SEXUAL SIZE DIMORPHISM AND SURVIVAL OF MALE AND FEMALE BLACKBIRDS (ICTERIDAE)

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ABSTRACT.—In a between-species comparison of icterids, male survival decreases relative to female survival as the degree of sexual size dimorphism increases. This result is consistent with the hypothesis that male size is limited by survival selection in icterids; the degree of size dimorphism is known to correlate with the degree of polygyny in icterids, however, so the decreased relative survival of males in dimorphic species may be caused by some correlate of polygyny other than large size.

Survival estimates based on records of recovery of dead birds show positive correlations between male size and male survival and between female size and female survival, but survival estimates based on recaptures of live birds fail to show such relationships. *Received 30 September 1980, accepted 21 February 1981.*

DARWIN (1871) noted that "amongst birds there often exists a close relation between polygamy and the development of strongly-marked sexual differences." Sexual size dimorphism is one of the most noticeable and easily quantifiable of such sexual differences. Since Darwin's time, a correlation between polygyny and the degree of size dimorphism has been shown in many groups of birds (Selander 1972). This correlation has been particularly well demonstrated for the blackbird species of the new world family Icteridae (Selander 1958, 1972; Orians 1961). The correlation between polygyny and size dimorphism implies that size dimorphism evolved largely in response to sexual selection, because variability in mating success is greater, and thus sexual selection is stronger, in polygynous species than in monogamous ones.

If males have evolved larger size than females in response to sexual selection, then it is reasonable to ask what stabilizing forces prevent further increases in size. A logical hypothesis is that increased size dimorphism entails a cost of decreased male survival (Selander 1965). Thus, size would stabilize at an optimum where the cost of decreased survival matches the benefit of increased mating success. One method of testing this hypothesis is to compare the survival of large and small males in dimorphic species. This test has been applied to several species of icterids, with mixed results. Lower survival of large males has been shown in Brown-headed Cowbirds (*Molothrus ater*) (Johnson et al. 1980) and Common Grackles (*Quiscalus quiscula*) (Baker and Fox 1979). On the other hand, studies of Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) have failed to demonstrate lower survival of large males (Searcy 1979a, 1979b; Johnson et al. 1980).

A second method of testing the hypothesis that increased size dimorphism lowers male survival is to compare male and female survival in dimorphic species. In the highly dimorphic Great-tailed Grackle (*Quiscalus mexicanus*), males have been shown to experience lower survival than females during the winter (Selander 1965). A more complete test can be made by comparing male and female survival in a number of species with varying degrees of size dimorphism. The stabilizing selection hypothesis predicts that the ratio of male size to female size should be negatively correlated

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with the ratio of male survival to female survival. An analysis of size dimorphism and survival in several species of grouse supports this prediction. The ratio of numbers of adult males to numbers of adult females declines as the ratio of male weight to female weight increases among grouse species (Wittenberger 1978). In the present paper, we provide a further test of this prediction by comparing male and female survival and degree of size dimorphism in a number of species of icterids.

Although we predict that increased size dimorphism entails a cost of decreased male survival, there is some apparently conflicting evidence. Interspecific comparisons within many taxonomic groups have shown that survival rate increases as body size increases. For example, maximum lifespans increase with body weight in interspecific comparisons of passerines, nonpasserines (S. Linstedt, cited in Calder 1974), and mammals (Gunther and Guerra 1955). If this relationship were to hold within species as well as between species, then one would expect that male survival would increase relative to female survival as males become larger relative to females. The relationship between size and survival need not be the same within and between species, however. We propose instead that there is an optimum size in terms of survival for each species and that, as this optimum increases between species, survival increases. Within a species, survival of individuals decreases as their size either increases or decreases relative to the optimum. Thus, the more sexual selection has pushed male size above the optimum, the lower should male survival be relative to female survival. At the same time, in between-species comparisons, male survival should increase with male size and female survival should increase with female size.

MATERIALS AND METHODS

Survival rates were calculated from banding return data obtained from the Bird Banding Laboratory of the United States Fish and Wildlife Service. Return records were of two general types: (1) recaptures—records of recaptures of previously banded birds caught alive, and (2) recoveries—records of recoveries of previously banded birds found dead. Recapture and recovery data were analyzed separately using a method similar to that of Fankhauser (1967, 1971).

