Viability selection against highly-ornamented males

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RH: NATURAL SELECTION OPPOSES SEXUAL SELECTION

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ABSTRACT

Hypothesis: Variation in ornamental traits, such as plumage coloration, is maintained by the opposing forces of sexual selection (increased ornamentation) and natural selection (decreased ornamentation).

Organisms: A wild population of western bluebirds (*Sialia mexicana*) in northwestern Oregon — the subject of longitudinal population studies since 1988.

Methods: We necropsied 47 adult birds recovered dead in 2002. We measured their plumage coloration with an Ocean Optics S2000 reflectance spectrophotometer. Using Mann-Whitney U-tests with Bonferroni correction, we compared these data to measurements collected from 43 adults recaptured alive.

Results: Necropsies suggested that birds died of an epidemic during 2002. Dead females did not differ from survivors in morphology or plumage. Dead males were significantly more highly ornamented (darker, redder breast patch) than males that survived.

Keywords: western bluebird, *Sialia mexicana*, natural selection, sexual selection, wildlife disease, natural mortality

INTRODUCTION

Sexual selection favors traits that increase performance in either male-male competition or in female mate choice, and indicator models predict that those traits will be honest indicators of physiological quality, parasite load, or immune response (Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Folstad and Karter 1992; Andersson 1994). Sexually selected traits, because they are dependent on individual condition, will require an allocation of resources that could be invested in other life history variables (Kokko 1998). An increase in the elaboration of condition-dependent traits may lead to a reduction in immune response (Folstad and Karter 1992). Although it has been argued that sexual displays require resource allocation and therefore should be regarded as life history traits (Höglund and Sheldon 1998), researchers rarely are able to demonstrate tradeoffs between sexual traits and other life history variables (but see Møller 1989; Møller and De Lope 1994). Because individuals have different energy budgets and employ different reproductive strategies, life history tradeoffs are often difficult to study (Reznick 1985). A level of investment in ornamentation that is a burden to one individual may not be so to another individual. Natural epidemics are unexpected and thus allow researchers to separate the natural covariance between sexually selected traits and viability.

Unusual occurrences of mass mortality provide a powerful way to study selection in the wild (Endler 1986). In a classic study, Bumpus (1899) compared the morphology of house sparrows (*Passer domesticus*) that survived a severe winter storm to those that did not. His data are often cited as an example of both directional and stabilizing selection (Buttemer 1992; Pugesek and Tomer 1996; Janzen and Stern 1998). A few researchers have been as fortunate as Bumpus to witness viability selection in action (Grant and Grant 1993; Brown and Brown 1998; Nolan et al. 1998; Brown and Brown 1999; Shine et al. 2001), but catastrophic events are rare. For many taxa, it is extremely unusual to recover large numbers of dead individuals. Often it is impossible to collect appropriate and comparable data on both individuals that survive and those that perish.

The western bluebird (*Sialia mexicana*) is a sexually dichromatic, socially monogamous passerine. Males are bright blue with a reddish-brown breast patch that can extend to the scapulars and over the back (Sibley 2000). Females are duller overall. The Prescott Bluebird Recovery Project has been monitoring a breeding population of western bluebirds in the Willamette Valley region of northwestern Oregon since 1975 and has conducted banding and recapture efforts since 1988. As a result of such intensive, longitudinal monitoring, dead adult bluebirds are recovered occasionally in or near nest boxes (e.g. a total of 29 birds from 1988-1997). However, as the population under observation grew, we recovered an increasing number of dead adults (Fig. 1). In 2001, 53 dead adults were recovered, more than in any prior year in this population and far more than in other large bluebird banding programs in North America (L. Siefferman, E. Eltzroth, J. Fair, J. Citta, pers. comm).

In anticipation of continuing high mortality and prior to the 2002 breeding season, we prepared to study the phenomenon in detail during 2002. Our goals were (1) to investigate cause of death through necropsies of dead adults, and (2) to uncover evidence of natural selection by comparing the morphology and ornamentation of birds that died with a random sample of birds that survived.

