Changing patterns of natural selection on morphology of Cliff Swallows during severe weather

Author(s): Charles R. Brown, Mary Bomberger Brown, Stacey L. Hannebaum, Patricia K. Hosack, Abigail J. Kucera, Catherine E. Page, Stephanie A. Strickler, and Gigi S. Wagnon

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Charles R. Brown,[1]* Mary Bomberger Brown,[1,2] Stacey L. Hannebaum,[1] Patricia K. Hosack,[1] Abigail J. Kucera,[1] Catherine E. Page,[1] Stephanie A. Strickler,[1,3] and Gigi S. Wagnon[1]

ABSTRACT—Extreme climatic events can often lead to intense selection and serve as catalysts for rapid evolutionary change. Cold and rainy weather during a 6-day period in spring 1996 led to massive mortality of Cliff Swallows (*Petrochelidon pyrrhonota*) in western Nebraska and selected for birds with shorter wings and tails, larger skeletal traits, lower levels of fluctuating asymmetry, and less phenotypic variance in all traits. Here we investigate whether the same patterns of selection occurred during 2 subsequent cold and rainy weather events in this population in 2004 and 2017. Directional selection on morphological traits in 2004 was generally the same as in 1996, but in 2017 selection on tarsus length and outer tail feather length was in the opposite direction. As in 1996, selection during both events reduced phenotypic variance in most traits. The results illustrate the potential for extreme weather events to act as drivers for fluctuating directional selection on morphological traits and for periodically removing phenotypic outliers. *Received 27 September 2017. Accepted 24 June 2018.*

Patrones cambiantes de selección natural en la morfología de la golondrina *Petrochelidon pyrrhonota* durante eventos climáticos severos

RESUMEN (Spanish)—A menudo, los eventos climáticos severos conllevan una selección intensa y pueden servir como catalizadores de rápido cambio evolutivo. El tiempo frío y lluvioso durante un periodo de 6 días en 1996 provocó una mortandad masiva de la golondrina *Petrochelidon pyrrhonota* en el occidente de Nebraska, y seleccionó aves con alas y colas más cortas, características esqueléticas más grandes, menores niveles de asimetría fluctuante y menor simetría fenotípica en todas sus características. Aquí investigamos si los mismos patrones de selección ocurrieron en dos eventos subsecuentes de tiempo severo en 2004 y 2017. La selección direccional de características morfológicas en 2004 fue generalmente la misma que en 1996, pero en 2017 la selección en la longitud del tarso y la longitud de la pluma caudal exterior fue en la dirección contraria. Como en 1996, la selección durante ambos eventos redujo la varianza fenotípica en la mayoría de las características. Los resultados ilustran el potencial de los eventos extremos del tiempo para actuar como operadores de selección direccional fluctuante en características morfológicas y para la remoción periódica de fenotipos atípicos.

Unusual weather events can serve as catalysts for rapid evolutionary change by causing nonrandom mortality and preferentially favoring individuals with certain characteristics (Endler 1986, Grant and Grant 2002, Brown and Brown 2011, Campbell-Staton et al. 2017, Grant et al. 2017). In birds, rapid change in traits such as bill dimensions or overall body size (Bumpus 1899; Grant and Grant 1993; Brown and Brown 1998, 1999; Acquarone et al. 2004; Clark 2009) has been documented during extreme weather (e.g., storms), with a population sometimes showing dramatic morphological differences after selection. Most such selection events, however, occur rarely and

unpredictably, and thus field studies are often unable to assess their repeatability or long-term evolutionary impact (Bailey and van de Pol 2016, Altwegg et al. 2017). An exception was Grant and Grant's (2002) study of bill evolution in Darwin's finches, in which relatively sudden climate-driven phenotypic change in one direction was sometimes reversed during later climatic events.