We obtained recapture and recovery data for all icterids banded after the postjuvenal molt. We limited analysis to returns of birds banded before 1975. Because return records were complete through August 1978, a bird had a minimum of $3\frac{2}{3}$ yr in which to be recaptured or recovered. In the analysis of recapture data, we used only records of birds recaptured at least 6 months after banding, because it appeared that, for all species, few banders bothered to report recaptures of birds banded in the same season. In the analysis of the recovery data, we included birds recovered within 6 months of banding. For both types of data, we calculated a survival rate for a given sex of a given species whenever we had at least 15 return records for that species-sex class.

Recapture records gave an estimate of the relative proportions of the banded populations still alive in each time period after banding. For recovery data, we requested only records of birds killed by human agency, so these records gave an estimate of the relative proportion of the banded populations that would have continued to survive except for human interference. We obtained recovery records for all icterids that had been shot (constituting the great majority of recoveries), trapped, poisoned, collected as specimens, killed in control or banding operations, killed by striking wires or towers, or killed by being struck by motor vehicles, trains, or airplanes.

Recapture data were assembled for analysis in the form of the number recaptured between 0.5 and 1.5 yr after banding, 1.5 and 2.5 yr after banding, etc. Recovery data were assembled in the form of the number recovered 0–1 yr after banding, 1–2 yr after banding, etc. For both types of data, annual survival rates for each species-sex class were calculated using the formula:

$$\% \text{ survival} = 100\left(\sum_{i=2}^{x} N_i \Big/ \sum_{i=1}^{x} N_i\right)$$

where N_i is the number encountered in the ith year and x is the last year a bird of a given species-sex class was encountered.

It is important to note that these survival estimates are not influenced by possible differences between males and females of the same species in the probability of recapture or recovery. It is undoubtedly true that, for most species, the chance that a given female will be encountered by a given sampling method is different from the chance that a given male will be encountered. For this reason, sex-ratio data are rarely trustworthy. Because our survival estimates are calculated using only within-sex data, however, and the bias due to differential encounterability appears in both the numerator and denominator of each survival rate estimate (and thus always cancels out), the differential vulnerability of the sexes to sampling has no effect on the survival estimates.

We calculated survival rates separately for Bullock's Oriole (*Icterus galbula bullockii*) and Baltimore Oriole (*Icterus galbula galbula*), which have recently been lumped as subspecies of the Northern Oriole. We felt justified in this separation because the subspecies are separate populations having different sizes and survival rates.

We used wing length as our measure of size because it correlates well with fat-free weight within species of birds (Connell et al. 1960) but is much less seasonally variable than live weight (e.g. Searcy 1979b). Average wing lengths used in interspecific comparisons were obtained from Ridgway (1902). In cases where Ridgway gives measurements for more than one subspecies, we used measurements of the nominate subspecies.

Ridgway also provides two other measurements that have been used previously as indices of size in birds: tarsus length and total length. For the 10 species of icterids considered in this paper (20 species-sex classes), there are very strong correlations between these two alternative measures and wing length (for tarsus length vs. wing length $r = 0.969$, $P < 0.01$; for total length vs. wing length $r = 0.951$, $P < 0.01$). These three measurements also give strongly correlated estimates of the degree of dimorphism, defined as the ratio of male size to female size (for dimorphism in tarsus length vs. dimorphism in wing length $r_s = 0.982$, $P < 0.01$; for dimorphism in total length vs. dimorphism in wing length $r_s = 0.966$, $P < 0.01$; r_s is the Spearman rank correlation coefficient). Thus, it matters little which size measurement is used.

As a check on whether geographic variation in male and female size affects the ratio of male size to female size, we also analyzed wing length data from widely distributed populations of Red-winged Blackbirds. Data were obtained from Power (1970), Searcy (unpublished), and Yasukawa (unpublished).

In the following sections, we use the term "relative male survival" to refer to the ratio of male survival to female survival. The term "relative male size" refers to the ratio of male wing length to female wing length.

RESULTS

Survival rates based on recapture data are given in Table 1. We were able to calculate survival rates for males and females in six species and for only males in an additional three species. Table 2 shows survival rates based on recovery data. We were able to calculate survival rates for both males and females in four species and for only males in an additional three species. Survival-rate estimates were obtained from both recaptures and recoveries for several species-sex classes, but the two sets of data gave quite different estimates of survival. Estimates from recapture data were consistently lower than those from recovery data. Estimates of relative male survival of Brown-headed Cowbirds, Red-winged Blackbirds, and Common Grackles were similar, however, despite these differences (cf. Tables 1 and 2).

