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Natural variation in the sexually selected feather ornaments of crested auklets (*Aethia cristatella*) does not predict future survival

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We evaluated whether sexually selected crest and auricular plume feather ornaments of crested auklet (*Aethia cristatella*) adults covaried with individual local survival over 11 years (1991–2001). Crested auklets ($n = 364$ total) were captured near breeding sites, marked with color rings, and local survival estimates were based on color ring resightings at a breeding colony. Survival estimates and relationships among local survival and crest length, auricular plume length, mass and tarsus were evaluated using the program MARK. The best models included four groups, defined by sex and ease of resighting, that differed in resighting rate (p) but not local survival rate (Φ). This model structure effectively explained sources of variation in local survival and resightability among individuals. The best fitting model showed local survival rate varying annually, while accounting for differences in resightability of marked individuals between the sexes and groups ($\Phi[t]$, p[sex*ease of resighting]). Annual local survival varied from 0.940 ± 0.029 (SE) in 1993–1994 to 0.767 ± 0.034 in 1997–1998 and averaged 0.859 ± 0.019. We found no evidence that crested auklet local survival covaried with continuous variation in individuals' ornaments. Simulations indicated that our data set was sufficient to detect a relationship between local survival and a covariate that equaled or exceeded a range of 8%. The implications for competing sexual selection mechanisms of empirically measured survival–ornament relationships are controversial, but our study emphasizes that survival estimates for such investigations must control for confounding factors such as resighting rate as well as have sufficient statistical power and time scale to be biologically meaningful. Our results are most consistent with the idea that the conspicuous variation in crested auklet's showy ornaments is arbitrary with respect to individual viability as quantified by their long-term survival.
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A widely cited explanation for the evolution of elaborate ornamental traits such as the showy plumes of some bird species is that they have been favored by mating preferences because they serve as viability indicators (Andersson, 1994). The logic is that individuals choosing mates benefit directly or indirectly by selecting a healthy, high-quality partner that can afford to display showy but costly adornments (also known as a "good genes" or "handicap" process; e.g., Andersson, 1986; Kirkpatrick and Ryan, 1991; Pomiankowski, 1988). In keeping with the predictions of this model, numerous studies have found correlations between ornament expression and health, parental ability, and so on (Andersson, 1994). For long-lived species that benefit from remating with the same partner from year to year and incur high costs if they lose their partner, survival ability might likely be a key attribute that would be the basis for mate choice.

Testing this hypothesis conclusively is problematic because, even if ornament expression honestly advertises individual quality, positive, neutral, or even negative relationships between ornament and survival rate are possible under varying scenarios (Jennions et al., 2001). Nevertheless, no study has used the latest survival estimation techniques (e.g., Burnham and Anderson, 1998; White and Burnham, 1999) to test whether ornaments of long-lived bird species relate to an individual's survival ability. For example, a recent comprehensive comparative analysis of the relationship between survival and sexually selected traits was based on studies in which survival was inferred from simple resighting of individuals between two time intervals (e.g., breeding seasons), or if individuals were known to be alive at the end of a (usually short-term) study or experiment (Jennions et al., 2001). Because emigration and other effects are confounded with survival in these approaches (Lebreton et al., 1992), their results are in effect return rates and should not be taken to represent true survival rates or survival ability. An approach that quantitatively detects and controls for effects of young individuals emigrating and for transient individuals is required (e.g., Burnham and Anderson, 1998; White and Burnham, 1999). We set out to rigorously quantify the relationship between expression of a spectacular feather ornament and true survival rate, a result crucial to the question of sexually selected ornament function.

Auklets (family Alcidae, tribe Aethiini) include five socially monogamous seabird species in which both sexes display similar ornaments during the breeding season (Gaston and Jones, 1998; Jones and Montgomerie, 1992). Crested auklets (*Aethia cristatella*) have a conspicuous black forehead-crest, white auricular plumes, an orange bill with accessory plates,

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Table 1

Crested auklet capture and resighting effort at Main Talus, Buldir Island, Alaska, 1991–2001, for individual birds from which complete sets of ornament measurements were obtained

