46 s; control, $\bar{x} = 5.8 \pm 0.34$ s; one-tailed nested ANOVA, $n = 355$ from 12 males [6 clipped and 6 unclipped] based on time budgets before 22 May; $P < 0.001$). The clipped males also acquired fewer mates (clipped, $\bar{x} = 0.67 \pm 0.49$ females, $n = 6$; control, $\bar{x} = 1.0 \pm 0.56$ females, $n = 13$; one-tailed t-test, $P < 0.05$).

Discussion

Male quality and display.—Clipped males had lower display durations and mating success compared with controls, suggesting that shorter displays adversely affect mating success. Among the controls, males that had longer displays also were in better condition and fledged more young. Thus, the existence of significant variation among individuals in display duration

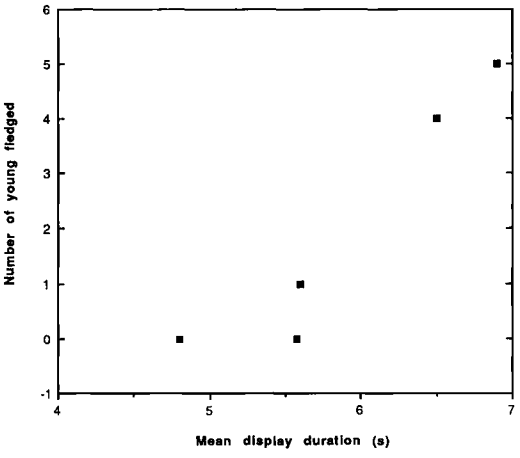

Fig. 3. Relationship between display duration and number of young fledged for control males (Spearman rank correlation = 0.98, one-tailed, $P < 0.01$).

could be used as a signal of male quality as a mate or a competitor. The apparent lack of difference in display duration between mated and unmated males was probably due to small sample sizes. Mating success has been shown to be positively correlated with display durations in other species (Halliday and Houston 1978, Clutton-Brock and Albon 1979, Gibson and Bradbury 1985, Hoglund and Lundberg 1987). Lambrechts and Dhondt (1987) and Lifjeld and Slagsvold (1988) noted that the intensity of the courtship display in Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*), respectively, may depend on the physical condition of the male. Evidence that vigorous displays correlate with greater male parental care has also been shown in Stonechats (*Saxicola torquata*; Greig-Smith 1982).

Flight display as an honest trait.—One measure of fitness is an individual's lifetime reproductive success. Obviously, animals on the breeding grounds cannot assess this directly. Instead, they rely on characteristics correlated with fitness (Searcy 1982). In our study, the existence of significant individual variation in display duration of the Bobolink shows that each male can be assessed based on his display behavior. The energy required for long display durations maintains the honesty of the signal as weaker males would not be capable of performing for such consistently long durations. Andersson (1982) and Jonsson (1987) showed that energetic factors limit the time spent displaying in the Long-tailed Widowbird (*Euplectes progne*) and Dunlin (*Calidris alpina*). The duration of display, thus, would reflect the overall condition of the male and his abilities to defend a territory, find food, care for young, etc.

Many studies have evaluated various aspects of courtship displays to see if there is variability among individuals and whether conspecifics use it as a cue to measure quality (Clutton-Brock and Albon 1979, Robertson 1986, Hoglund and Lundberg 1987). However, few studies have looked at the flight display as a signal of male condition in birds (Jonsson 1987). At least 15 species of North American passerines and most waders use song-flight displays in courtship (Bent 1958, 1968, Dabelsteen 1978). Because this behavior is so common in a wide variety of species nesting in open habitats, considerable selective pressures may exist for highly visible, energetically costly, courtship behavior. Further investigations into the adaptive significance of these displays may offer insights into the importance of the habitat in shaping the evolution of reliable signals.

In Bobolinks, the question of whether the display duration was used primarily in male-male competition or female choice was not directly addressed. However, because displaying begins well before females return to the breeding sites, and appears to be encouraged by the presence of other males, we suspect the display to be important in providing information about the status and strength of male competitors for good breeding territories. Studies involving more direct tests of whether energy limits courtship displays are also needed. More accurate energy reserve measurements and feeding experiments would determine if energy was truly the limiting factor in display duration.

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