METHODS

The western bluebird is an obligate, cavity-nesting passerine. The species is distributed throughout western North America, but the focal population is disjunct from the rest of the species range (Guinan et al. 2000). The Prescott Bluebird Recovery Project maintains and monitors nearly 1800 nest boxes in a 122,375 hectare region of northwestern Oregon, USA. During the breeding season (April-September), we check boxes weekly and record standard nesting data. Nestlings are banded between 7-13 days of age, and adults are trapped in Potter live traps. Live recapture rate was 45% averaged across years, age classes, and phenotypes (for population details see Keyser et al. 2004).

During the 2002 breeding season, as soon as we recovered a dead adult bluebird, the bird was stored on ice in a clean plastic bag and then under refrigeration until examination. For each bird, we measured culmen length, right tarsus length, unflattened wing chord length, and tail length. We sampled the outer two tail retrices and 6-8 feathers from the breast and rump region. When birds were in good condition, we performed a gross necropsy. After dampening feathers and exposing the breast region, we assigned a body condition score as follows: 1, breast muscle extremely concave, keel very pronounced; 2, breast muscle slightly concave, keel obvious; 3, breast muscle flat or slightly convex, keel flush with breast musculature; 4, breast muscle bulging, keel nearly invisible. Upon opening the thoracic and abdominal cavities, we recorded the presence or absence of hemorrhagic lungs, liver, or other major organs. We removed the entire gastrointestinal tract and examined the contents of the ventriculus, small intestine, and large intestine. For each region, the contents were scored as follows: 0, empty; 1, some food or feces; 2, full of food or feces; 3, full of blood. In addition, we recorded the number and location of intestinal macroparasites and stored samples in 10% formalin for later identification.

In conjunction with the examination of dead recoveries, we collected as much comparable data as possible from a random sample of live, breeding adults captured using Potter traps. For each bird, we measured culmen, tarsus, wing, and tail length. All morphological measurements of both dead and live birds were made by one of us (AJK) using identical techniques. Each bird was only measured once so it was not possible to quantify repeatability of these measurements. We sampled retrices and body plumage from live birds immediately upon capture in the same manner as described above for dead birds. Because this study was conducted in an at-risk population, birds were not sacrificed for internal examination and thus, were released unharmed within 10 minutes.

We quantified plumage coloration of breast, rump and tail feathers using an Ocean Optics S2000 reflectance spectrophotometer (Dunedin, FL, USA). Body feathers from each individual were taped in an overlapping fashion to a piece of black cardboard prior to spectrophotometric analysis. A sheathed, fiber-optic probe delivered illumination from a deuterium-tungsten-halogen lamp to a plumage region 2 mm in diameter, and feather reflectance was measured at a 90° angle to the feather surface. We expressed all reflectance measurements as the proportion of the total reflectance of Ocean Optics W-1 white standard measured before and after each feather sample. To smooth the curve, each reading was constructed from an average of 20 reflectance curves, which reduced measurement error due to mechanical fluctuations in the spectrometer readings. We took 5 readings from each region, moving the probe by at least 3 mm before taking each new reading. Finally, we averaged the five readings from each body region of each individual, which reduced measurement error due to slight fluctuations in plumage color across the measured body region. Spectrometer readings from the same body region (i.e. the five described above) were strongly correlated (all r's >0.92, all p's << 0.05).

We summarized reflectance data by calculating three standard descriptors of reflectance spectra: brightness, chroma, and hue. Brightness (total amount of light reflected by the feather) was calculated as the summed reflectance from 300 to 700 nm. We calculated hue and chroma differently for blue (rump and tail) and chestnut (breast) plumage because of the inherent reflectance properties of the two colors. For the rump and tail feathers, UV chroma, a measure of spectral purity, was calculated as the ratio of the total reflectance in the ultraviolet range to the total reflectance of the entire spectrum (∫300-400/∫300-700). For breast feathers, red chroma was calculated as the ratio of the total reflectance in the red range to the total reflectance of the entire spectrum (∫645-700/∫300-700). Hue is the principal color reflected by the feather. For structural coloration, hue was calculated as the wavelength at peak reflectance. Because hue of breast (calculated as the wavelength of maximum slope) did not vary among males, we do not report hue for breast coloration.