Year	Individuals newly marked	Individuals resighted
1991	47	47
1992	106	165
1993	3	134
1994	0	106
1995	34	139
1996	90	188
1997	84	248
1998	0	209
1999	0	151
2000	0	124
2001	(68)	169
Total	364	

and a citruslike plumage odor (Jones, 1993a). These ornaments are displayed by both sexes during courtship at the colony and at sea, and mate choice follows from the performance of sexual displays by both members of courting pairs (Hunter and Jones, 1999; Jones, 1993a). The feather ornaments become greatly reduced and the brightly colored bill plates drop off after the breeding season (Jones, 1993a). Long crests are favored by mutual mating preferences of both sexes and signal high dominance status, evidence that mutual inter- and intrasexual selection favor the crest ornament (Jones and Hunter, 1993, 1999). Ornament variability across the crested auklet population is extreme, but individuals maintain similar ornament size across years (e.g., Jones et al., 2000: Figure 3), indicating that ornament expression is a stereotyped characteristic maintained across individuals' life spans. The objectives of the present study were to quantitatively evaluate whether individuals' ornament size was correlated with their subsequent survival rate and to evaluate the result in terms of competing explanations for the evolution of similar sexually selected display traits.

METHODS

Study area

Fieldwork was carried out at a mixed colony of more than 200,000 least, crested, and other auklets species at Main Talus, Buldir Island, western Aleutian Islands, Alaska (52°22.577′N, 175°54.326′E; Byrd and Day, 1986; Byrd et al., 1983) during mid-May to early August of 1991–2001.

Auklet captures and measurements

We captured auklets for marking using noose carpets set on the colony surface within a single 100 m^2 (surface area) study plot over talus occupied by more than 1000 nesting pairs of crested auklets and 100 pairs of least auklets (Table 1). We believe noose carpets selected breeding and nonbreeding auklets randomly from the population (Jones, 1992a,b). Each captured adult auklet was given a numbered stainless-steel leg ring and a unique combination of three plastic color rings. Upon capture, we weighed birds to the nearest 1 g using a spring scale, sexed them using bill shape (Jones, 1993b), and took measurements of tarsus length, crest length (length of the longest straightened crest shaft), and the auricular plume length to the nearest 0.1 mm (Jones et al., 2000). We measured auricular plumes on the right side only in 1991, and both right and left sides were measured in 1992–1998. We used the right-side measurement (1991) and the mean value of left and right auricular plume measurements (1992–2001) to index auricular plume expression. To test whether ornaments predict future survival ability, we tested for a relationship between ornament size at initial capture (the marking occasion) and subsequent survival.

Repeatability and measurement error were calculated on birds measured twice within a year, and on birds measured by two of us to compare intermeasurer measurement reliability. Repeatability within and between measurers was high, and measurement error was low (e.g., r_{I} within/between measurers for crest 0.95/0.91, for auricular plume 0.92/0.89; Jones et al., 2000). Individuals tended to retain their relative ornament size across years, with repeatability, r_{I}, across years for crest 0.79 and for auricular plume 0.13 (there was a notable population-wide increase in auricular plume during the study period; Jones et al., 2000). Crest and auricular plume were weakly correlated across individuals ($r = .16$ for males, .21 for females) and had no relationship with body size as indicated by tarsus length ($r = -.11, -.09$; Jones et al., 2000). Other than 36 birds captured in subadult plumage (2 year olds; Bédard and Sealy, 1984; Jones et al., 2000), as judged by worn brownish flight feathers and greater coverts and dull orange bills, all individuals measured in our study were adults 3 or more years old.

Auklet resightings

To quantify survival rigorously, resightings of color-marked auklets were made daily (except during the most severe weather conditions) during mid-May to early August 1991–2001 (Table 1), encompassing 11 entire breeding seasons. We observed birds from a plywood blind during their morning activity period (0900–1300 h) and during the brief evening activity period (2300–0030 h, mostly during early chick-rearing) and recorded the color-ring combinations of all marked individuals.