In several of the species analyzed, yearling males are readily distinguishable from adults by plumage. Returns from such birds have been included in Tables 1 and 2. Only in the Red-winged Blackbird did yearling males contribute a substantial portion of the returns: 20.8% of recaptured males and 22.8% of recovered males were first banded as yearlings. Inclusion of the yearling data does not have a substantial effect on survival-rate estimates. Using only the returns of male redwings banded as adults, the recapture data gave a survival-rate estimate of 43.4% (645/1,485) versus an estimate of 42.2% (792/1,876) using both yearlings and adults, a difference of 1.2%. The recovery data gave a survival estimate of 53.0% (287/541) using only

TABLE 1. Survival estimates based on recapture data. N_i is the number encountered in ith year, and x is last year in which a bird was encountered.

Species	Sex	$\sum_{i=2}^{x} N_i \Big/ \sum_{i=1}^{x} N_i$	Percentage survival	Male survival/ female survival
Brown-headed Cowbird	Males	903/2,421	37.3	1.19
(*Molothrus ater*)	Females	375/1,195	31.4	
Red-winged Blackbird	Males	792/1,876	42.2	1.05
(*Agelaius phoeniceus*)	Females	251/623	40.3	
Baltimore Oriole	Males	67/170	39.4	0.84
(*Icterus galbula galbula*)	Females	41/87	47.1	
Bullock's Oriole	Males	28/57	49.1	1.09
(*Icterus galbula bullockii*)	Females	22/49	44.9	
Brewer's Blackbird	Males	22/58	37.9	1.27
(*Euphagus cyanocephalus*)	Females	20/67	29.9	
Common Grackle	Males	855/1,720	49.7	1.04
(*Quiscalus quiscula*)	Females	731/1,522	48.0	
Orchard Oriole	Males	12/23	52.2	—
(*Icterus spurius*)				
Yellow-headed Blackbird	Males	30/48	62.5	—
(*Xanthocephalus xanthocephalus*)				
Tricolored Blackbird	Males	1/27	3.7	—
(*Agelaius tricolor*)				

males banded as adults versus 54.1% (379/701) using both yearlings and adults, a difference of 1.1%.

Male and female wing lengths and the relative male size estimates obtained from Ridgway (1902) are given in Table 3. Geographic variation in size had little effect on estimates of relative male size. Table 4 shows that the ratio of male size to female size changed little despite interpopulational differences in wing lengths of male and

TABLE 2. Survival etimates based on recovery data. N_1 is the number encountered in ith year, and x is last year in which a bird was encountered.

Species	Sex	$\sum_{i=2}^{x} N_i \Big/ \sum_{i=1}^{x} N_i$	Percentage survival	Male survival/ female survival
Brown-headed Cowbird	Male	482/1,038	46.4	1.10
(*Molothrus ater*)	Female	113/269	42.0	
Red-winged Blackbird	Male	379/701	54.1	1.00
(*Agelaius phoeniceus*)	Female	74/137	54.0	
Common Grackle	Male	1,105/1,980	55.8	0.98
(*Quiscalus quiscula*)	Female	692/1,220	56.7	
Great-tailed Grackle	Male	9/15	60.0	0.80
(*Quiscalus mexicanus*)	Female	12/16	75.0	
Yellow-headed Blackbird	Male	61/105	58.1	—
(*Xanthocephalus xanthocephalus*)				
Baltimore Oriole	Male	14/27	51.9	—
(*Icterus galbula galbula*)				
Brewer's Blackbird	Male	19/35	54.3	—
(*Euphagus cyanocephalus*)				

TABLE 3. Wing lengths of icterid species; wing length taken from Ridgway (1902); sample sizes in parentheses.