To analyze associations between categorical variables, we used Fisher's exact tests following Sokal and Rolf (1995). Because many variables were non-normally distributed, we used non-parametric, Mann-Whitney U tests with Bonferroni correction to compare the morphology and plumage of dead and live birds (SPSS 10.0.5). We used logistic regression where appropriate to quantify selection gradients for variables that differed significantly between dead and live birds (Janzen and Stern 1998) using the correction for bias suggested by Blanckenhorn (1999).

RESULTS

In total, we recovered 94 dead adult bluebirds from April-July 2002, nearly twice as many as in 2001 (53 vs. 94; Fig. 1). Of the 94 dead adults, 34 were too decomposed to examine further. Of the remaining 60 dead adults, 13 were killed by external cause (e.g. impact with automobiles or predation). These birds were excluded from further analysis, and the results discussed below refer to the 47 birds (21 females, 26 males) that were recovered in good condition and to which no obvious, external cause of death could be attributed.

There was no evidence for a high incidence of death by starvation because only six birds were in the lowest body condition category. Average body condition score was 2.61 ± 0.93 and did not differ between males and females (Mann-Whitney $U = 113.5$, $p = 0.43$). Additionally, only five birds had completely empty gastrointestinal tracts (Table 1), and of these five, only one was in the lowest body condition category.

Fifty-five percent of birds had at least one acanthocephalan intestinal parasite (mean ± SD: 1.83 ± 3.33; range: 1-19). B. Nickol confirmed the species identification as *Plagiorhynchus cylindraceus* (*formosus*). This level of incidence is comparable to that found in starlings (*Sturnus vulgaris*), in which they appear to be non-pathogenic (Moore and Bell 1983). We found no other macroendoparasites.

Sixty-six percent of birds examined showed signs of hemorrhage in either the gastrointestinal tract or major organs (Table 1), a finding consistent with the action of an infectious agent (Samour 2000), suggesting death by enteritis. Prior work supporting this conclusion comes from a geographically adjacent population in which enteritis was documented as a cause of death in western bluebirds (Thompson-Cowley et al. 1979;

Bildfell et al. 2001). We found no association between the presence of *P. cylindraceus* and internal hemorrhage ($p = 0.27$).

In order to compare the morphology and plumage of the birds that died with a random sample of birds that survived, we captured 21 breeding males and 22 breeding females during the 2002 breeding season. For females, dead birds did not differ significantly from live birds for any morphological or plumage variable that we measured (Table 2). However, dead males had significantly darker breast patches than live males ($U = 111.00$, $p = 0.001$; Table 3). In addition, the breast patches of dead males were significantly redder than those of live males ($U = 113.00$, $p = 0.002$; Table 3). We found no significant differences in ornamental blue plumage on the rump or tail between dead and live birds of either sex (Tables 2 and 3). The observed plumage differences in males were not related to age (average age for live males = 1.6 years, for dead males = 1.8 years; $t = 0.59$, $p = 0.56$). The culmen length of dead males was significantly shorter than culmen length in live birds ($U = 78.00$, $p \leq 0.001$; Table 3). Otherwise, the two groups were similar morphologically.

After standardizing each variable to mean = 0 and SD = 1, we calculated linear selection differentials for male culmen length, male breast brightness, and male red chroma (Table 4). Estimates of selection can be biased in several ways. First, if the variables in question are altered at or after the time of death (e.g. through tissue degradation), measurement error could imitate selection. This is an unlikely source of bias in this case because the morphological and plumage differences between dead and live birds were evident in males but not females. If post-mortem changes were driving the statistical patterns we observed, they would be evident in males and females. Second, dead birds could disappear differentially prior to recovery if scavengers locate dead birds non-randomly with respect to phenotype. In this case, 46 out of 47 dead birds were recovered in nest boxes and out of reach of most scavengers. Third, immigration by morphologically distinct individuals that are mistaken for local survivors could lead to apparent selection. The majority of birds in this study, both selected individuals and survivors, were breeders with established territories during the 2002 breeding season. Typically, little immigration or dispersal occurs during the breeding season. Fourth, when the true proportion of breeding individuals that die is unknown, estimates of selection will be biased (e.g. Price et al. 2000). Specifically, if selected individuals are overrepresented in the data set, selection will be underestimated (Blanckenhorn et al. 1999).