We kept track of the number of times each individual was resighted each year. It was evident that topography of the study plot, nest-site location, and behavior of individuals created heterogeneity in our ability to resight individuals. Birds with breeding-site entrances obscured by boulders or at the far corners of the plot were more difficult to see. Survival estimation techniques include the assumption that each individual is equally likely to be resighted in each year it is alive (Lebreton et al., 1992), so it was necessary to account for variation in ease of resightability by grouping individuals according to ease of resighting (Jones et al., 2002). We classified individual birds as hard to see by default until they were resighted at least three times in one year, then they were classified as easy to see if they were observed at least three times in each year they were alive excepting the last year they were observed (e.g., resightings of a hard-to-see individual during 5 years, 1-0-3-0-4; resightings of an easy-to-see individual, 3-7-5-9-2). We excluded frequency of resighting in the last year from the group classification criteria to allow for individuals in the easy-to-see groups to die during a breeding season and consequently be seen less than three times. Thus, our marked population was divided into four groups for analysis: easy-to-see males, hard-to-see males, easy-to-see females, and hard-to-see females. We used the four-group criterion because we believed more complex grouping methods, use of an individual covariate for resightability, or modeling encounter histories within years (e.g., Pollock's robust design models) would be unnecessarily complex and overparameterize the models, making it more difficult to make inferences about survival.

Survival rate estimation and model selection

We estimated local adult annual survival (Φ) and resighting (*p*) rates using methods described by Lebreton et al. (1992), Burnham and Anderson (1998), and Jones et al. (2002) with the program MARK (White and Burnham, 1999). In the terminology of capture-mark-recapture analysis (e.g., Lebreton et al. 1992), confirmation that a marked individual is alive in a year of the study is referred to as a "recapture," whether the bird was caught and its band read or the bird's band was read visually from a distance. In our study, these recaptures were obtained by color-band resighting, so to avoid confusion we refer to resighting rate rather than to recapture rate. Our estimate of local survival, referred to as Φ following Lebreton et al. (1992), includes losses due to mortality and any permanent emigration of marked individuals. Because strong site fidelity is a characteristic of the biology of auklets in general and of crested auklets in particular (Fraser et al., 1999; Jones, 1992b, 1993a; Jones et al., 2002), we assumed that permanent emigration would be negligible or absent and that our local survival estimate would be close to true survival. Nevertheless, during our 11-year study we looked for marked crested auklets outside the study plot and throughout Main Talus to detect emigration.

We began by first defining a global model (Anderson and Burnham, 1999a; Burnham and Anderson, 1998), which is an inclusive model that contains all possible explanatory terms that a priori are expected to influence survival and/or resighting rates. Heterogeneity in resighting rate can create problems in estimating survival rates (Prévot-Juilliard et al., 1998); therefore, we included a group effect in resighting rates, with hard-to-see individuals and easy-to-see individuals treated in different groups in our global model. We looked for an effect of sex on both resighting rate and survival rate. Resighting rates were also allowed to vary over time. For our global model, we used a survival model with time dependence and a sex effect, and a resighting model with a group effect (ease of sighting and sex) and time dependence. In the notation of Lebreton et al. (1992), this model was Φ ($t \times$ sex), *p*(sex × ease × *t*), using *t* for time effects, sex for a sex effect, and ease for a resightability effect.

We determined the goodness-of-fit of this global model to the data using a parametric bootstrap approach, based on 1000 bootstraps, described by Cooch and White (2001). From these bootstraps, we extracted a mean of the model deviances and a mean c-hat. C-hat is a measure of overdispersion, or extra-binominal variation, in the data. It arises when some model assumptions are not being met, such as heterogeneity in survival or resighting rates varying among individual animals (Burnham and Anderson, 1998). The observed deviance and c-hat were divided by the mean of bootstrapped values, and the higher of the two values was taken as an estimate of c-hat (Cooch and White, 2001).

We restricted our candidate models to the global model, plus a series of reduced parameter models, including Cormack-Jolly-Seber (Lebreton et al., 1992) models. We did not construct every reduced parameter model, as this would have led to hundreds of models, many of which had very poor fit. Instead, we used the approach in Lebreton et al. (1992) by first modeling resighting rates to determine the best structure for resighting rates and then modeling survival rates.

Relationships among factors were indicated using standard linear models notation. Capture-mark-recapture analysis uses a model selection framework to infer whether parameters are useful in explaining variation in survival and resighting rates, rather than traditional hypothesis-testing–based approaches that rely on arbitrarily selected *p* values (Burnham and Anderson, 2001). Model selection was based on comparison of the quasi–Akaike Information Criterion (QAICc), where the models with lowest QAICc values suggest the best compromise between good-fitting models and models with relatively fewer explanatory variables (i.e., statistically parsimonious; Anderson and Burnham, 1999a; Burnham and Anderson, 1998). QAICc was used instead of AICc to rank models, as an acknowledgment of the extra-binomial variation in the data set, represented by c-hat (Anderson and Burnham, 1999b; Burnham and Anderson, 1998). We also calculated QAICc weights, as they provide a relative measure of how well a model supports the data compared with other models (Anderson and Burnham, 1999a).

