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## SEXUAL SELECTION AND SURVIVAL IN NORTH AMERICAN WATERFOWL

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In a recent study, we showed that the sex bias (male/female) in mortality rates increased with plumage brightness in passerine birds, thus suggesting an important cost resulting from sexual selection for bright plumage (Promislow et al. 1992). However, mortality rate estimates for most passerine species have not been determined using modern methods and may therefore be unreliable (Lebreton et al. 1992). Mortality esti-

mates for waterfowl, on the other hand, are among the best available for any free-living animal population. Here, we focus on the costs of bright plumage coloration in waterfowl as an independent assessment of the costs of sexual selection, and we find the same general pattern as we described for passerines (Promislow et al. 1992). These results suggest that bright plumages may be generally costly to survival in birds.

Models of sexual selection usually assume that ornamental traits impose a survival cost on the bearer (e.g., Fisher 1930; Zahavi 1975). Despite this assumption, most studies of sexually selected traits have failed to find any such cost within species (Harvey and Bradbury 1990), possibly

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because of the difficulty in controlling for variation in individual quality (see Promislow et al. 1992). As an alternative, we have used the comparative method (Harvey and Pagel 1991) to study how ornamentation and survival vary across species, assuming that species' mortality rates represent individuals of average quality.

Although interspecific analyses of mortality and ornamentation could help us to identify the costs of sexual selection (e.g., Promislow et al. 1992), recent work suggests that many reported mortality rates based on mark-recapture studies may be unreliable (Lebreton et al. 1992). For example, most demographic studies of passerine birds are based on banded individuals and have not corrected for the effect of recapture probability on estimates of mortality rate. Because the probability of recapture can vary between sexes and years within species, as well as between species (Lebreton et al. 1992), mortality estimates from passerines may not be reliable. Thus, the results from previous work on sex-related differences in passerine mortality rates (Searcy and Yasukawa 1981; Dobson 1987; Promislow et al. 1992) must be interpreted with caution.

Recent models allow us to correct for potential biases in the estimates of mortality rates from marked individuals that were later recovered after they had died, or were recaptured when still alive (Brownie et al. 1985; Lebreton et al. 1992). With few exceptions, the best mortality estimates for birds come from studies of waterfowl that employ these new models for analysis. The mortality rate estimates for some waterfowl are particularly good because they are based on large samples of banded birds (up to  $2.3 \times 10^5$ ) taken over long periods (up to 39 yr) from many populations of each species. In addition, because of hunting, the recovery rate of banded birds is high compared with that of passerines. Thus, the waterfowl are potentially an ideal group in which to look at the relation between male plumage brightness and sex-biased mortality across species.

#### METHODS

Among waterfowl, only the ducks (subfamily Anatinae) are largely sexually dichromatic; thus, we restricted our analysis to that taxon. Among the ducks, reliable adult mortality rates have so far been calculated for both sexes of ten North American species, representing three genera (table 1).

Male and female plumage colors were scored

from paintings in field guides (Robbins et al. 1966; National Geographic Society 1983) by six different birdwatchers naive to both the mortality data and the purpose of our study. Overall plumage brightness (as defined by Endler 1980) was scored subjectively on a scale from 1 (dull) to 5 (bright), based on the hue and intensity of the color and the extent of coloration on the bird.

Though the mortality estimates for these waterfowl species are quite reliable, most North American ducks are also subject to considerable hunting pressure comprising a significant source of mortality. To evaluate the influence of hunting on mortality rates, we calculated the ratio of male to female recovery rates of ducks banded before the hunting season. This provides a reasonable estimate of sex-biased mortality as a result of hunting (J. Nichols pers. comm. 1992). For nine of the ten species in our sample, recovery rates were obtained from the same source as the mortality rates (see table 1). The average sex-biased recovery rate (i.e., ratio of male to female recovery rate) was  $1.063 \pm 0.24$  (mean  $\pm$  SD), with a range from 0.68 in the canvasback to 1.44 in the widgeon (table 1).