One example of weather-mediated selection on morphology was that of Cliff Swallows (*Petrochelidon pyrrhonota*) during a severe weather event in the western Great Plains (Brown and Brown 1998). During a 6-day period of unusually cold and rainy weather in late spring 1996, >50% of the population perished, and mortality was nonrandom with respect to body size metrics. Birds with shorter wings and tails but larger skeletal dimensions were favored (Brown and Brown 1998). During the subsequent 14 years, the population maintained the same directional trajectories in morphological traits established during

[1] Department of Biological Sciences, University of Tulsa, Tulsa, OK, USA
[2] Current address: School of Natural Resources, University of Nebraska, Lincoln, NE, USA
[3] Current address: Department of Biological Sciences, Murray State University, Murray, KY, USA
* Corresponding author: charles-brown@utulsa.edu

the weather event, suggesting that the 1996 event might have led to a relatively permanent micro-evolutionary change (Brown and Brown 2011, Brown et al. 2013b).

Two additional (although less severe) mortality events driven by cold and rainy weather occurred in this Cliff Swallow population in the 21 years following the 1996 selection episode. Given the potential role of rare climatic events in reversing patterns of directional selection (Gibbs and Grant 1987, Bailey and van de Pol 2016), we investigated whether the post-1996 weather events caused detectable selection on Cliff Swallow morphology and, especially, whether any such selection might have reversed the trait trajectories established by the earlier event. We measured morphology of birds succumbing and of those surviving the severe weather and used a selection gradient analysis to identify which morphological traits were potential targets of selection. We compare the results to the earlier selection event to gain insight into drivers of morphological change in Cliff Swallows and the evolutionary processes that potentially either promote or prevent stasis in these traits over the long term.

Methods

Study animal and study site

Cliff swallows are highly colonial passerines that build gourd-shaped mud nests, often in high density, underneath cliff overhangs or the eaves of bridges and buildings or inside highway culverts throughout much of North America (Brown et al. 2017). The species is highly migratory, arriving in our study area beginning in late April, with most nesting completed by late July. Colonies at most sites are initiated in May and early June. Cliff Swallows winter in southern South America, primarily Argentina. The sexes exhibit little sexual dimorphism in size, although males have a larger patch of blue feathers at the base of the throat (Brown et al. 2017).

Beginning in 1982, we studied Cliff Swallows near the Cedar Point Biological Station (41.2097°N, 101.6480°W) in western Nebraska, USA, along the North and South Platte rivers. The study area includes all of Keith County and portions of Garden, Deuel, Lincoln, and Morrill counties (Brown and Brown 1996). Our work was conducted primarily at Cliff Swallow colonies on highway bridges and box-shaped culverts underneath roads or railroad tracks (Brown et al. 2013a). Colony size varied widely, ranging from 2 to 6,000 nests (mean 404 [SE 13], $n = 2318$ colonies), with some birds also nesting solitarily.

Weather events and field collections

Cliff Swallow mortality during the breeding season occurs during periods of 4 or more consecutive days with daily maximum temperatures ≤ 15 °C, daily minimum temperatures ≤ 8 °C, and rain on most days (Brown and Brown 1998). These conditions so severely reduce activity of flying insects, the birds' exclusive food source (Brown et al. 2017), that individuals starve. Our annual presence in the study area from early May to late July each year allowed us to document that the 2 periods of cold and rainy weather in 2004 and 2017 were the only ones since the 1996 weather event (Brown and Brown 1998) to cause Cliff Swallow mortality.

During 17–20 June 2004, daily temperature ranges were 10–15, 5.5–11.6, 6.6–10.5, and 10.5–12.8 °C (at noon), respectively, daily rainfall was 0–0.35 cm (only one day without rain), and daily maximum wind speeds were 22.5–37 kmph. Foraging conditions were extremely poor for Cliff Swallows until about noon on 20 June. During 17–20 May 2017, daily temperature ranges were 10–18, 7.2–10, 2.8–9.4, and 2.8–8.9 °C, respectively, daily rainfall was 0.33–2.71 cm, and daily maximum wind speeds were 33.6–41.6 kmph. Cliff Swallows foraged for brief periods in the afternoon of 17 May, but conditions largely precluded any foraging during the remaining times on these days.