Finally, once an appropriate set of models was constructed, we modeled the relationship of ornaments and local survival by treating them as individual covariates. This approach greatly helps control for the confounding effects of temporary emigration on survival estimates (e.g., low-quality individuals with small ornaments having low resighting rates, *p*, vs. low survival rates, Φ). We only modeled the covariates with survival after the initial capture period, as we were not interested in the ornaments of birds not resident to the study area. Also, as with the candidate model set above, we did not model the covariates with every parameterization possible. Rather, we modeled these covariates with the best fitting parameterizations of Φ and *p*. We used simulations to evaluate the statistical power of our analysis and thus indicate the strength of our conclusion about an ornament–survival relationship.

RESULTS

We captured and completely measured 364 crested auklets at Main Talus, of which 313 were resighted at least once at the study plot (Table 1). During our 11-year study, no marked bird resighted at least once at the study plot was observed away from the study plot, but eight birds (prospectors) that were marked but never seen again at the study plot were observed elsewhere on Main Talus or Crested Point (1 km west of the Main Talus, 1 bird). These data help confirm the very high site-fidelity and low rate of permanent emigration of marked birds from the study plot. The data set provided a reasonably good fit to a reduced global model with time dependence in local survival rates and four groups and time dependence in resighting rates. From the parametric bootstrap, c-hat was calculated to be 1.184, suggesting the presence of only minor amounts of extra-binomial variation. This value of c-hat was used to adjust all QAICc values. Without the groups included, c-hat was calculated to be 1.408.

After constructing Cormack-Jolly-Seber and reduced parameter models, it was clear that resighting rate was best modeled with differences among the groups but with no time dependence. Therefore, we used only this parameterization in building subsequent models. Our index of ease of sighting did not bias our efforts to model local survival rate: we found no evidence for a difference in local survival rate between the easy- and difficult-to-resight groups (ease), nor by sex, as indicated by the relatively poor fit of the model Φ(sex × ease), *p*(sex × ease). Therefore, we believe our method of identifying easy- and hard-to-see birds proved useful in reducing unexplained heterogeneity in *p* while not biasing estimates of Φ. Therefore, we used time-dependent local survival rate and a resighting rate that allowed for groups (ease of sighting and sex) to model individual covariates.

The most parsimonious model in the final candidate model set was a time-dependent model in which resighting rate differed between the previously classified hard-to-see and easy-to-see birds grouped by sex (Φ[*t*], *p*[sex*ease]; Table 2). This model was 32 times better supported by the data compared

Table 2

Model results for crested auklet survival (Φ) at Buldir Island, Alaska, 1990–2000 (c-hat adjusted to 1.184), in decreasing order of fit

Model	QAICc	ΔQAICc	QAICc weight	Parameters	Deviance
$\Phi(t)$ p(ease × sex)	1840.6	0.00	0.957	14	1812.3
$\Phi(.)$ p(ease × sex)	1848.8	8.23	0.016	5	1838.8
Φ(crest) p(ease × sex)	1850.6	9.96	0.007	6	1838.5
Φ(plume) p(ease × sex)	1850.7	10.09	0.006	6	1838.6
Φ(sex) p(ease × sex)	1850.7	10.11	0.006	6	1838.7
Φ(tarsus) p(ease × sex)	1850.9	10.25	0.006	6	1838.8
Φ(tarsus) p(ease × sex)	1850.9	10.25	0.006	6	1838.8
Global model					
Φ(sex × t) p(ease × sex × t)	1870.3	29.72	<0.001	58	1749.2

Models with survival varing over time, and constant survival, fit better than models incorporating ornaments as covariates.

with the next most parsimonious model, a model with constant survival rate over time (Table 2).

By using a method that takes into account annual variance and sampling variance in local survival rate (based on the model $\Phi[t]$, p[sex*ease]), our estimate of mean crested auklet adult local survival rate at Main Talus from 1991 to 2000 was 0.859 ± 0.019, corresponding to a mean adult life span of 6.6 ± 1.0 years.