Since the putative selective event described here occurred during the breeding season in a relatively closed population (Keyser et al. 2004), we have a reliable estimate of the true fraction of birds that died, which can be used to bracket our estimates of the strength of selection. Of 213 breeding males, 44 died of intrinsic causes (i.e. not due to predation or impact), and 26 were recovered in good condition. We used these two estimates of the true fraction dying ($p_1 = 44/213 = 0.21$, $p_2 = 26/213 = 0.12$) to correct our estimates of selection (Table 4) following Blanckenhorn (1999).

Because our fitness measure was binomial (dead or alive), and both culmen and brightness were normally distributed (culmen: Kolmogorov-Smirnov statistic = 0.117, df = 44, p = 0.16; brightness: Kolmogorov-Smirnov statistic = 0.08, df = 45, p = 0.20), we used logistic regression to calculate linear selection gradients (Janzen and Stern 1998) for these two variables. We did not include red chroma in this analysis because it was non-normally distributed and highly correlated with brightness (Spearman's R = -0.66, $p < 0.001$; negative correlation indicated that birds with more red were also darker). Both culmen length and breast brightness were significant predictors of survival (logistic regression coefficient, $\alpha \pm$ SE, Wald's χ^2 and significance level for culmen and brightness respectively: 1.43 ± 0.53, $\chi^2 = 7.39$, $p = 0.007$; 0.82 ± 0.43, $\chi^2 = 3.53$, $p = 0.060$). Logistic regression coefficients were transformed following Janzen and Stern (1998) into β, which is equivalent to the selection gradient calculated via multiple linear regression (Lande and Arnold 1983). Both the uncorrected and corrected (Blanckenhorn et al. 1999) selection gradients are reported in Table 4. The true selection gradients should be bracketed by these intervals (culmen: 0.22-0.45; brightness: 0.12-0.22) and are consistent with selection gradients reported in the literature (mean $| \beta | = 0.22$, median $| \beta | = 0.16$, Kingsolver et al. 2001). Our analysis indicated that directional selection for larger bills relative to body size will occur if culmen length is heritable and not confounded by environmental effects (Mauricio and Mojonnier 1997; Stinchcombe et al. 2002). Similarly, the linear selection gradient for brightness is positive, which indicates that if heritable, natural selection will favor males that display reduced ornamental plumage on the breast (i.e. less dark and less red).

Discussion

It is unusual to find large numbers of dead vertebrates in the wild. Typically, predation is an isolated, rarely witnessed event, and it is even more uncommon to document death caused by illness or starvation except in mass mortality events such as after extreme weather (Bumpus 1899; Grant and Grant 1993; Brown and Brown 1998) or exposure to anthropogenic contaminants (Carson 1962; Anspaugh et al. 1988). In this study, we documented high mortality, apparently due to illness, in a wild population of western bluebirds. Furthermore, we showed that this episode of viability selection differentially affected males bearing darker, redder breast plumage and those with smaller bills relative to body size. This result is consistent with the interpretation that natural selection for reduced ornamentation opposed sexual selection for increased ornamentation during an epidemic.

Illness as cause of death

Two lines of evidence led us to conclude that the most probable explanation for high bluebird mortality in 2002 was an infectious agent sweeping through the population. First, we documented nearly twice the mortality of previous years in spite of the fact that the population size in 2002 was comparable to that in 2001. The majority of these birds were found dead in nest boxes but had obviously fed within the 12 hours prior to death. Second, the finding that 66% of birds necropsied suffered internal bleeding without external trauma (i.e. impact) strongly suggested that illness was responsible (Samour 2000).

Selection against highly-ornamented, small-billed males

The only morphological difference we documented was that dead males had significantly shorter bills than live males. It is not immediately obvious why bill length should be associated with mortality. However, we propose two possible explanations. First, if the range of suitable prey items is determined by bill size (Van Valen 1965; Smith 1987; Grant and Grant 1996), small-billed males could be less able to forage sufficiently to meet their own metabolic needs (Blanckenhorn 2000). Second, if bill size reflects nutritional condition during the nestling period, small-billed males could be those that started life under nutritional stress and pay for this stress with a concomitant reduction in immune function later in life (Metcalfe and Monaghan 2001).