After the severe weather ended (and the birds resumed foraging), we visited colony sites on the afternoons of 20 June 2004, and 21 May 2017 to collect fatalities. Dead birds were found on the ground underneath nests or floating in water nearby. Fatalities were collected throughout the study area from 8 colonies in 2004 and from 17 colonies in 2017. These sites were assumed to be representative of all of those in the study area and were selected (by us) mostly for their spatial proximity to each other, allowing us to visit them quickly after the bad weather before scavengers had removed most of the carcasses. Quantifying per capita mortality at these sites was impossible

because most colony sizes at the time of the event were unknown. Birds dying inside nests and thus not visible to us were generally not collected, although in 2017 we found 4 such specimens included among the fatalities for that year. All dead birds, unless partially decomposed when collected, were prepared as study skins and deposited in the University of Tulsa bird collection.

As in 1996 (Brown and Brown 1998), birds designated as survivors were those captured in mist nets in the days immediately following the severe weather event. During 21–26 June 2004 we netted adults at 7 colonies, and during 22–28 May 2017 we netted adults at 7 colonies. Some colony sites in each year were ones where we found both fatalities and captured survivors. Using only birds caught in close temporal proximity to the weather event ensured that the individuals included were likely ones that had experienced and survived the event. Birds were captured by dropping mist nets over the top of a bridge to catch adults as they flushed out of nests or by placing stationary nets in front of nests on a bridge or in a highway/railroad culvert. All Cliff Swallows captured in nets were sexed based on the presence of a brood patch or cloacal protuberance and given a USGS band.

Measurements

For both survivors and nonsurvivors, we measured the length of each unflattened, closed wing (from the anterior most part of the wrist joint to the tip of the outermost primary) to the nearest 1 mm with a stoppered wing ruler; the length of the middle tail feather and the outermost tail feather (from their emergence from the skin to the distal most point) on each side to the nearest 1 mm with a ruler; the length of each tarsus (from the proximate end of the tarso-metatarsus to the hallux) to the nearest 0.1 mm with calipers; and the length and width of the exposed bill (length from the proximate end of the exposed culmen to the tip along the upper mandible and width of the exposed mandibles at the nostrils) to the nearest 0.1 mm with calipers. Fluctuating asymmetry in wing and tail length was expressed by the unsigned difference between the right and left wing and between the right and left outermost tail feathers, respectively. Wing length, outer tail length, and tarsus length reflect the mean of the

right and left values for each bird. Further details on measuring birds and statistical descriptors of asymmetry are given in Brown and Brown (1998, 2011) and Brown et al. (2013b).

Survivors were measured in the field at the time of capture. Nonsurvivors of both weather events were measured before preparation as museum skins. One person (MBB) measured all birds in 2004 and another (CRB) measured all birds in 2017. Because of differences in the way different people hold and measure birds (Price and Grant 1984, Bryant and Jones 1995), direct comparison of mean trait values between 2004 and 2017 are not warranted, and thus all analyses were done separately for the 2 weather events. In 2004, we measured 72 nonsurvivors and 127 survivors, and in 2017, we measured 50 nonsurvivors and 105 survivors, although not all traits could be measured for some birds (e.g., because of missing heads or tarsi). Sexes of nonsurvivors were determined by dissection during skinning, but some specimens (especially in 2017) lack sex designations because of partial decomposition.

Selection analyses

To facilitate comparison to the 1996 event, we analyzed selection generally as in Brown and Brown (1998), with the major exception that here we doubled the nonlinear (quadratic) selection coefficients (γ) and their standard errors (Stinchcombe et al. 2008). All trait values were transformed to mean 0 and SD 1, yielding standardized selection differentials and gradients. Linear (directional) selection gradients (β) were determined from the partial regression coefficients of a multiple regression (Lande and Arnold 1983) containing only linear terms, whereas the nonlinear (variance) gradients (γ) were estimated from a quadratic regression that also included the linear terms. Correlational selection gradients consisted of regressions using the linear, quadratic, and all cross-product terms, with the cross-products indicating potential evidence for correlational selection. A potential effect of sex was investigated by including sex as both a main effect and an interaction in both the linear and nonlinear gradients, with significant interaction terms indicating that patterns of selection differed between the sexes. Selection gradients and differentials were calculated using SAS software (SAS Institute

2016). We present significance values for all traits without correction for multiple tests (Rothman 1990, Armstrong 2014) and indicate which traits remained significant at $P = 0.05$ after sequential Holm-Bonferroni corrections.