We modeled individual covariates within the structure of the best model ($\Phi[t]$, p[sex × ease]) and also with a simpler model (Φ[covariate], p[sex × ease]) to remove the necessity of modeling the individual covariate separately within each year and to improve our ability to detect any effect of the individual covariates on local survival. All models with the individual covariates crest, plume, and tarsus were ranked below a model with constant local survival (Table 2), providing little support that these traits were useful in explaining variation in local survival. The slope β (based on a logit linked analysis) of the relationship between local survival and crest length was negative at −0.038 ± 0.073 SE (95% CI, −0.018 to +0.105). The slope b (based on a logit linked analysis) of the relationship between local survival and auricular plume length was also negative at −0.030 ± 0.076 SE (95% CI, −0.179 to +0.119). In both cases, the confidence intervals included 0.

Table 3

Parameter estimates and standard errors for model $\Phi(t)$, p(ease × sex) for crested auklets marked and resighted at Main Talus, Buldir Island, Alaska, during 1991–2000

Parameter		SE
Survival		
1990–1991	0.931	0.050
1991–1992	0.904	0.032
1992–1993	0.825	0.038
1993–1994	0.940	0.029
1994–1995	0.836	0.037
1995–1996	0.908	0.026
1996–1997	0.832	0.028
1997–1998	0.767	0.034
1998–1999	0.839	0.037
1999–2000	0.783	0.047
Resighting rate		
Easy-to-see males	0.952	0.015
Hard-to-see males	0.657	0.030
Easy-to-see females	0.979	0.010
Hard-to-see females	0.768	0.029

Model averaging procedures of program MARK, corrected for c-hat = 1.184, were used.

To assess our ability to detect true effects of ornament size on survival, we simulated data with known relationships between local survival and ornament length. Simulated data sets were based on the model (Φ[covariate], p[sex × ease]), as we believed our best ability to detect effects would be in models without time variation. Simulated capture histories were constructed based on the values of Φ (0.848) and p (Table 3) obtained from the above model, and sample sizes were the same as those in the study. Three sets of simulations were conducted. In the first, there was no relationship between local survival and the covariate randomly drawn from a normal distribution. In the second set, a random normal deviate was drawn for each individual, and we modeled local survival to have the relationship of an increase of 0.01 for every 1 standard deviate increase in the covariate (i.e., across the range of the covariate, 95% of the individuals would vary in local survival rates by 0.0392 [or 2 × 0.0196]). Similarly, in the third set, the relation of local survival to the covariate was a 0.02 increase for every increase of 1 standard deviate of the covariate (for a 95% range of 0.0784). For each run, the slope of the relationship and which model was selected (based on QAICc) was extracted, and 100 runs were done for each condition. With no relationship, the slope was estimated at 0.003 (95% CI; −0.159 to +0.171), and the model with the covariate was selected 17 times out of 100. For the model with a +0.01/SD relationship with local survival, the mean slope was 0.078 (95% CI; −0.051 to +0.205), and the model with the covariate was selected 37 times. For the model with a +0.02/SD relationship between the covariate and local survival, the mean slope was 0.147 (95% CI; −0.022 to +0.328), and the model with the covariate was selected 70 times, indicating respectable power to detect the relationship when it was present. Given our estimates of −0.038 and −0.030, we believe that we would not likely have detected a weak relationship between local survival and a covariate (such as a 0.04 range in local survival across the population), but a relationship between local survival and a covariate equal to or exceeding a range of 0.08 would have likely been detected.

DISCUSSION

We believe our approach provided a rigorous quantification of crested auklet survival and its relation to variation in feather ornament size. Because permanent emigration of marked auklets resighted at least once was absent or extremely low (Fraser et al., 1999; Jones, 1992, 1993a; Jones et al., 2002), our estimates of local survival must be close to true survival estimates and thus appropriate for a biologically meaningful test of the survival-ornament relationship. Our best fitting model suggested that resighting rate of marked individuals varied between groups defined by ease of resighting and that resighting rate also differed between the sexes (Table 2). However, we found no evidence that survival rate varied between the groups defined by ease of resighting or between the sexes. These findings were partly related to the techniques used in the study. Individuals using areas in clear view or close to our observation blind would be expected to be seen more often than individuals farther away, and our separation of the data set into two groups appeared to have the desired effect of reducing this resighting heterogeneity. Our best model also indicated a sex effect on resighting rate, with males being generally easier to resight than females. This result is consistent with previous observations of behavior differences between male and female crested auklets (Fraser et al., 1999; Jones, 1993a).

