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Natural Selection after Severe Winter Favors Larger and Duller Bluebirds

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ABSTRACT: Extreme cold events, which have become more frequent, can revert the direction of long-term responses to climate change. In 2021, record snowstorms swept the United States, causing wildlife die-offs that may have been associated with rapid natural selection. Our objective was to determine whether the snowstorms caused natural selection in Eastern Bluebirds (*Sialia sialis*). To test which mechanism most influenced their survival, we measured the morphology and coloration of fatalities and survivors at three sites. Survival was associated with a longer tarsus and with a wider, longer, and deeper beak, in support of the starvation and thermal endurance hypotheses. Additionally, bluebirds with more-ornamented plumage were less likely to have survived, perhaps because of an early energy investment in mate and site acquisition. As bluebirds encounter increasingly warm summer conditions, the longer extremities favored during the snowstorms may continue to be favored through their thermoregulatory benefits. However, the dull plumage coloration favored by natural selection during the snowstorms may be opposed by sexual selection benefits of more-ornamented plumage. Overall, responses to extreme events are difficult to predict from responses to long-term climate change, and responses to one event, such as the 2021 snowstorms, may not predict responses to a future extreme event.

Keywords: Eastern Bluebirds, extreme weather, ornamentation, morphology, mortality, *Sialia sialis*.

Introduction

Climate models predict an increase in the frequency and intensity of extreme weather events, such as droughts and floods, heat waves and cold snaps, and severe fire seasons (Cohen et al. 2014; IPCC 2018). When such extreme events cause high mortality, there may be strong nonrandom selection for individuals with specific traits (Bumpus 1899; Boag and Grant 1981; Brown and Brown 1998, 1999; Campbell-Staton et al. 2017; Hasegawa and Arai 2017). Conditions during those events can be so intense that they can accelerate or reverse the direction of long-term natural selection (Endler 1986; Bailey and van de Pol 2016; Brown et al. 2018).

Extreme cold conditions not only affect thermoregulatory ability but can lead to food shortages that greatly increase the risk of starvation (Lima 1986; McNamara et al. 2016). To survive such conditions, high fasting endurance and thermal tolerance are crucial. First, individuals with greater energy stores may be less likely to starve (Rogers 1987; Chapman et al. 2011). Furthermore, larger individuals may be able to consume a greater variety of prey sizes (Dickman 1988; Cohen et al. 1993). Finally, a large body confers a thermal endurance advantage in cold conditions (Chapman et al. 2011). Thus, natural selection should favor large-bodied individuals in severely cold weather. Accordingly, after cold events in 1992 and 1996, surviving Barn Swallows (*Hirundo rustica*) and Cliff Swallows (*Petrochelidon pyrrhonota*) tended to have longer culmen and tarsi (i.e., be larger individuals; Brown and Brown 1998, 1999). Although used as indices of skeletal size in these swallow studies, beak and tarsus are also exposed areas with the highest heat exchange in birds (Tattersall et al. 2017). Consequently, smaller extremities might alternatively be advantageous in cold conditions. Accordingly, Silver-throated Tits (*Aegithalos glaucogularis*) that survived harsh winters had smaller beaks (Wang et al. 2023).

Natural selection can also act on sexually selected traits, such as plumage ornamentation in sexually dimorphic species. Energetically expensive, these traits are the product of a trade-off between investment in reproduction and other life history variables like survival (Höglund and Sheldon 1998; Kokko 1998). In normal conditions, sexual selection favors more-ornamented birds that invest more in

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reproduction; in Eastern Bluebirds (*Sialia sialis*), more-ornamented males acquire nest sites and pair earlier than less-ornamented males (Siefferman and Hill 2003, 2005*a*), and more-ornamented females nest earlier (Siefferman and Hill 2005*b*). By contrast, under extreme and unfavorable conditions, high ornamentation can be selected against; in a mass mortality event in Western Bluebirds (*S. mexicanus*), dead males were more ornamented than survivors (Keyser and Siefferman 2005), while an extreme cold event led to reduced survival of more-ornamented male Great Tits (*Parus major*; Moore et al. 2015).

Two snowstorms in February 2021 (Uri on February 12–16 and Viola on February 15–20) swept the United States and set new or near records of snowfall and low temperature in both magnitude and duration (NOAA 2021). For example, cities in Oklahoma neared or broke their records with temperatures at or below −25°C and wind chills as low as −44°C (Oklahoma Climatological Survey 2021) but also with the longest period (7–11 days) below −7°C (Erdman 2021). Across the coastal southern region, temperatures remained below freezing for more than a week (Whaley 2021; table 1). These extreme conditions severely impacted wildlife, including birds (Flesher and Stengle 2021), likely because the conditions exceeded their tolerance for cold temperatures (thermal tolerance) and scarce resources (fasting endurance; Ketterson and Nolan 1976; Chapman et al. 2011). For example, in Cliff Swallows severe weather (i.e., high of <15°C, low of <8°C, and rain) must last at least 4 days to cause mortality (Brown and Brown 1999).

Following the 2021 snowstorms, reports suggested a mass mortality event for Eastern Bluebirds (Flesher and Stengle 2021), which had historically suffered population declines due to severe winter weather (Musselman 1941; James 1962; Pitts 1981; Sauer and Droege 1990). Populations in southern states consist mostly of resident individuals with some partial migrants (Gowaty and Plissner 2020), and winter mortality in resident populations seems strongly correlated with the number of days with subfreezing temperature (Pitts 1981).

In cold conditions, Eastern Bluebirds can lower their body temperature by 5°C–8°C through nocturnal hypothermia (Reinertsen 1996; Ritchison 2000) and roost in cavities, including nest boxes (Thomas 1946; Frazier and Nolan 1959; Pitts 1979), to use 13%–28% less energy (even at −30°C) than if roosting outside (Kendeigh 1961; Cooper 1999). Additionally, Eastern Bluebirds can roost communally in groups of up to 16 individuals (Pitts 1976; Fowler Neal 2014) to increase the temperature within the cavity or nest box and reduce heat transfer to the environment through bodily contact among birds (Du Plessis and Williams 1994). However, when severely cold conditions are long lasting and the scarce resources are buried under a thick layer of snow or ice, these strategies may not be enough to survive, and mortality from hypothermia and starvation increases (Pitts 1978*a*).