Ornamental breast plumage differed significantly between males that died and males that survived. Specifically, there was viability selection against males with darker, redder plumage. The chestnut breast patch in bluebirds is a melanin-based ornament (McGraw et al. 2004), it is much more dramatic in males than in females, and by analogy with other species, it is likely to be involved in sexual selection. In house sparrows (Møller 1988; Veiga 1993), great tits (*Parus major*, Norris 1990b; Norris 1990a), and pied flycatchers (*Ficedula hypoleuca*, Sætre et al. 1994; Sætre et al. 1995), melanin-based ornaments are positively correlated with reproductive success and are involved in male-male competition and female choice. While we did not quantify the potential for sexual selection directly in this study, male eastern bluebirds (*Sialia sialis*; a closely-related congener of the western bluebird) with darker, redder breast plumage paired earlier, provided more parental care, and fledged heavier offspring than less ornamented males (Siefferman and Hill 2003). Based on this evidence, and because western bluebirds express more extensive and darker melanin plumage that do eastern bluebirds, we think it likely that sexual selection may favor increased male ornamentation in western bluebirds.

Thus, if we suppose that sexual selection favors increased ornamentation in western bluebirds, why might natural selection favor duller males? From a life history perspective, individuals make dynamic trade-offs when allocating internal resources to reproduction and survival (Williams 1966; Van Noordwijk and Dejong 1986; Stearns 1992; Westendorp and Kirkwood 1998). Folstad and Karter (1992) proposed that increased testosterone led to increased sexual display but decreased immunocompetence. Evans et al. (2000) demonstrated that increased testosterone was directly correlated with increased melanin-based ornamentation and increased corticosterone levels, which led, in turn, to reduced immune function in house sparrows. Also in house sparrows, a positive relationship between ornamentation and immune response exists during the non-breeding season, but the relationship is reversed during the breeding season (Gonzalez et al. 1999; Buchanan et al. 2003). Verhulst et al. (1999) used selection experiments with domestic fowl (*Gallus domesticus*) to demonstrate the link between immunocompetence and testosterone-based sexual ornamentation. These examples are best explained in terms of a life history trade-off between sexual ornamentation and survival (for an invertebrate example see Siva-Jothy 2000).

We propose that there are underlying costs of ornamentation that require individuals to gamble on future survival when allocating resources to ornamentation. If immune response is the currency in this trade-off, then the apparent epidemic that we documented represents an unpredictable, and perhaps infrequent, challenge to breeding males. In the case of the males in our study, the most highly-ornamented individuals lost the bet and were selected against. It appears that this episode of natural selection opposed the putative action of sexual selection, a relationship that has been documented in house sparrows and barn swallows (*Hirundo rustica*) as well (Møller 1989; Møller and De Lope 1994). If there is a heritable basis to male breast plumage (e.g. Norris 1993; Roulin et al. 1998; but see Griffith et al. 1999), the counteracting forces of natural selection and sexual selection could maintain additive genetic variation for male plumage ornamentation.

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TABLE 1. Summary of necropsy findings for adult western bluebirds recovered dead in 2002.[1] To the extent possible relative to decomposition of the specimen, we examined the major organs for signs of hemorrhage and the entire gastrointestinal (GI) tract for food, feces, hemorrhage, and endoparasites (*P. cylindraceaus*). This table gives the counts in each category for each sex. In total, 21 females and 26 males were necropsied, but not all data could be collected for all individuals thus sample sizes vary.

		Males	Females	Total
Contents of GI tract	Empty (0)	4	1	5
	Food (1,2)	5	5	10
	Blood (4)	7	7	14
P. cylindraceaus present	Yes	13	7	20
	No	6	10	16
Hemorrhagic GI or organs	Yes	10	11	21
	No	8	3	11

[1] Currently there is national concern over the spread of West Nile Virus (Petersen and Roehrig 2001), but it had not been reported in Oregon as of January 2003 nor was the pathology of the necropsied birds consistent with West Nile Virus (E. DeBess, pers. comm).

TABLE 2. Morphological and plumage differences between females that died and females that survived. Units on all morphological measurements are in mm. See text for plumage variable details. For each variable, mean ± SD (n) is given for each group (dead vs. alive). The groups were compared with non-parametric Mann-Whitney U tests.