Results

Linear selection differentials (*i*) during both weather events (Tables 1, 2) indicated evidence of net directional selection on morphological traits of Cliff Swallows; survivors in 2004 had longer tarsi, wider and longer bills, and less wing asymmetry than nonsurvivors, and in 2017 survivors had longer outer tail feathers, shorter tarsi, and less tail asymmetry. In 2004, the linear selection gradient (β) generally indicated that these traits were independent targets of selection (Table 1). In 2017, however, the linear selection gradient indicated significant directional selection for shorter wings and wider bills not apparent from examination of the differentials, and tail asymmetry was not significant in the linear gradient (Table 2). Distributions of actual tarsus lengths overlapped little between nonsurvivors and survivors of each event, although in different directions (Fig. 1).

Nonlinear selection differentials (*j*) for all but one trait in both years were negative, indicating a net reduction in trait variances (Tables 1, 2) and suggesting stabilizing selection on these morphological characters. In 2004, the nonlinear differentials for outer tail length, tarsus length, bill width, and tail asymmetry were significant, as were those for tarsus length and tail asymmetry in 2017. These traits were, for the most part, significant targets of apparent stabilizing selection in the nonlinear selection gradient (γ; Tables 1, 2).

We found no evidence for any correlational selection; no cross-product terms were significant ($P > 0.05$) in the correlational selection gradient for either the 2004 or 2017 weather events (not shown).

In 2004, 47.5% of fatalities were male ($n = 59$; $P = 0.99$, binomial test), whereas in 2017, 75.9% of fatalities were male ($n = 29$; $P = 0.07$). In both the linear and nonlinear analyses, we found no significant interaction terms that included sex (or sex as a main effect) after correcting for multiple comparisons (not shown), and thus regressions without sex were used for estimating the selection gradients (Tables 1, 2).

Discussion

Our main objective was to determine if 2 unusual weather events that followed the intense selection on morphology of Cliff Swallows in 1996 led to the same patterns of natural selection. In both events, selection differentials and gradients were, in general, similar in magnitude to those from 1996 (Brown and Brown 1998), suggesting similar intensities of selection, although the much smaller sample sizes in the latter events yielded less statistical significance. The results of the 2004 event matched generally those seen in 1996, with directional shifts toward less wing asymmetry and larger skeletal measurements and reduced phenotypic variance in all traits. In 2017, however, directional selection on tarsus length was strongly reversed (Fig. 1), favoring shorter tarsi; in addition, some evidence indicated selection for longer outer tail feathers. Along with annual climatic variability (Brown et al. 2013b, Roche et al. 2014), these results implicate severe weather events in spring as a potential driver for opposing selection on morphological traits in this species.

Tarsus length seemed to be the trait under the most intense selection in the 1996 event (Brown and Brown 1998, Price et al. 2000), and based on the differentials and gradients presented here, tarsus was also subject to the strongest selection in both of the subsequent weather events (Fig. 1). In 1996, a 1.5 mm average difference in tarsus length was found between survivors and nonsurvivors (Brown and Brown 1998), and this increase was maintained during the subsequent decade with no evidence of opposing directional selection for smaller tarsi (Brown and Brown 2011). This finding prompted speculation that tarsus length (and other morphometric traits under selection in 1996) had crossed to another fitness peak in the adaptive landscape and were unlikely to return to those seen before 1996. The selection event in 2004 supported that conclusion by reinforcing the patterns observed earlier. However, the 2017 event reversed the trajectory of increasing tarsus size observed since 1996. The mean difference in tarsus length in 2017 was >2 mm, roughly equivalent to the change in 1996 but in the

Table 1. Measurements of morphological traits of Cliff Swallows (sexes combined) succumbing and surviving a 2004 severe weather event in western Nebraska, with standardized directional (i) and nonlinear (j) selection differentials, linear (β) and nonlinear (γ) selection gradients, and significance levels of each ($P < 0.05$ in boldface).