By comparing morphological characteristics between nonsurviving and surviving bluebirds, we addressed the following question: Which morphological traits in Eastern Bluebirds were associated with a higher survival probability during the severe winter storms of February 2021? We hypothesized that conditions during a severe winter storm could lead to a microevolutionary change. Specifically, we predicted two alternative scenarios for body size. Following the thermal and fasting endurance hypotheses, these February winter storms should have favored individuals with bigger skeletal size (with beak and tarsus as proxies); or if survival was driven primarily by heat retention, survivors should have had smaller extremities (beak and tarsus) to minimize heat loss. We further expected birds with more-ornamented plumage color to have been disadvantaged from a too-early investment in reproduction to acquire mates and territories. We also measured wing and tail length; symmetry in wing, tail, and tarsus; and coloration metrics of the white belly but predicted no pattern of natural selection on those traits.

Methods

Study Species and Locations

We conducted the project at three sites that were within the path of the February 2021 snowstorms: Jonesboro, Arkansas; Stillwater, Oklahoma; and Oxford, Mississippi.

Table 1: Eastern Bluebird (*Sialia sialis*) fatalities from nest boxes and weather data at three sites during snowstorms Uri and Viola, February 2021

Site	No. monitored nest boxes	No. bluebird fatalities	No. consecutive days less than 0°C/−7°C	Snowfall (cm)
Jonesboro, AR	150	77	11/4.5	27.9
Oxford, MS	218	69	8/1	14
Stillwater, OK	106	17	12/5	19.3

Note: Weather data were obtained from the National Climatic Center Data.

At all sites, Eastern Bluebirds have been banded and their nests monitored in 106–218 nest boxes since 2003, 2009, and 2017, respectively. Nest boxes are placed on metal poles, 100 m apart, in a linear or grid-like fashion (when not constrained by private landowners or habitat). Depending on the site, nest boxes are located in a combination of walking trails, roadsides, areas with short grass (e.g., private mowed yards, golf course, city park), grassland, hay fields, and pastures, interspersed with mixed coniferous-deciduous forest lots.

Within a season, between late March and August, Eastern Bluebirds typically have up to three successful clutches of up to six eggs each, and both parents are involved in parental care (Gowaty and Plissner 2020). The Eastern Bluebird is a migratory species, but their migratory behavior depends on the climate at their nesting grounds. In Stillwater, the average maximum temperature in January and February is 3.5°C–5.5°C, with total snowfall averaging 7.3 cm (range: 0–19.0 cm), between 2003 and 2020. The Stillwater bluebird population is made of partial migrants; a band recovery indicates that some overwinter in Texas, but the proportion of migrants is unknown. In Jonesboro, the average maximum temperature is 4°C–5.9°C, with an average snowfall of 6.7 cm (range: 0–32.5 cm), in January and February. In Oxford, the average maximum temperature is 5.7°C–7.7°C, with an average snowfall of 4.3 cm (range: 0–32 cm), in January and February. Bluebirds of the Jonesboro and Oxford populations are mostly year-round residents, although a few partial migrants cannot be excluded.

During the nesting season, Eastern Bluebirds are mostly insectivorous (Beal 1915; Pinkowski 1978; Pitts 1978*b*). Between late summer and early spring, they may still feed on arthropods, but they also eat berries (e.g., sumac, mulberry; Pinkowski 1977; Pitts 1978*b*). In snow or ice conditions, both prey and berries become inaccessible (Pitts 1978*a*).

Eastern Bluebirds are sexually dichromatic: males display bright ultraviolet (UV) blue color on most of their bodies and have chestnut breast and white belly plumage. Females are duller overall. The UV-blue and white coloration is structural (Shawkey et al. 2003), whereas the chestnut coloration is melanin based (McGraw et al. 2004). Plumage coloration is likely a sexually selected trait in Eastern Bluebirds; birds with more colorful blue coloration achieve higher reproductive success (Siefferman and Hill 2003, 2005*a*) and tend to be in better body condition (Grindstaff et al. 2012). Their breast coloration may also respond to sexual selection (Siefferman and Hill 2003; but see Grindstaff et al. 2012). Bluebirds experience trade-offs between producing colorful plumage and investing energy in other energetically expensive life history traits. Siefferman and Hill (2005*b*) increased the cost of reproduction, which caused a reduction in blue color in the following breeding season. To date, no study has tested whether white color is sexually selected.

Field Procedures

At all sites, we checked all nest boxes for dead bluebirds between the last week of February and the first week of March 2021. We collected up to 77 specimens at a given site (table 1). All specimens were rolled into a piece of paper towel and placed into resealable plastic bags that we stored in a −20°C freezer on return to the laboratory. Later, from late March to early August 2021, we captured adults 1–3 days following hatching using the trap design by Robinson et al. (2004).

For both dead (after they had completely thawed) and live (in the field) individuals, we recorded band number and color band combination, nest box and date of capture, age, and sex. In addition, with a wing ruler we measured wing chord (left and right) and tail length (left and right outer tail feather) as well as the middle-right tail feather (±1 mm). With a caliper we also measured tarsus length (left and right) and beak width, depth, and length (±0.01 mm). We did not use body mass because dead individuals had already started degrading when we collected them.