Species	Male wing length	Female wing length	Male wing length/ female wing length
Brown-headed Cowbird (BHC)	110.5 (14)	101.1 (15)	1.09
Red-winged Blackbird (RWB)	120.9 (14)	98.3 (10)	1.23
Baltimore Oriole (BAO)	97.0 (12)	88.9 (8)	1.09
Bullock's Oriole (BUO)	99.8 (12)	93.7 (12)	1.07
Brewer's Blackbird (BRB)	128.5 (8)	117.6 (9)	1.09
Common Grackle (COG)	143.8 (10)	127.8 (10)	1.13
Orchard Oriole (ORO)	78.2 (30)	73.2 (9)	1.07
Yellow-headed Blackbird (YHB)	141.2 (11)	113.8 (7)	1.24
Tricolored Blackbird (TCB)	121.2 (9)	106.7 (10)	1.14
Great-tailed Grackle (GTG)	182.4 (8)	142.7 (9)	1.28

female Red-winged Blackbirds. Further, the estimates of relative male size shown in Table 4 were quite similar to the estimate for Red-winged Blackbirds calculated from Ridgway (Table 3).

Wing length and survival data support the predicted positive correlation between size and survival of male and female icterids. Using estimates of survival calculated from recovery data, we found a statistically significant positive correlation between body size and survival of male icterids ($r_s = 0.929$, $n = 7$, $P < 0.01$; see Fig. 1a). Using estimates from recapture data, we found the correlation between male size and survival to be near zero and not significant ($r_s = 0.067$, $n = 9$, $P > 0.10$; see Fig. 1b). Similarly, we found a strong, positive correlation between female size and survival using recovery data, though this correlation is not significant ($r_s = 0.800$, $n = 4$, $P > 0.10$; see Fig. 2a). The correlation found between female size and survival when we used recapture data was near zero and not significant ($r_s = -0.143$, $n = 6$, $P > 0.10$; see Fig. 2b).

Wing length and survival data also support the predicted negative correlation between relative male size and relative male survival. Using recovery data, we found a strong negative correlation between the ratio of male to female size and the ratio of male to female survival, but again this correlation is not significant ($r_s = -0.800$, $n = 4$, $P > 0.10$; see Fig. 3). Using recapture data, we found the corre-

TABLE 4. Relative male sizes in various populations of Red-winged Blackbirds. Sample sizes are in parentheses.

| Male wing length (mm)	Female wing length (mm)	Male wing length/ female wing length	Locality	Source
126.6 (7)	103.4 (8)	1.22	Alberta	Power (1970)
125.7 (38)	103.3 (8)	1.22	Alberta	Power (1970)
125.7 (24)	103.3 (8)	1.22	Saskatchewan	Power (1970)
124.6 (15)	101.5 (10)	1.23	Nebraska	Power (1970)
123.1 (40)	101.2 (5)	1.22	Wisconsin	Power (1970)
121.9 (29)	99.4 (25)	1.23	Kansas	Power (1970)
129.4 (16)	106.1 (17)	1.22	Colorado	Power (1970)
130.0 (46)	108.0 (9)	1.20	Washington	Searcy (unpublished)
125.9 (37)	102.1 (34)	1.23	Indiana	Yasukawa (unpublished)
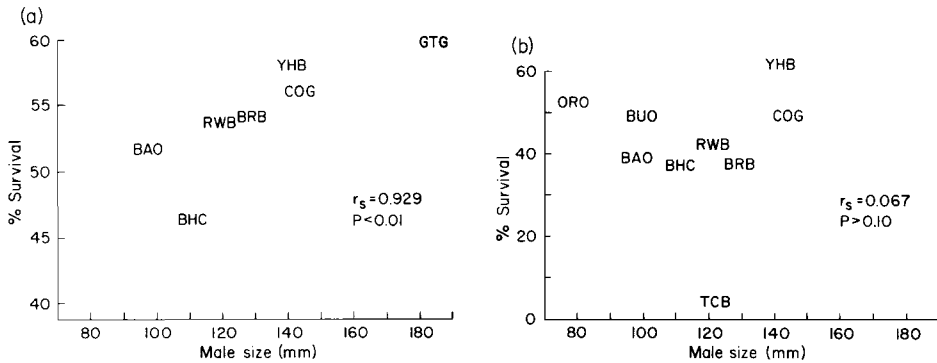
Fig. 1. Percentage survival versus size (wing length) for male icterids. (a) survival estimates from recovery data, $r_s = 0.929$, $n = 7$, $P < 0.01$; (b) survival estimates from recapture data, $r_s = 0.067$, $n = 9$, $P > 0.10$. Species codes are given in Table 3. Note that survival is scaled differently in (a) and (b).

lation between relative male size and survival to be again negative, but far from significant ($r_s = -0.334$, $n = 6$, $P > 0.10$; see Fig. 3). Because the survival rates from recovery and recapture data were based on separate data sets and were thus independent estimates, we tested for the predicted negative correlation between relative male size and relative male survival using all 10 estimates of the ratio of male survival to female survival (Tables 1 and 2). Using both data sets, we found a statistically significant correlation between relative male size and relative male survival ($r_s = -0.592$, $n = 10$, $P < 0.05$; see Fig. 3).