Closely related species often resemble one another because of shared ancestry. For this reason, species are not independent in a comparative analysis (Harvey and Pagel 1991). To control for this phylogenetic effect, we used a computer application written by A. Purvis (University of Oxford), based on Felsenstein's (1985) method and more recent enhancements (see Harvey and Pagel 1991) to calculate independent scores for each variable of interest. A number of recent papers have applied this or similar methods to a variety of biological questions (Blackburn et al. 1990; Harvey et al. 1991; Briskie and Montgomerie 1992; Martin 1993), with worked-through examples in Promislow (1991a) and Pagel (1992).

Statistics presented are from least-squares regressions of contrast scores calculated using Purvis's program. All regressions were forced through the origin (Harvey and Pagel 1991). Mortality rate and body-size data were both log-transformed to make distributions closer to normal (the untransformed data are listed in table 1). Since previous work has shown that mortality rates co-vary negatively with adult body mass in passerines (Sæther 1989), body mass was controlled statistically using partial regression. We controlled for female, rather than male, body mass (data from Johnsgard 1975) on the assumption that the body mass of females is not

TABLE 1. Male plumage brightness, hunting season recovery rates, and annual mortality rates for waterfowl species used in this study.

Species	Male brightness	Recovery rate		Mean annual mortality rate		Method†	Source
		Male	Female	Male	Female		
Wood duck <i>Aix sponsa</i>	4.33	5.14	4.02	0.46	0.51	2	Johnson et al. 1986
Pintail <i>Anas acuta</i>	1.83	4.84	3.99	0.28	0.4	3	Rienecker 1987
Widgeon <i>Anas americana</i>	2.67	4.68	3.24	0.36	0.39	1	Rienecker 1976
Green-winged teal <i>Anas crecca</i>	2.67	3.06	2.72	0.47	0.57	3	Chu et al. 1995
Blue-winged teal <i>Anas discors</i>	2.33	1.50*	2.08*	0.41	0.48	3	Schroeder in Johnson et al. 1991
Mallard <i>Anas platyrhynchos</i>	3.83	6.95	6.13	0.37	0.44	1	Anderson 1975
Black duck <i>Anas rubripes</i>	1.83	5.30	5.90	0.37	0.53	2	Krementsz et al. 1987
Gadwall <i>Anas strepera</i>	1.17	2.14	1.86	0.25	0.31	3	Szymczak and Rexstad 1991
Ring-necked duck <i>Aythya collaris</i>	2.5	6.10	6.20	0.3	0.53	2	Conroy and Eberhardt 1983
Canvasback <i>Aythya valisineria</i>	2.17	3.43	5.05	0.24	0.39	2	Nichols and Haramis 1980

\* J. Nichols (pers. comm. 1992).

† 1. Seber (1970); 2. Brownie et al. (1978); 3. Brownie et al. (1985).

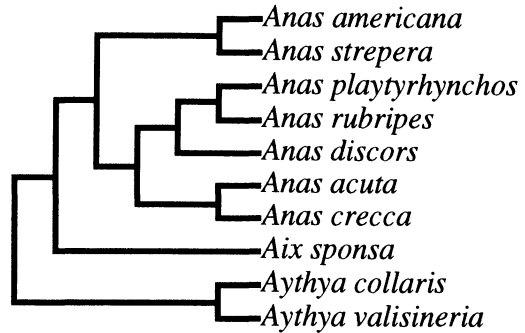


FIG. 1. Phylogeny of waterfowl species used in the analysis of mortality rates (after Livezey 1986, 1991).

directly influenced by sexual selection. The phylogeny for this study (fig. 1) was constructed from Livezey's (1986, 1991) cladistic studies based on morphological traits.