From both dead and live individuals, we collected the right outer tail feather in addition to eight feathers from each of the following regions: chestnut breast, white belly, and blue rump. We taped region-specific feathers from each individual together in an overlapping fashion to a piece of black cardboard. Using an Ocean Optics S2000 reflectance spectrophotometer (Dunedin, FL), we quantified plumage coloration as the proportion of the total reflectance of Ocean Optics W-1 white standard measured before and after each feather sample. We took five readings from each sample, and each reading was an average of 20 reflectance curves for each body region. We then averaged the five readings from each body region of each individual (for more details, see Keyser and Siefferman 2005). From reflectance data, we calculated (1) brightness (total amount of light reflected by the feather) as the summed reflectance from 300 to 700 nm (for overall reflectance of each body region); (2) UV chroma (measure of spectral purity for blue rump and tail feathers) as the ratio of the total reflectance in the UV range to the total reflectance of the entire spectrum ($\int 300–400/\int 300–700$); (3) red chroma (for chestnut breast feathers) as the ratio of the total reflectance in the red range to the total reflectance of the entire spectrum ($\int 645–700/\int 300–700$); and (4) hue (for blue rump and tail feathers) as the wavelength at peak reflectance using the R package pavo (Maia 2013). For UV-blue plumage, more-ornamented birds have greater brightness, greater

UV chroma, and hues with shorter wavelengths (Siefferman and Hill 2003). For the chestnut breast coloration, more-ornamented birds have darker (lower brightness) and redder (greater red chroma) breasts (Siefferman and Hill 2003). A more-ornamented belly would have greater brightness (Doucet et al. 2005).

At a given site, a single trained individual (i.e., V. Rolland in Arkansas, J. L. Grindstaff in Oklahoma, and S. L. Balenger in Mississippi) took the measurements the same way and with the same set of tools for all birds (dead and alive) to avoid interobserver variability and minimize intraobserver variability at a site. Although repeating the measurements on live individuals was not feasible, measurements were taken two to three times on the dead specimens. Additionally, not all monitored sites around Oxford yielded survivors. Therefore, for comparison purposes, we included dead specimens only from sites where we also had survivors, leading to a reduction in sample size from 69 to 36 nonsurvivors for Oxford.

This study was conducted under state scientific collection permits (011420203 and 1221120211 for Arkansas; 4116217, W2312, and 2210 for Oklahoma; 0507191 for Mississippi) and with the approval of the Institutional Animal Care and Use Committee of Arkansas State University (FY17-18-484 and FY20-21-268), Oklahoma State University (OSU AS-18-2 and IACUC-21-18), and Mississippi State University (18-015). All authors own a banding permit with an authorization to collect feathers and were permitted to access landowners' properties.

Data Analyses

For each of our study sites, we calculated decline rates as the number of birds captured, recaptured, or resighted during the 2021 nesting season divided by the number of birds captured, recaptured, or resighted during the 2019 and 2020 nesting seasons (if available). For reference, we also calculated state-level decline rates using 2019 and 2021 point count data from the Breeding Bird Survey (https://www.pwrc.usgs.gov/BBS/PublicDataInterface/index.cfm) for three states within and three states outside the path of the 2021 snowstorms.

In addition to the morphometrics recorded directly on the birds, we derived an asymmetry score (i.e., absolute difference between left and right) from the bilateral measurements (e.g., right and left wing chord; Brown and Brown 1998). We also derived beak volume and surface area from depth, width, and length, using volume and surface area formulas for an elliptic cone.

We performed four analyses, all of them in R statistical software (R Core Team 2022). Data and scripts for all analyses are shared in a data repository (https://doi.org/10.5061/dryad.2ngf1vhwh). First, we assessed repeatability of the original morphometrics recorded on dead individuals using Nakagawa and Schielzeth's (2010) function from the rptR package (Stoffel et al. 2017) with 1,000 bootstraps. We used bird ID as a grouping (random) effect, and a Gaussian distribution was the most appropriate for our measurement data. The repeatability index ranges from 0 to 1 and is assessed at $\alpha = .05$, with a significant index representing a repeatable variable. All measurements were highly repeatable; the repeatability index for two asymmetry variables was <0.5 but still indicated repeatability ($P < .001$; table S1; tables S1–S6 are available online).

Second, to visually assess patterns of natural selection in the distribution of morphology and coloration between bluebirds that died versus those that survived, we performed two principal component analyses (PCAs), one on standardized morphological measurements and the other on standardized plumage coloration measures. We used the packages FactoMineR (Lê et al. 2008) and factoextra (Kassambara and Mundt 2020). For the morphological measurements, we included averages and asymmetry scores rather than the original side-specific variables. For both PCAs, more than three principal components (PCs) were needed to meet any of the common stopping rules (i.e., latent root, scree plot, broken stick, and relative percent variance; McGarigal et al. 2000; Husson et al. 2017), but we could easily interpret only the first two. The first two PCs accounted for 49% of the variation in the morphological measurements and for 57% of the variation in the coloration measures.

Third, to determine whether natural selection acted on bluebird morphology and plumage coloration, we built generalized linear mixed models (GLMMs) with a binomial error distribution, using the lme4 package (Bates et al. 2015). The dependent variable was survival (yes or no). To avoid multicollinearity issues resulting from strong correlations among the original variables (tables S2, S3), fixed effects were the two morphology PCs or the two coloration PCs; morphology and coloration were analyzed separately because the datasets differed in sample sizes. We also used sex as a fixed effect. We created five types of models: PC alone, PC with an additive effect of sex, PC with an interaction effect of sex, both PCs (additive), and both PCs with an additive effect of sex. One random effect was site ID to avoid confounding effects of interobserver variability and other site differences. Another random effect was whether a bird was newly captured or recaptured so as to further reflect potential interpopulation differences; new captures likely represent immigrants (through dispersal), although some birds already in the population may have nested in nearby natural cavities and been missed in the previous season. Although populations consist of both nest box and natural cavity nesters, we cannot determine whether an unbanded individual was born in a natural cavity of the population or immigrated into the population. Similarly, although mostly composed of year-round resident individuals, populations at the three sites include an unknown proportion of seasonal migrants. However, a study on the closely related Western Bluebird indicated that body size does not differ between residents and migrants (Dale et al. 2019). Assuming that Eastern Bluebirds follow similar migratory patterns in populations of partial migrants, the inclusion of partial migrants likely does not bias our analyses.

For both morphology and coloration, we selected the best model using an information-theoretic approach based on the Akaike information criterion (AIC) corrected for small sample size (AICc; Burnham and Anderson 2002). The best model was the model with the lowest AICc, but if two models were equivalent (i.e., $\Delta\text{AICc} \leq 2$), we applied the principle of parsimony and retained the model with the fewest parameters (Burnham and Anderson 2002). Furthermore, considering the PC in the selected model, we built post hoc models containing each original (morphology or coloration) variable with which the selected PC was highly correlated ($|\text{loading}| > 0.5$). From these post hoc models, we extracted slope estimates ($\beta \pm 1$ SE) to provide a more straightforward interpretation.