Trait	Dead mean (SE)	Alive mean (SE)	i	i P	j	j P	β	β SE	β P	γ	γ SE	γ P
Wing length	105.53 (0.026)	105.72 (0.19)	0.03314	0.77	−0.01936	0.46	−0.001724	0.02475	0.94	−0.01831	0.02808	0.52
Middle tail	45.61 (0.22)	45.52 (0.16)	−0.01735	0.88	−0.05119	0.39	0.01011	0.02880	0.73	−0.03384	0.03232	0.30
Outer tail	49.93 (0.33)	50.28 (0.17)	0.05596	0.60	**−0.3085**	0.012	−0.02613	0.03818	0.49	0.02332	0.04520	0.60
Tarsus length	10.90 (0.029)	11.57 (0.029)	**0.5435***	<0.0001	**−0.4393***	0.0003	**0.2377***	0.03183	<0.0001	**−0.1367***	0.04546	0.0031
Bill length	7.20 (0.036)	7.60 (0.029)	**0.3446***	0.0021	−0.1784	0.11	−0.01184	0.03032	0.70	0.01506	0.03162	0.63
Bill width	5.85 (0.036)	6.40 (0.027)	**0.4428***	<0.0001	**−0.3902***	0.0015	**0.1581***	0.02875	<0.0001	**−0.1369***	0.03472	0.0001
Wing asymmetry	1.38 (0.12)	0.74 (0.075)	**−0.2430**	0.027	−0.1959	0.09	**−0.06278***	0.02323	0.0076	−0.01129	0.02818	0.69
Tail asymmetry	1.72 (0.56)	0.52 (0.070)	−0.1464	0.11	**−0.9293***	<0.0001	−0.02278	0.03298	0.49	0.02062	0.02438	0.40

* significant at $P < 0.05$ after sequential Holm-Bonferroni correction.

Table 2. Measurements of morphological traits of Cliff Swallows (sexes combined) succumbing and surviving a 2017 severe weather event in western Nebraska, with standardized directional (i) and nonlinear (j) selection differentials, linear (β) and nonlinear (γ) selection gradients, and significance levels of each ($P < 0.05$ in boldface).

Trait	Dead mean (SE)	Alive mean (SE)	i	i P	j	j P	β	β SE	β P	γ	γ SE	γ P
Wing length	108.36 (0.32)	106.88 (0.22)	−0.2048	0.10	−0.08682	0.32	**−0.04084**	0.02000	0.043	0.01836	0.02692	0.50
Middle tail	44.96 (0.32)	45.09 (0.15)	0.02216	0.85	−0.2414	0.06	−0.01038	0.01898	0.58	0.006966	0.01602	0.66
Outer tail	49.23 (0.25)	50.65 (0.16)	**0.2569**	0.037	−0.1786	0.14	**0.04631**	0.02128	0.031	−0.005818	0.01769	0.74
Tarsus length	12.30 (0.091)	10.17 (0.046)	**−0.6075***	<0.0001	**−0.8288***	<0.0001	**−0.3676***	0.02103	<0.0001	**−0.07436**	0.03440	0.032
Bill length	7.21 (0.069)	7.16 (0.050)	−0.03720	0.77	0.03125	0.43	−0.01053	0.01835	0.57	0.006996	0.02422	0.77
Bill width	5.72 (0.060)	6.01 (0.044)	0.2022	0.11	−0.04751	0.40	**0.05614***	0.01898	0.0036	−0.01685	0.02830	0.55
Wing asymmetry	1.07 (0.12)	0.69 (0.075)	−0.1518	0.22	−0.1108	0.26	−0.004470	0.01800	0.80	**0.04934**	0.02416	0.043
Tail asymmetry	2.06 (0.33)	0.78 (0.10)	**−0.2449**	0.028	**−0.5901***	<0.0001	−0.02000	0.01925	0.30	**0.02350**	0.01041	0.026