## RESULTS

Male brightness scores were positively correlated among all observers, with a mean Pearson correlation coefficient ( $r$ ) of  $0.61 \pm 0.05$  SE (range 0.21–0.93,  $n = 15$  pairwise comparisons). In all subsequent analyses, we used the arithmetic mean of brightness scores from the six observers.

Average male color score ranged from a low of 1.2 in the gadwall to a maximum of 4.3 in the wood duck (table 1). Female color scores were, on the average, much less bright, ranging from 1.0 in the gadwall and pintail to 2.0 in the widgeon. The average female color score was about 60% that of males.

Though males were brighter than females, male mortality was lower than female mortality in all species examined, ranging from a difference of 5% in the widgeon to almost 50% in the ring-necked duck (table 1). On the average, male mortality was about 20% lower than that of females. This female bias in mortality in the Anatinae is consistent with that found in blackbirds (Shutler and Weatherhead unpubl. data) and in passerines in general (Promislow et al. 1992), two other avian taxa in which males are generally more colorful than females.

Sex-biased mortality rates (i.e., the ratio of male to female mortality) were positively related to male plumage brightness scores across species (fig. 2, table 2). Thus, relative male mortality increased with plumage brightness, as in passerine birds (Promislow et al. 1992). The mortality of male ducks, unlike that of passerines, was positively related to male brightness, and there was

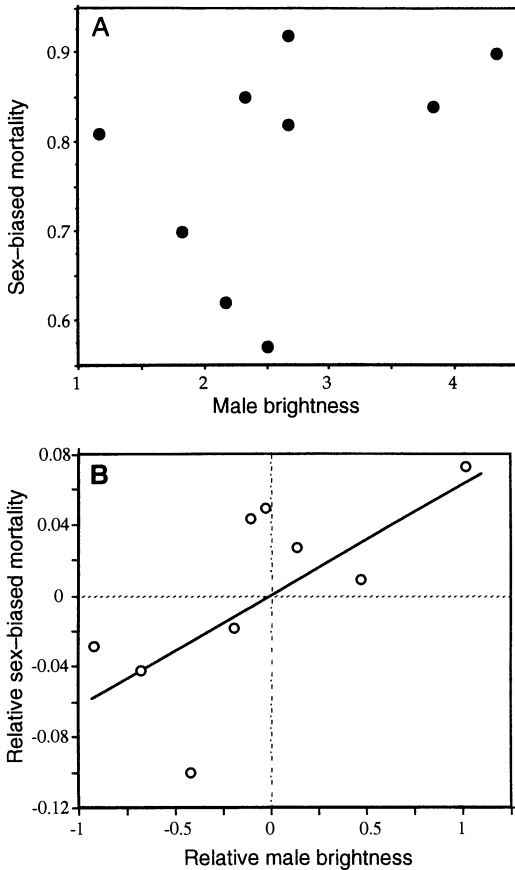


FIG. 2. Relation between sex-biased mortality (i.e., the ratio of male to female mortality rates) and male plumage brightness in waterfowl, shown as (a) raw data for each species (see table 1) and (b) contrast scores controlling the influence of phylogeny and female body mass.

no relation between female mortality and male brightness (table 2). Thus, sex-biased mortality is a consequence of male mortality increasing with male brightness, whereas female mortality remains relatively constant across species. In passerines, female mortality was negatively correlated with male brightness, whereas male mortality was not correlated with male brightness across species (Promislow et al. 1992).

The sex bias in recovery rates (during the hunting season) was not significantly correlated with the sex bias in mortality (partial slope  $b = 0.18 \pm 0.15$  SE,  $P = 0.25$ ,  $n = 7$  contrasts), after controlling for the effects of phylogeny and body mass. We conclude from this that hunting did not significantly influence our measure of sex-biased mortality, even though mortality rates

TABLE 2. Relation between mortality rates and male plumage brightness. Statistics here are from the analysis of contrast scores used to control for phylogeny (see text for details). In each analysis, the effect of female mass has been removed using partial regression.