Last, to better characterize selection, we analyzed selection differentials (total selection on a trait) and selection coefficients, also called selection gradients (selection on a trait independent of other traits), using standardized morphology and coloration variables (Brodie et al. 1995). Following Endler (1986) for selection differentials, we calculated i as a measure of directional selection and j as a measure of stabilizing ($j < 0$) or disruptive ($j > 0$) selection, using survivors and nonsurvivors as the group before selection and survivors only as the group after selection. However, we compared the survivors (selected) to the nonsurvivors (unselected) for a more sensitive test (Endler 1986; Brown and Brown 1998), using a two-independent-sample t-test if normality and variance assumptions were met or a Wilcoxon rank sum test if normality was violated.

For selection coefficients, we estimated i^* (also commonly denoted β), the coefficient of directional selection, and j^* (also commonly denoted γ), the coefficient of variance (stabilizing or disruptive) selection (Lande and Arnold 1983) from GLMMs using the lme4 package (Bates et al. 2015). GLMMs were built with a binomial error distribution for the response variable, which was the relative fitness defined as 1 for survivors and 0 for nonsurvivors. For morphology, we extracted the coefficients i^* from a GLMM that included all traits except beak surface area and volume because these variables were derived from the combination of the other beak measurements, creating complete collinearity. For coloration, we used two GLMMs to circumvent model convergence issues: one GLMM with belly and breast variables, the other with rump and tail variables. The coefficients j^* were the quadratic coefficients from the same GLMMs in which we also included a nonlinear term for each test trait X as $X = (X - \bar{X})^2$ (Endler 1986). Finally, the random factors were site ID and whether the bird was newly captured or recaptured. For both selection differentials and selection coefficients, P values were evaluated at $\alpha = .05$; $\alpha = .0042$ was used for morphology and $\alpha = .0056$ was used for coloration after Bonferroni correction.

Results

Although other cavity nesters (e.g., Carolina Chickadees *Poecile carolinensis*) use nest boxes, we found fatalities only among bluebirds. We recovered 17–77 fatalities per site (table 1), alone or in groups of up to 16 birds in one nest box. Among the 130 fatalities we measured, 57% were females. Only 6 birds in Oklahoma, 33 in Arkansas, and 42 in Mississippi nested in 2021. The number of adults, combining new and recaptured individuals, declined by 87% from 2020 to 2021, or 81%–92% from 2019 to 2021 at the studied populations, corresponding to the state-level decline of up to 62%–87% recorded by the Breeding Bird Survey from 2019 to 2021 (table S4).

Selection on Morphology

The first morphology PC (hereafter, "beak PC"), which increased with beak and tarsus measurements, discriminated survivors with positive scores from dead individuals with negative scores (fig. 1). Loadings were highest for beak volume (0.97), beak surface area (0.87), beak depth (0.76), beak width (0.71), and beak length (0.67), followed by tarsus length (0.53). The second morphology PC (hereafter, "wing PC"), which increased with wing and tail measurements, did not discriminate survivors from dead birds. Loadings were highest for outer tail feather length (0.85), wing chord (0.83), and middle tail feather length (0.76).

In morphological models of survival, random effects of state and recapture status were important (table S5). The model with the wing PC did not perform better than the null model (table S6). The best model included a positive effect of beak PC ($\beta = 1.19 \pm 0.21$; table S6) without a sex effect, suggesting that survival was higher for males and females with overall greater beak and tarsus measurements. The post hoc models specifically indicated that bluebirds were more likely to survive the snowstorms if their beak was deeper ($\beta = 8.03 \pm 1.32$), wider ($\beta = 4.32 \pm 0.94$), and longer ($\beta = 1.26 \pm 0.47$), thus having larger surface area ($\beta = 0.06 \pm 0.01$) and volume ($\beta = 0.07 \pm 0.01$; fig. 2), as well as longer tarsus ($\beta = 1.11 \pm 0.32$; fig. 2). Mean beak depth, width, length, surface area,