TABLE 2 (CONT).

	Dead	Alive	U	p
Morphology				
Culmen	9.40 ± 0.41 (20)	9.53 ± 0.59 (22)	197.50	0.570
Wing chord	99.52 ± 2.66 (21)	99.18 ± 2.36 (22)	214.50	0.686
Tarsus	20.59 ± 0.61 (20)	20.42 ± 1.09 (22)	208.00	0.762
Tail	58.19 ± 2.29 (21)	58.82 ± 2.20 (22)	205.00	0.522
Breast Plumage				
Brightness	3664.38 ± 822.74 (20)	3916.82 ± 928.37 (22)	187.50	0.413
Red chroma	58.27 ± 4.48 (20)	56.15 ± 4.01 (22)	158.50	0.121
Rump Plumage				
Hue	436.77 ± 9.84 (20)	436.45 ± 9.58 (22)	216.50	0.930
Brightness	6157.63 ± 996.94 (20)	6171.60 ± 1337.63 (22)	218.00	0.960
UV chroma	28.59 ± 3.08 (20)	29.41 ± 2.22 (22)	173.00	0.237
Tail Feathers				
Hue	475.99 ± 17.76 (20)	477.81 ± 17.81 (22)	207.50	0.753
Brightness	5731.58 ± 695.17 (20)	5462.42 ± 511.03 (22)	165.00	0.821
UV chroma	21.77 ± 1.92 (20)	21.34 ± 1.84 (22)	202.00	0.650

TABLE 3. Morphological and plumage differences between males that died and males that survived (as in Table 2 for females). The groups were compared with non-parametric Mann-Whitney U tests. Significant differences are in bold.

TABLE 3 (CONT).

	Dead	Alive	U	p
Morphology				
Culmen	**9.02 ± 0.41 (24)**	**9.60 ± 0.47 (20)**	**78.00**	**≤ 0.001**
Wing chord	103.48 ± 2.89 (25)	103.33 ± 3.02 (21)	248.50	0.754
Tarsus	20.70 ± 0.59 (25)	20.51 ± 1.04 (21)	249.50	0.774
Tail	61.58 ± 3.36 (24)	61.48 ± 2.71 (21)	242.50	0.828
Breast Plumage				
Brightness	**2252.28 ± 511.82 (25)**	**2721.63 ± 448.98 (20)**	**111.00**	**0.001**
Red chroma	**63.54 ± 4.12 (25)**	**58.20 ± 6.40 (20)**	**113.00**	**0.002**
Rump Plumage				
Hue	408.34 ± 12.77 (25)	403.50 ± 9.00 (20)	189.50	0.167
Brightness	8570.05 ± 1559.05 (25)	8423.53 ± 1283.16 (20)	222.00	0.522
UV chroma	39.41 ± 4.39 (25)	41.00 ± 3.27 (20)	174.00	0.083
Tail Feathers				
Hue	438.86 ± 10.43 (25)	435.94 ± 13.25 (20)	226.50	0.591
Brightness	5487.37 ± 462.62 (25)	5373.36 ± 605.73 (20)	212.50	0.392
UV chroma	25.87 ± 1.98 (25)	25.55 ± 2.32 (20)	235.50	0.740

TABLE 4. Comparison of selection statistics before and after correction for fraction of birds dying. All three variables were standardized to mean = 0, SD = 1. Thus, the selection differential, S, was the mean of the selected (i.e. dead) males after standardization. Following Blanckenhorn (1999), the uncorrected mean was weighted by the fraction of the population that died (p_1 = number of males that died divided by the number of breeding males, 44/213; p_2 = number of males that died from intrinsic causes divided by the number of breeding males, 26/213). The selection gradients were calculated through logistic regression, transformed following Janzen and Stern (1998), and corrected as above (see text for details Blanckenhorn et al. 1999).