DISCUSSION

Recapture and recovery data gave quite different estimates of male and female survival. The tendency for recapture data to give lower estimates of survival than recovery data has been noted by others (Fankhauser 1969, 1971; Franks 1975) and
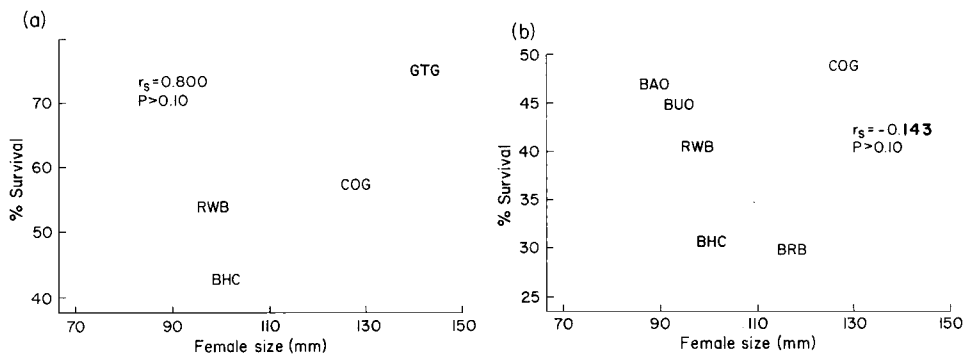

Fig. 2. Percentage survival versus size (wing lengths) for female icterids. (a) survival estimates from recovery data, $r_s = 0.800$, $n = 4$, $P > 0.10$; (b) survival estimates from recapture data, $r_s = -0.143$, $n = 6$, $P > 0.10$. Species codes as in Fig. 1. Note that survival is scaled differently in (a) and (b).
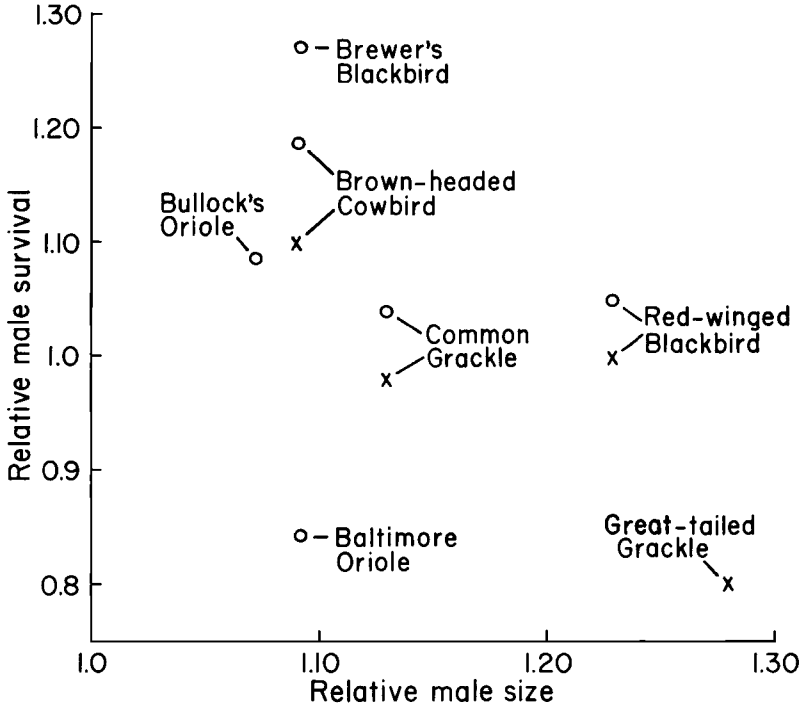
Fig. 3. Relative male survival (male survival/female survival) versus relative male size (male size/female size) in icterids. For recapture data (o's): $r_s = -0.334$, $n = 6$, $P > 0.10$. For recovery data (x's): $r_s = -0.800$, $n = 4$, $P > 0.10$. For combined: $r_s = -0.592$, $n = 10$, $P < 0.05$.

is usually attributed to the fact that a large proportion of recaptures are made by the same banders who originally marked the birds. Because banding operations are of finite duration, recaptures of long-lived birds are underrepresented. By contrast, a smaller proportion of recoveries are made by the original banders, so the finite duration of banding operations has less effect on survival estimates based on recoveries.