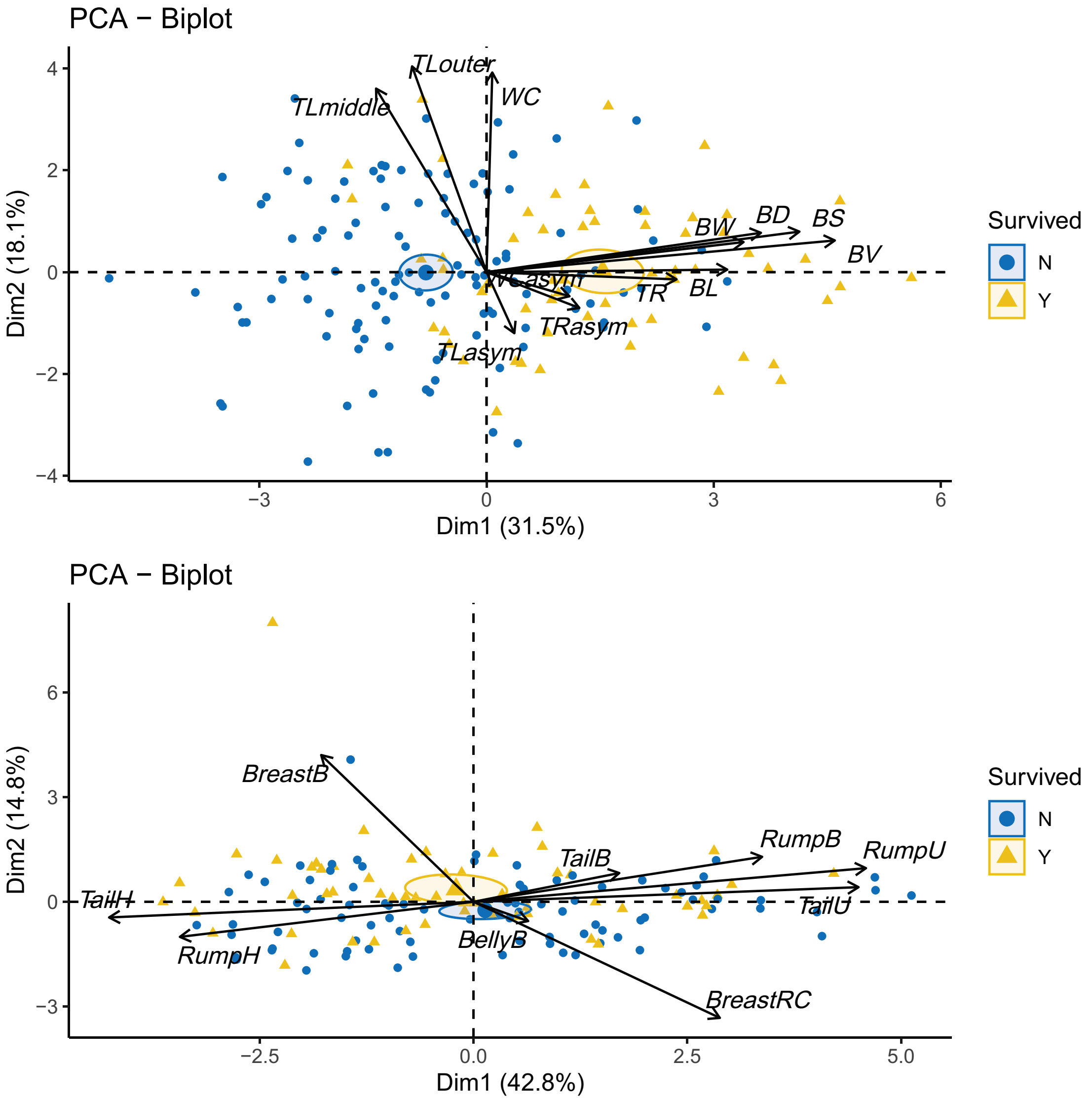

Figure 1: Principal component analyses (PCAs) of morphological characteristics (*top*) and plumage coloration (*bottom*) in Eastern Bluebirds (*Sialia sialis*) that did (Y) or did not (N) survive the February 2021 snowstorm in Jonesboro (Arkansas), Oxford (Mississippi), and Stillwater (Oklahoma). Confidence ellipses are indicated for individuals that died versus those that survived; their centers represent average morphology and plumage coloration. Variables were wing chord (WC), tail feather length (TL), tarsus length (TR), and beak width (BW); depth (BD), length (BL), surface area (BS), and volume (BV); breast brightness (BreastB) and red chroma (BreastRC); belly brightness (BellyB), rump brightness (RumpB), hue (RumpH), and UV chroma (RumpU); and tail brightness (TailB), hue (TailU), and UV chroma (TailU).

and volume increased by 4%, 3%, 2%, 5.6%, and 9.5%, respectively, whereas tarsus length increased by 1.6%.

The selection differentials and coefficients corroborated these patterns. We detected directional selection for the same six beak measurements as well as for tarsus length, although the variance was not reduced (table 2, pt. A). Coefficients (selection once correlations are removed) suggested that selection acted only on tarsus length and beak depth (table 2, pt. A). We also found disruptive selection for wing asymmetry, but the selection coefficient analysis provided no evidence that this selection was strong (table 2, pt. A).

Selection on Plumage Ornamentation

The first coloration PC (hereafter, "blue PC"), which decreased with tail and rump hue but increased with their brightness and UV chroma, attributed a slightly lower