More interesting, however, was the result that crested auklets survival was not related to crest or auricular plume length or body size, as indicated by tarsus length. A variety of models with and without time dependence effects all fit better than models with these ornaments and other traits as individual covariates. We assessed the power of our analysis to evaluate the data set's ability to detect biologically significant links of the covariates and survival rate. These simulations suggested we would have been able to detect relationships with respectable strength (anything over an 0.08 range in survival from the shortest to longest ornamented individuals), and thus our negative results suggest the lack of any obvious or strong survival-indicator function for crested auklet ornaments. Our confidence in this conclusion is supported by the fact that the results come from a long-term survival data set spanning 11 years and comprising more than 300 marked individuals. Our simulations were conservative in that covariates were drawn from a normal distribution, which produces mostly individuals close to population averages in survival and covariate length. Using flatter or uniform distributions (thereby producing more extreme individuals in the simulations) would have increased our power. An interesting, and unexpected, result was that in 17 cases of 100, the model-fitting procedure would have selected a model with the covariate, when, in fact, there was no relationship (i.e., a Type I error). Further theoretical work on this potential issue may prove worthwhile. The lack of fit of a model incorporating tarsus length as a covariate suggests there is no survival-related directional selection on body size acting in our population.

Crested auklet crests and plume ornaments showed relatively stereotyped expression within individuals over time, extreme variability among individuals, little sexual dimorphism, and little evidence of condition dependence (Jones et al., 2000), although the crest ornament is favored by mutual mating preferences and signals dominance status (Jones and Hunter, 1993, 1999). Our results indicating a lack of a correlation between survival rate and the ornaments continue an enigmatic stream of results (i.e., an elaborate sexually selected ornament without condition dependence; Andersson, 1994). Ornament variability may be arbitrary with respect to measures of individual variation in phenotypic quality such as condition and survival. Ornaments may have evolved under a mechanism independent of "viability indication" (Jones and Hunter, 1998). Alternatively, these ornaments may signal aspects of quality or viability that we have not yet measured. Furthermore, although there are hypothetical benefits to mating with a potentially long-lived partner, a trade-off between survival and reproductive effort might negate this benefit. The trade-off could also have produced a situation where we would find no relationship between individuals' survival and adornments even though ornaments per se do indicate individual viability controlled for reproductive effort. Similarly, a trade-off between sexual attractiveness and mortality (e.g., due to predation) might also lead to lack of a relationship between ornaments and survival.

What implications do studies of covariation between sexually selected ornaments and survival have for tests of competing hypotheses to explain the evolution of these adornments and preferences for them? Jennions et al. (2001) suggested that an overall trend indicating a positive relationship between ornaments and survival across 69 studies is inconsistent with Fisherian (i.e., Fisher, 1930; Kirkpatrick, 1982; Lande, 1980, 1981) or other models that are not based on quality-dependent trait expression (but see Balmford and Read, 1991; Jones, 1992c; Kokko, 2001). Leaving aside the controversy over whether a positive relationship does in fact refute some putative sexual selection mechanisms, a major issue related to the quality of empirical evidence remains unresolved. Most studies of the relation of ornamental traits with survival have in fact examined the ornaments' relationship with return or resighting rates or used a survival estimate confounded by resighting rate (see Lebreton et al., 1992). This is particularly problematic because if low-quality individuals are more likely to emigrate from a study area or if they are less conspicuous and thus less likely to be resighted than studies in which resighting is not controlled for (e.g., most of those used by Jennions et al., 2001), it would tend to report a (spurious) positive relationship between ornament expression and survival. As pointed out by Jennions et al. (2001), the question of whether sexually selected ornaments generally have positive, neutral, or negative relationships with survival rate is an important issue that will not be solved by single studies. Our study provides a clear case, based on a rigorous survival estimate, of a survival-neutral ornament. Further empirical effort to examine variation of long-lived species' ornaments and their relation to survival rate is required to further test the hypothesis that showy sexually selected displays might predict survival ability. This will require more long-term data sets, such as ours, that span time periods greater than the life span of the study species. Further theoretical development is required to clear up the issue of how ornament-survival relationships (or lack thereof) bear on Fisherian, viability indicator, and other sexual selection mechanisms.

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