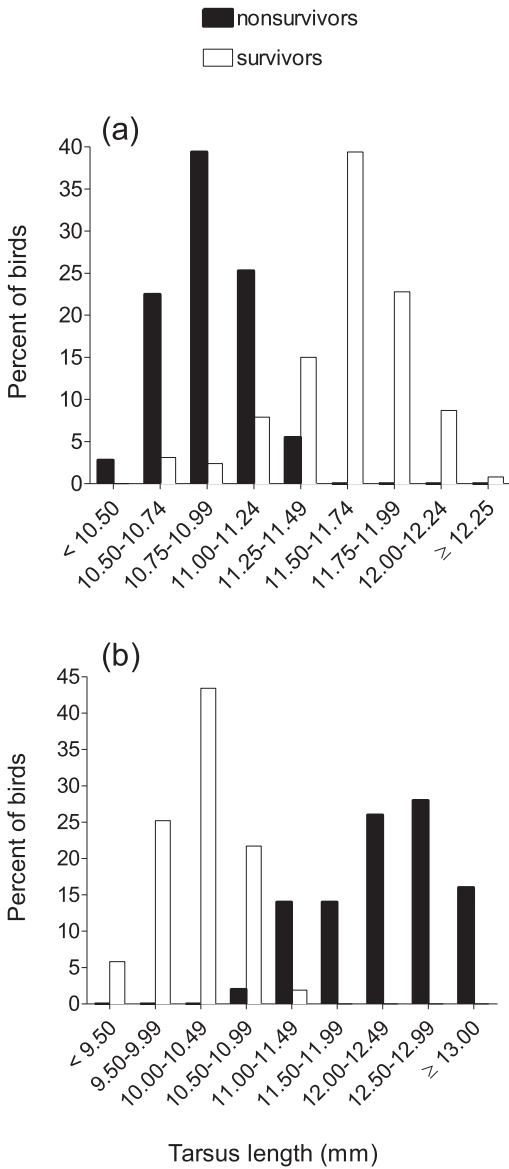* Significant at $P < 0.05$ after sequential Holm-Bonferroni correction.

Figure 1. Percentage distributions of tarsus lengths (mm) for Cliff Swallows that survived (light bars) and did not survive (dark bars) a severe weather event in (a) 2004 and (b) 2017. Sample sizes were 127 and 71 for survivors and nonsurvivors, respectively, in 2004; and 103 and 50 for survivors and nonsurvivors, respectively, in 2017. Significant selection on tarsus length occurred during both events (Tables 1, 2). Actual trait values are not comparable between events because of different measurers.

opposite direction, suggesting that opposing selection can work on this trait. A similar trend was found for outer tail length, which had earlier been under weak negative directional selection (Brown and Brown 1998) but exhibited evidence of positive directional selection in 2017.

Tarsus length was also under apparent stabilizing selection in both 2004 and 2017, with the nonlinear differentials in those years roughly equivalent in magnitude to those seen in 1996. Most traits in these selection events exhibited a reduction in variance following the extreme weather, including many of those showing directional shifts. This stabilization suggests that morphological outliers are at a disadvantage during unusual conditions, even when a trait's average value changes through directional selection.

In 1996, reconstruction of the population before selection suggested a strongly bimodal distribution of tarsus lengths, based on our samples of living and dead birds (Price et al. 2000). This bimodality most likely reflected nonrandom sampling of nonsurvivors, perhaps because only the birds with the smallest tarsi were likely to be found and salvaged. In that event, costs were associated with shorter legs, possibly because such birds were on average smaller and thus competitively inferior and had not secured nesting sites at the time of the weather event. Without a nest in which to shelter, they were more likely to die and be found by us (Price et al. 2000).