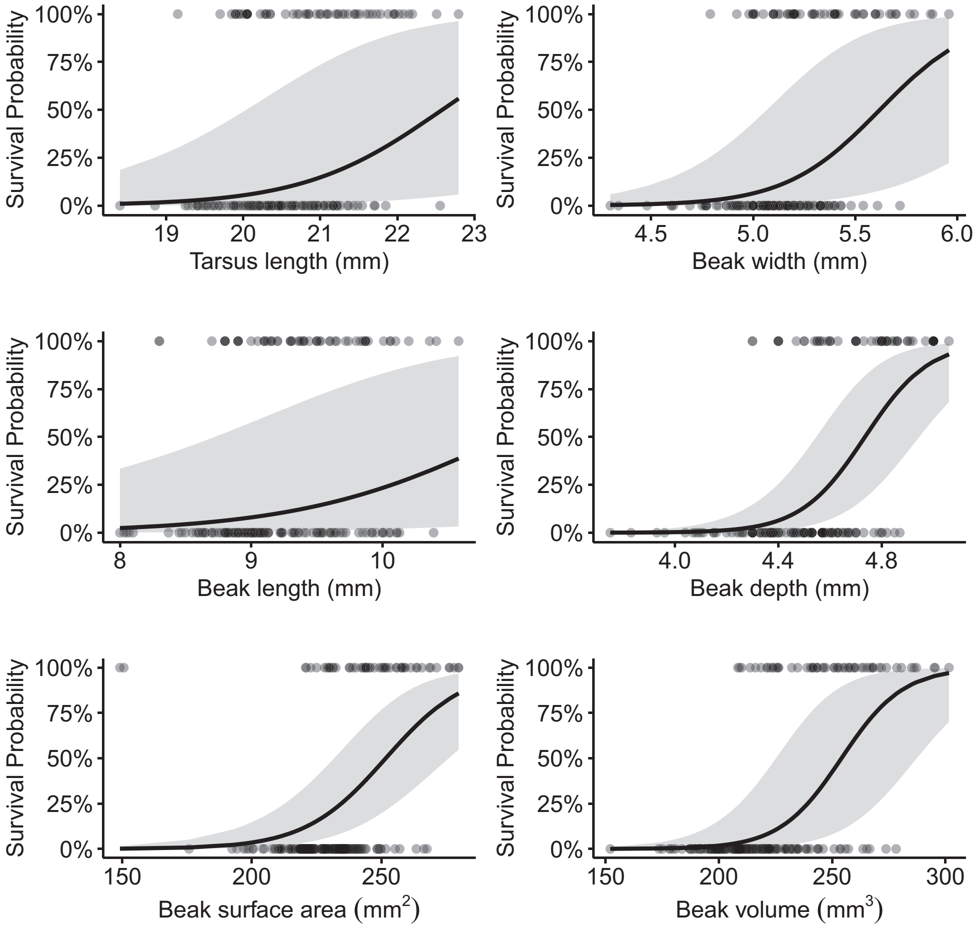

Figure 2: Observed (points) and predicted (line) survival probability of Eastern Bluebirds (*Sialia sialis*), based on tarsus length and beak dimensions ($n = 175$ birds), during the 2021 February snowstorm in Jonesboro (Arkansas), Oxford (Mississippi), and Stillwater (Oklahoma). The shaded area represents the 95% confidence interval around the predicted line from the generalized mixed models of survival with a given morphological variable as a fixed effect and with state and whether a bird was recaptured as random effects.

score to survivors than to dead birds. Loadings were highest for rump UV chroma (0.91), tail UV chroma (0.90), tail hue (−0.84), rump hue (−0.68), and rump brightness (0.67). The second coloration PC (hereafter, "inverse chestnut PC"), which decreased with breast red chroma but increased with breast brightness, discriminated survivors with a higher score from dead individuals with a lower score (fig. 1). Loadings were highest for breast brightness (0.84) and breast red chroma (−0.66).

In coloration models of survival, random effects of state and recapture status were important (table S5). The model with the blue PC and the null model performed equally (table S6). The most parsimonious model included a positive effect of the inverse chestnut PC ($\beta = 0.48 \pm 0.21$; table S6) without an effect of sex, suggesting that survival was higher for both males and females with a less-ornamented chestnut coloration. The post hoc models specifically indicated that survival probability during the snowstorm increased with breast brightness ($\beta = 0.17 \pm 0.06$) and decreased with breast red chroma ($\beta = -13.86 \pm 5.27$; fig. 3).

The selection differentials or coefficients also revealed patterns of selection for breast brightness and tail UV chroma but not for breast red chroma. Selection was directional on breast brightness but not strong—partial selection was not significant (table 2, pt. B). Tail UV chroma seemed under strong selection, but the selection differential analysis did not detect it as significant (table 2, pt. B).

Discussion

Mass mortality events can be associated with rapid natural selection (Bumpus 1899; Boag and Grant 1981; Brown and Brown 1998, 1999; Campbell-Staton et al. 2017; Hasegawa and Arai 2017). Extreme weather, including severe winters,

Table 2: Selection differentials and coefficients for Eastern Bluebirds selected during the two 2021 severe snowstorms in Arkansas, Oklahoma, and Mississippi

Trait	i	P^a	j	P^b	i^*	P^c	j^*	P^c
A. Morphological traits ($n = 175$ birds)								
Wing chord	.007	.950	−.21	.148	.121	.746	.150	.612
Outer tail length	−.244	.019	−.09	.657	−.526	.193	.250	.378
Middle tail length	−.120	.254	.275	.070	.300	.398	.168	.537
Tarsus length	**.438**	**<.001**	.171	.054	**1.154**	**.001**	.154	.578
Wing asymmetry	.127	.994	**.456**	**<.001**	.056	.840	.676	.012
Tail asymmetry	.164	.060	.115	.215	.384	.133	.032	.777
Tarsus asymmetry	.195	.180	.364	.443	−.035	.913	−.173	.394
Beak length	**.365**	**<.001**	−.092	.860	.325	.371	−.264	.297
Beak depth	**.775**	**<.001**	−.367	.008	**1.934**	**<.001**	.636	.039
Beak width	**.596**	**<.001**	−.054	.128	.845	.010	−.222	.535
Beak volume	**.785**	**<.001**	−.292	.773	...	...	...	...
Beak surface area	**.619**	**<.001**	.270	.013	...	...	...	...
B. Coloration traits ($n = 145$ birds)								
Belly brightness	.263	.009	−.207	.428	.437	.050	.070	.689
Breast brightness	**.370**	**<.001**	.438	.349	.641	.163	−.097	.223
Breast red chroma	−.187	.066	.129	.308	−.193	.563	−.011	.947
Rump brightness	.163	.042	−.199	.077	.317	.287	−.141	.424
Rump hue	.014	.798	−.299	.014	.144	.668	−.203	.439
Rump UV	−.007	.948	−.116	.316	.545	.312	−.204	.553
Tail brightness	.013	.898	−.230	.097	.151	.518	−.593	.010
Tail hue	.124	.302	−.009	.602	−.614	.178	.190	.564
Tail UV	−.210	.038	−.086	.668	**−1.751**	**.001**	.191	.390

Note: Standardized directional (i) and variance (j) selection differentials capture total selection on a trait, whereas selection coefficients (i^* and j^*) represent selection on a trait independent of selection on other, correlated traits. Directional (i^*) and variance (j^*) selection coefficients were estimated from linear and quadratic partial regression coefficients, respectively. Coefficients j and j^* indicate stabilizing or disruptive selection if they are negative or positive, respectively. Boldfaced coefficients are significantly selected at $\alpha = .0042$ and .0056 for morphological and plumage coloration traits, respectively, after Bonferroni correction. UV = ultraviolet.

[a] P values are from a two-independent-sample t-test or Wilcoxon rank sum test, depending on the normality of the samples.

[b] P values are from a variance test or Mood's test, depending on the normality of the samples.

[c] P values are from a generalized linear mixed model of survival with state and recapture status (yes or no) as random effects.

can cause high mortality of birds (Robbins et al. 1986; Sauer et al. 1996), including bluebirds (up to 78% regionally between 1976 and 1978; Pitts 1978*a*, 1981; Pinkowski 1979). All three study populations experienced drastic declines in breeding bluebirds locally (81%–92% decline) and at the state level (62%–97% decline) during the spring of 2021. During these weeks, the central southern region of the United States experienced extreme snowfall and low temperatures, in both magnitude and duration. This was the fourth most severe winter in all metrics (Bolinger et al. 2022), with new records in some metrics (Earley 2021; Erdman 2021). Notably, the maximum temperature remained below freezing for 8–12 consecutive days at all sites. Such a prolonged period of extreme cold likely exceeded many of the birds' fasting endurance and/or their ability to maintain homeostasis, resulting in high mortality (Pitts 1978*a*, 1981). By sampling across three sites impacted by the storms, we found phenotypic differences between the birds that died and survived the inclement weather, suggesting natural selection. Male and female bluebirds that survived the storm had longer tarsi, larger beaks, and less-ornamented plumage coloration.