	Partial slope	SE	<i>P</i>
Male mortality	0.044	0.014	0.016
Female mortality	0.017	0.023	0.487
Male/female mortality	0.063	0.025	0.040

caused by hunting can be as high as 40% or more of the fall population in some species (Patterson 1979). In addition, the sex bias in recovery rates was not significantly correlated with male plumage brightness ( $b = 0.12 \pm 0.06$  SE,  $P = 0.10$ ,  $n = 7$  contrasts).

#### DISCUSSION

Our analysis of waterfowl plumage color accords with the major findings of our previous study (Promislow et al. 1992) on the relation between plumage color and mortality in the passerine birds: sex-biased mortality increases with male plumage brightness. Thus, we conclude from both of these studies that sexually selected plumage brightness exacts a mortality cost on male birds.

Though hunting is an important source of mortality in these species, our analyses of hunting recovery rates suggest that it is unlikely that hunting could explain the patterns we found. First, there was no correlation between sex-biased mortality and sex-biased recovery rates. Second, we failed to find a significant correlation between sex-biased (male : female) recovery rates and male brightness, further suggesting that the influence of hunting mortality on our results is slight.

In our previous study of passerine birds (Promislow et al. 1992), we suggested that our results be interpreted with caution because of two related problems with the available mortality estimates. First, mortality rates for passerines were all calculated from banding returns and were therefore subject to a variety of potential errors (Lebreton et al. 1992). Second, the apparent female bias in passerine mortality could simply be an artifact of male-biased philopatry (Greenwood 1980). The waterfowl data have neither of these problems—the mortality rates have been estimated from models that take into account the errors inherent in using return and recovery data and, in waterfowl, females are the philo-

patric sex (Greenwood 1980). The similarity of patterns found in both ducks and passerines suggests to us that the passerine mortality data are reasonably accurate, at least for the analysis of sex-biased mortality.

Though sex-biased mortality was positively correlated with male plumage brightness in both passerines and ducks, the relations between male brightness and both male and female mortality differed between these taxa. In particular, the relation between male mortality and male brightness was positive in ducks (table 2), whereas there was no significant relation in passerines. In passerines, female mortality was negatively correlated with male brightness but there was no such correlation in the ducks (table 2). Such differences among taxa underline the value of using sex-biased, rather than sex-specific, mortality rates for interspecific analyses of the relative costs of traits influenced by sexual selection.

Past comparative studies of the costs of sexual dimorphism and ornamental traits have relied on sex ratios as an index of relative mortality rates (Wiley 1974; Clutton-Brock et al. 1977; Alexander et al. 1979; Clutton-Brock et al. 1985). These studies have found that the degree of female bias in adult sex ratios increases with increasing sexual size dimorphism. On the basis of these results, it has been argued that sexual selection for increased male size has resulted in increased male mortality. Female-biased sex ratios, however, provide only an indirect indication of sex-biased mortality patterns (Promislow et al. 1992). For example, female-biased adult sex ratios may be due to male-biased mortality among juveniles (Clutton-Brock et al. 1985) rather than among adults.

As reliable mortality data for more species become available, we can begin to ask direct questions about the relationship between mortality patterns and a variety of biological phenomena. For example, comparative studies have recently used mortality data to further our understanding of life-history strategies, brain size, flight, and senescence (Pagel and Harvey 1989; Sæther 1989; Pomeroy 1990; Promislow and Harvey 1990; Promislow 1991b). Because past estimates of mortality may be unreliable (Lebreton et al. 1992), the results from these analyses must also be interpreted with caution.

Most studies of sexually selected traits have focused on their benefits, rather than their costs (Harvey and Bradbury 1990). These analyses have furthered our understanding of the variation in

traits within species but interspecific variation has been more difficult to explain. The results presented here and in our previous work (Promislow 1992; Promislow et al. 1992) suggest that the analysis of mortality costs of sexually selected traits may be a valuable way to understand variation among species in the expression of these traits.

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