	Culmen	Brightness	Red Chroma
S, Uncorrected selection differential	-0.51	-0.39	0.41
S_1*, Corrected selection differential, $p_1 = 0.21$	-0.90	-0.64	1.96
S_2*, Corrected selection differential, $p_2 = 0.12$	-1.03	-0.71	2.68
B, Uncorrected selection gradient	0.22	0.12	
β_1*, Corrected selection gradient, $p_1 = 0.21$	0.40	0.20	
β_2*, Corrected selection gradient, $p_2 = 0.12$	0.45	0.22	

FIGURE 1. Proportion (± SE) of all adult birds censused in each study year that were recovered dead. Note the standard errors are large due to small sample sizes in the early years of the study. All proportions may slightly underestimate the true proportion of birds dying because prior to 2002, only banded birds were reported dead. The star for 2002 represents the proportion of birds recovered dead if unbanded recoveries are included (76 banded birds and 18 unbanded birds died out of 415 adults censused). The horizontal line at 0.08 is the average mortality across all years of the study.

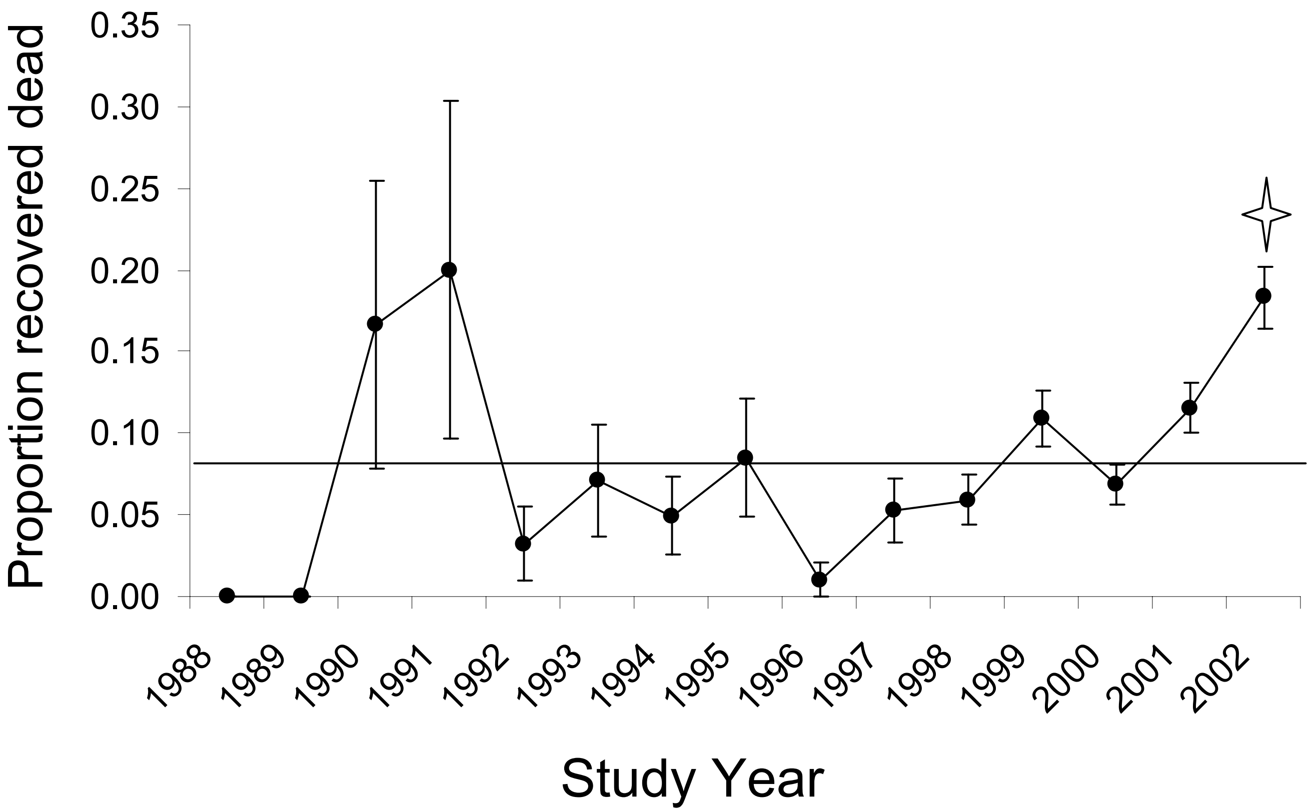
Proportion recovered dead
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
Study Year

Figure 1