Selection on Morphology

Our data are consistent with predictions of the fasting endurance hypothesis that larger individuals can store more fat reserves and endure longer periods of fasting, assuming that bluebirds with longer tarsi and larger beaks also had a greater body mass. Although we did not have body mass data for our study period, studies report body size as positively correlated with tarsus length (Siefferman et al. 2006) and beak depth (Grant 1991). Chapman et al. (2011) hypothesized that fasting endurance ability explains why some birds remain on the breeding grounds during the winter.

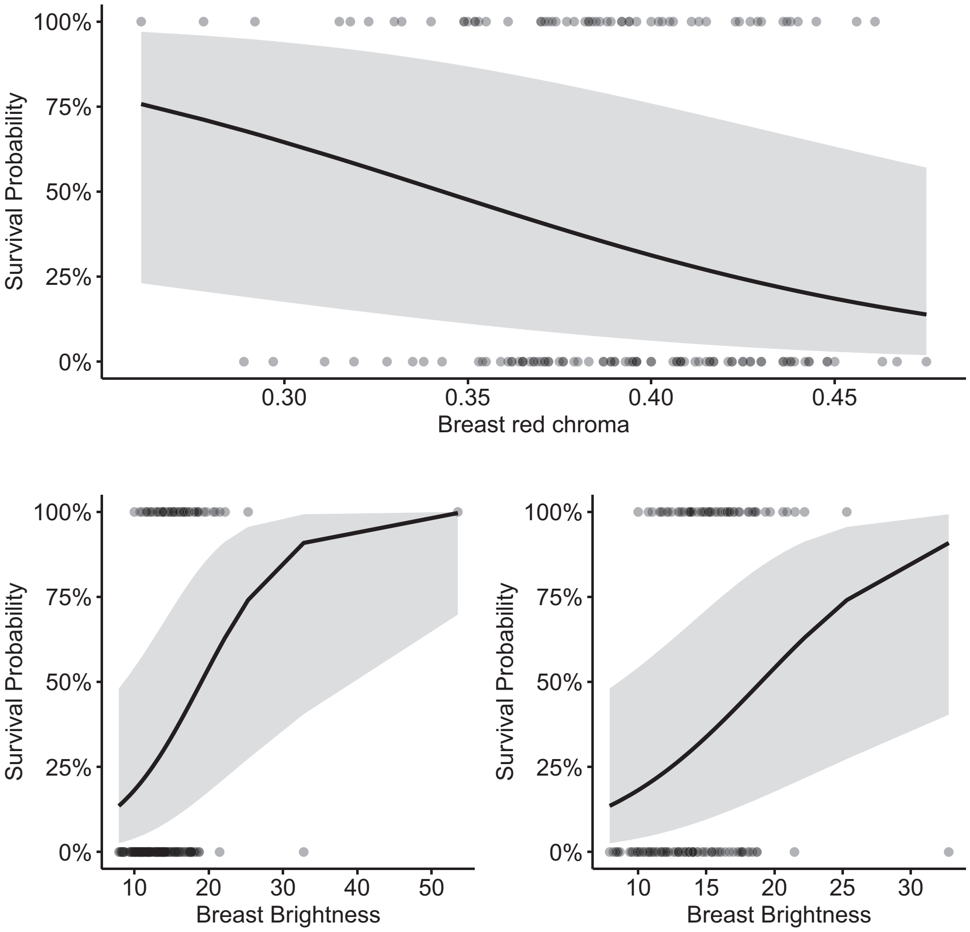

Figure 3: Observed (points) and predicted (line) sex-specific survival probability of Eastern Bluebirds (*Sialia sialis*), based on plumage coloration variables ($n = 145$ birds), during the 2021 February snowstorm in Jonesboro (Arkansas) and Oxford (Mississippi). The shaded area represents the 95% confidence interval around the predicted line from the generalized mixed models of survival with an additive effect of sex and a given color variable and with state and whether a bird was recaptured as random effects.

With the same assumption that beak and tarsus lengths are measures of skeletal body size, our data also support the thermal endurance hypothesis that a larger body size is more advantageous in cold weather because the smaller surface area–to–volume ratio helps conserve body heat and avoid hypothermia (Chapman et al. 2011). Accordingly, the Vinous-throated Parrotbill's (*Sinosuthora webbiana*) culmen and tarsus lengths and beak volume increased as the minimum temperature of the coolest month decreased (Lee et al. 2021). This larger-body advantage also explained the longer beaks in Cliff and Barn Swallows that survived a cold spell (Brown and Brown 1998, 1999). Similarly, if individuals with larger beaks and longer tarsi also had larger pectoralis muscles, they would have benefitted from improved shivering endurance because muscle mass, especially pectoralis muscle mass, is positively associated with summit metabolism (a measure of maximal shivering thermogenic capacity; Swanson et al. 2013; Petit and Vezina 2014). By contrast, our data appear inconsistent with the hypothesis that thermoregulation in cold conditions is aided by smaller extremities (e.g., legs). Although individuals with shorter beaks lose heat to the environment less readily (e.g., Friedman et al. 2017), animals, including birds, can constrict blood vessels in their extremities (Scholander 1955; McQueen et al. 2023) and adjust their posture to minimize heat loss. Birds with long legs tend to bring one or the other into their belly plumage, whereas those with long bills may tuck it into their back plumage (Pavlovic et al. 2019).