We found the same sort of bimodal pattern in tarsus length in both subsequent mortality events (Fig. 1). The interpretation of smaller, competitively inferior birds being less likely to survive without nests seems reasonable for 2004; however, the cause of reversed selection on tarsus length in 2017 is unclear. One possibility is that the birds with the longest tarsi were also at a disadvantage in settling, possibly because the largest body sizes (coupled with shorter wing lengths) may affect average wing-loading, which in turn influences flight efficiency and can result in later spring arrival in other species of swallows (Bowlin and Winkler 2004, Matyjasiak 2013). The largest Cliff Swallows (that thus arrived later) may not have had enough time to have secured ownership of a nest prior to the 2017 weather event and were selected against. Severe weather events could favor, in general, intermediate-sized birds that

can effectively compete for nesting sites while at the same time not arrive too early (and be at a greater risk of experiencing a weather event; Brown and Brown 2000) or too late (and be at a greater risk of not having settled before a late-spring weather event does occur). Regardless of cause, the distribution of tarsus lengths in the 2 events (Fig. 1) seems to offer strong evidence of fluctuating directional selection. We acknowledge, however, that the potential nonrandom sampling of nonsurvivors in 1996 (Price et al. 2000) may have applied in 2004 and 2017 as well.

Wing and tail asymmetry in this study showed the same patterns documented earlier (Brown and Brown 1998), with survivors being less asymmetric, possibly reflecting advantages associated with more efficient foraging, especially in marginal weather conditions (Brown and Brown 1998). In contrast to most other morphological traits, average levels of wing asymmetry in this population have been gradually shifting back to levels found in 1996 (Brown and Brown 2011), suggesting relaxation of selection for reduced wing and/or tail asymmetry in the absence of severe weather. Conclusions about selection on asymmetry must be made with caution, however, given that fluctuating asymmetry may reflect mostly nongenetic individual quality, nutrition, or environmental conditions during molt (Brown and Brown 2002), and given its low heritability (Markow and Clarke 1997, Whitlock and Fowler 1997).

The 2 weather events in this study differed in important ways from that of 1996. Both caused far less mortality than in 1996 when thousands of birds perished, some colonies had 100% mortality, and the population size did not recover for 5 years (Brown et al. 2013a). The mortality in 2004 and 2017 was not high enough to have had any obvious effect on total population size, as assessed by combined active nest counts across all colony sites in the study area later in each summer (Brown et al. 2013a; CRB, unpubl. data). In addition, the 2004 event occurred when many birds were provisioning nestlings, likely presenting a different (or additional) stress. Mortality among nestlings 5–15 days old occurred in 2004, whereas in 1996 few eggs had hatched at the time of the weather event, and many birds had not laid.

We detected evidence for sex-biased mortality in 2017, with a near-preponderance of males succumbing, unlike in 2004 (this study) or in 1996 (CRB and MBB, unpubl. data) when mortality was equal among the sexes. This finding likely reflects the 2017 event occurring earlier in the season than the others, at a time when the population was probably male-biased due to males' arriving earlier than females in general (Brown and Brown 1996). However, this study found no evidence that selection acted differently on morphology of males vs. females, despite average trait values differing slightly between the sexes (Brown et al. 2013b). An effect of sex on selection was not investigated in the 1996 event (Brown and Brown 1998).

Despite their relatively small respective effects on overall population size, these 2 events nevertheless illustrate that unusual weather can affect morphological evolution in Cliff Swallows, and different events may lead to fluctuating (opposing) patterns of directional selection on certain traits. These sorts of events are rare; the 2 documented here bring to 13 the total number (as either directly observed or judged from the climatic record) that have presumably affected Cliff Swallows in our study area in the last 142 years (Brown and Brown 1998). At an average frequency of about one per decade in western Nebraska, severe weather events could be a regular driver of morphological change that periodically adjusts both the mean and variance of trait distributions in Cliff Swallows. Our results add to others that emphasize the potential evolutionary consequences of extreme events (reviewed in Grant et al. 2017). Furthermore, if extreme events such as these increase in frequency, as models of climate change predict (Mitchell et al. 2006, Bailey and van de Pol 2016, Kingsolver and Buckley 2017) and the occurrence in the last 29 years of 5 (38%) of the documented severe weather events (Brown and Brown 1998; this study) might suggest, morphology of Cliff Swallows may show more frequent and perhaps more dramatic directional shifts in the future.

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