Use of recovery data resulted in strong, positive correlations between size and survival in both sexes, while recapture data gave weak correlations. We have seen that survival estimates based on recapture data probably underestimate actual survival. If the degree of underestimation varies from species to species, then any relationship between size and survival would be obscured. The degree of underestimation probably does vary from species to species because of species differences in the degree of site fidelity. Because a large proportion of recaptures are made by the original banders in the original localities, survival would be more strongly underestimated in species in which individuals are less faithful in returning to the same wintering and breeding localities. The lowest survival estimate obtained in this study was the estimate (3.7%/yr) based on recapture data for male Tricolored Blackbirds (*Agelaius tricolor*). Tricolored Blackbirds are a nomadic, colonial species in which the site of breeding colonies changes from year to year (Orians 1961). Thus, site fidelity is exceptionally low, and it is not surprising that recapture data give such a low survival estimate. Again, because a smaller proportion of recoveries are made

by the original banders, survival estimates based on recovery estimates would be less influenced by such species differences in site fidelity.

If we tentatively accept recovery data as being more reliable, then we may conclude that survival tends to increase with size in males, and probably in females as well. There was a statistically significant, positive relationship between male size and the recovery estimates of male survival and a positive, though not significant, correlation between female size and the recovery estimates of female survival.

We have argued that recapture data underestimate survival because of the finite duration of banding operations and that the degree of this bias probably varies from species to species because of variation in site fidelity. These biases should have much less effect on the ratios of male to female survival than on the separate survival estimates for males and females. The short duration of banding operations means that recaptures of long-lived birds will be underrepresented, but this underrepresentation should be the same for males as for females within a species. Similarly, differences in site fidelity may be smaller between males and females within a species than between two species; for example, the difference in site fidelity between adult male and adult female redwings is probably considerably less than the difference in site fidelity between male redwings and male tricolors. Thus, the estimate of the ratio of male survival to female survival should be more reliable than the separate survival estimates for the two sexes.

Despite the tendency for male survival to increase with size in interspecific comparisons, we nevertheless found that relative male survival tended to decrease as relative male size increased within a species. Taken together, these findings are in accordance with the hypothesis that there is an optimal size in terms of survival for the males of each species and that, as this optimal size increases, absolute male survival increases. As the size of males within a species increases above the optimum, male survival decreases relative to female survival. Females are presumably closer to their own optimal size for survival, because they are not as strongly subject to sexual selection. The optimum size (for survival) of males of one species must be at least close to the optimum for females of the same species, because the ecologies (diet, habitat, predators, etc.) of males and females of the same species are usually very similar.

Note that relative male survival is not 1 in those species with little sexual dimorphism; rather, relative male survival is substantially greater than 1. In other words, in monomorphic, monogamous species, female survival is substantially lower than male survival, probably because female parental investment is greater than male parental investment (Trivers 1972). Why females in monogamous species of birds have been selected to exhibit greater parental investment than males has not been adequately explained. Nevertheless, it should be clear that our hypothesis that males pay an increasing cost in survival as their size increases relative to females is compatible with the idea that females in general pay a cost in survival for their greater levels of parental investment.

We have stated that our results are consistent with the hypothesis that male size is limited by survival selection. Our test of this hypothesis was valid in that negative results would have been good evidence against the hypothesis; that is, if relative male survival had not declined as relative male size increased, it would have been hard to maintain that male icterids pay a cost in survival for being large. As is commonly true in hypothesis testing, however, confirmation of the predictions does

not necessarily confirm the hypothesis. In this case, the major problem is that the degree of size dimorphism is correlated with the degree of polygyny (Selander 1958), so the decreased survival of males in dimorphic species may be caused by some other correlate of polygyny (such as behavior or plumage) rather than by large size. Thus, a conservative interpretation of the relationship between relative male size and relative male survival is that some characteristic favored by sexual selection tends to depress male survival.

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