Forces other than thermoregulation may also have driven selection. Although speculative, bluebirds with longer tarsi and/or larger beaks might have had a foraging advantage during the 2021 snowstorm. Snow (1954) showed that morphology associated with feeding and movement efficiency can override thermal constraints. Moreover, foraging ability influences the evolution of beak morphology (Grant 1979; Boag and Grant 1981). Bigger beaks (and associated greater bite force) allow birds to feed on a wider variety of food items (Grant 1979; Lefebvre et al. 2017) and to forage more efficiently (i.e., larger items in less time; Snow 1954). Notably, the selection we documented on beak depth was equivalent to the previously documented selection on beak depth in Medium Ground Finches (*Geospiza fortis*; Grant 1991). Although bluebirds can switch from insects to fleshy fruit on colder days (Pinkowski 1977; Pitts 1978*a*), these fruits are difficult to access in snow or ice conditions. Thus, perhaps bluebirds with a larger beak were better able to access new foods. Similarly, longer tarsi might have helped them forage in snow or on new substrate. For example, Blue Tits (*Parus caeruleus*) with longer tarsi tend to forage while hanging, while those with shorter legs tend to forage while standing (Carrascal et al. 1994).

Selection on Plumage Ornamentation

As predicted, male and female bluebirds that survived the storms displayed less-ornamented plumage (i.e., lighter chestnut breasts and less blue tails) than those that died. These data are consistent with the assumption that energetically expensive sexually selected traits are the product of a life history trade-off between reproductive and somatic investment (Höglund and Sheldon 1998; Kokko 1998). We argue that these unpredictable back-to-back winter storms disproportionately challenged the more highly ornamented birds after they had allocated energy toward an early start to reproduction acquiring mates and territories. Bluebirds mate assortatively for blue tail coloration, and in both sexes bluer birds nest earlier and achieve greater reproductive success (Siefferman and Hill 2003, 2005*c*; Grindstaff et al. 2012).

Our results for melanin-based breast coloration mirror those in Western Bluebirds, in which males that survived an epidemic were duller than nonsurvivors (Keyser and Siefferman 2005). Whether the melanin-based chestnut coloration is sexually selected in bluebirds is not as clear as the blue structurally based coloration. Siefferman and Hill (2003) found that males that achieved higher reproductive success in an Alabama population displayed more-ornamented breast coloration, whereas Grindstaff et al. (2012) did not find this relationship in our Oklahoma study population. Similarly, breast coloration of females was not related to body condition or reproductive success (at least in the metrics tested) in Alabama (Siefferman and Hill 2005*a*), but females with less colorful breasts had higher fledging success in Oklahoma (Grindstaff et al. 2012). Similar trends between sexually selected plumage coloration and survival in the face of unpredictable and extreme events have been documented in other species (Van Oort and Dawson 2005; Moore et al. 2015).

Neither brightness of the white plumage on the belly nor body symmetry differed between bluebirds that died and survived the winter storms. Whether sexual selection has shaped the brightness of the white belly coloration and body symmetry of bluebirds has not yet been studied. In fact, such traits allow us to contrast the strength of natural selection for traits that are currently under directional sexual selection versus those that are likely not. Our results differ from those of Brown and Brown (1998, 1999), who found that aerial-foraging swallows with greater tail symmetry were more likely to survive a cold spell in the 1990s. But tail symmetry may be less important to ground-foraging bluebirds. Sexual selection could also drive tail asymmetry in swallow species (Møller and De Lope 1994; but see Safran and McGraw 2004). Finally, low repeatability (although significant) in asymmetry parameters may have prevented us from detecting a difference (Brown and Brown 1998).

Implications

Overall, although the avian beak is a site of constant heat loss (McQueen et al. 2023), bluebirds with larger beaks and longer tarsi were selected during the 2021 winter storms in the southeastern United States. Similarly, Dark-eyed Juncos (*Junco hyemalis*) have beaks with larger surface area at greater relative temperature extremes, such as in unusually cold years in regions with warm climates (LaBarbera et al. 2020). We speculate that the winter storms favored bluebirds with these traits because of the synergistic effects of greater fat reserves, increased shivering thermogenesis, improved foraging abilities, and more favorable surface area–to–volume ratios.

After catastrophic events such as extreme weather or epidemics, newly selected phenotypes, including the deeper beaks observed here, may persist in populations for several years (Brown and Brown 2011). Studying persistence, however, requires recapture of the survivors' descendants, which can be challenging after a population bottleneck. Additionally, recapture rates of second-year birds are typically low (up to 13%; Gowaty and Plissner 2020)—only five offspring born in 2021 were recaptured as adults in 2022 at the Arkansas site.

In the long term, in increasingly warmer summer conditions (IPCC 2018), we might anticipate that deeper beaks and longer tarsi could persist because of thermoregulatory advantages through heat dissipation (McQueen et al. 2023). In Cliff Swallows, tarsus length and bill dimensions were consistently linked with fitness for many years after a severe spring storm (Brown et al. 2013). However, selection on tarsus length in response to a subsequent spring storm was in the opposite direction than in the initial 1996 event

(Brown et al. 2018). Therefore, not only may the response to extreme events be difficult to predict from the response to longer-term climate change, but responses to one event may not predict responses to a subsequent event. This is also true for responses of plumage ornamentation traits, in which interactions between natural and sexual selection may be critical in determining the overall response to selection during extreme events. Extreme winter weather events have increased in frequency in northern temperate regions since the 1990s (Cohen et al. 2014; IPCC 2018). If natural selection favoring duller plumage in extreme winter weather acts against sexual selection favoring brighter and more vivid plumage in normal weather conditions, the expression of plumage ornamentation traits may stabilize.

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Statement of Authorship

All authors conceived the study. V.R., S.L.B., and J.L.G. collected the data, whereas L.S. analyzed the feathers. V.R. obtained funding, curated the data, performed all the data analyses, and wrote the first draft. V.R., J.L.G., and L.S. contributed significantly to the writing and editing of the manuscript.

Data and Code Availability

Data files and R code to reproduce the figures and the results presented in text and tables in this article have been archived in the Dryad Digital Repository (https://doi.org/10.5061/dryad.2ngf1vhwh; Rolland et al. 2024) and Zenodo (https://doi.org/10.5281/zenodo.10329630).

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