

Fluctuating viability selection on morphology of cliff swallows is driven by climate

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Abstract

The extent to which fluctuating selection can maintain evolutionary stasis in most populations remains an unresolved question in evolutionary biology. Climate has been hypothesized to drive reversals in the direction of selection among different time periods and may also be responsible for intense episodic selection caused by rare weather events. We measured viability selection associated with morphological traits in cliff swallows (*Petrochelidon pyrrhonota*) in western Nebraska, USA, over a 14-year period following a rare climatic event. We used mark-recapture to estimate the annual apparent survival of over 26 000 individuals whose wing, tail, tarsus and bill had been measured. The fitness functions associated with tarsus length and bill dimensions fluctuated depending on annual climate conditions on the birds' breeding grounds. The oscillating yearly patterns may have slowed and occasionally reversed directional change in trait trajectories, although there was a trend over time for all traits except tarsus to increase in size. The net positive directional selection on some traits, despite periodic climate-associated fluctuations, suggests that cliff swallow morphology in the population is likely to keep changing and supports recent work contending that selection in general does not fluctuate enough to be an effective driver of stasis.

Introduction

A central problem in evolutionary biology is evaluating the role of fluctuating selection – regular reversals in directional selection that occur across different time periods – in maintaining the evolutionary stasis seen in most populations (Bell, 2010). Although patterns of oscillating selection have been well demonstrated in some taxa (e.g. Price *et al.*, 1984; Hairston & Dillon, 1990; Losos *et al.*, 2006; Carlson *et al.*, 2007), much of the evidence for widespread fluctuating selection (Siepielski *et al.*, 2009; Bell, 2010) is equally consistent with relatively stable directional selection obscured by sampling variance (Kingsolver & Diamond, 2011; Morrissey & Hadfield, 2012). Thus, what prevents continued directional change in many traits believed to be under selection remains unclear in most cases (Merilä *et al.*, 2001; Estes & Arnold, 2007).

Changing climatic conditions have been suggested as a likely cause of potential fluctuating selection in general, and the relatively few studies that have investigated drivers of temporal selection dynamics have identified climate as likely being involved to various degrees (Siepielski *et al.*, 2009). Normal climatic variation can indirectly affect food supply or predation that in turn influences both fecundity and viability in sometimes opposing ways (Price *et al.*, 1984; Hairston & Walton, 1986; Grant & Grant, 1989, 1993, 2002; McAdam & Boutin, 2003; Carroll *et al.*, 2007). In other cases, climatic extremes may directly affect organisms' survival (Bumpus, 1899; Brown & Brown, 1998; McKechnie & Wolf, 2010) and serve as catalysts for evolutionary change through intense episodic viability selection (Grant & Grant, 2002). With global climate change, both the magnitude of climatic variation and the frequency of extreme events are predicted to increase (Easterling *et al.*, 2000; Greenough *et al.*, 2001; Rosenzweig *et al.*, 2001), and thus understanding the effect of climate as a driver of selection becomes especially important.

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Small insectivorous birds are known to be particularly sensitive to variation in climate and thus are good candidates to investigate the dynamics of climatically driven selection. Variation in temperature and moisture affects insect populations that in turn determine survival and fecundity of birds that feed on these insects (Szep, 1995; Cowley & Siriwardena, 2005; Stokke *et al.*, 2005; Robinson *et al.*, 2008). Fluctuating selection driven in part by climate-related changes in food supply occurred in insectivorous bank swallows (*Riparia riparia*), in which directional shifts in body morphology varied in sign at different times (Bryant & Jones, 1995). In addition, unusually cold and wet weather can lead to extensive mortality in insectivorous birds (Anderson, 1965; Löhrl, 1971; Littrell, 1992), and these events can exert strong episodic viability selection on morphology (Bumpus, 1899; Brown & Brown, 1998, 1999c).

Our objective in this study is to examine patterns of viability selection on morphology of cliff swallows (*Petrochelidon pyrrhonota*) and identify whether any directional selection on morphological traits has fluctuated in response to climatic variation. Our work was motivated by the documenting of strong episodic directional selection on morphology of cliff swallows during a rare climatic event in 1996 (Brown & Brown, 1998) and our interest in knowing whether the directional selection occurring then has been reversed, potentially by climatic variation, in years subsequent to this event. A 6-day period of unusually cold and wet weather in late May reduced these birds' food supply to the extent that thousands of individuals starved to death (Brown & Brown, 1998). A comparison of morphological measurements of the birds that died with those that survived revealed strong directional selection on tarsus length, wing length, bill length and bill width; in addition, birds that had arrived earlier in the spring were selected against (Brown & Brown, 1998, 2000). Comparison of historical weather records showed that only two such climatic events have occurred since record-keeping began 135 years ago (Brown & Brown, 1998).

This study uses a data set of over 26 000 individual cliff swallows from 10 yearly cohorts that were measured, banded and subsequently recaptured repeatedly during the 14 years following the climatic event. We employ mark-recapture statistical methodology to estimate apparent survival and study viability selection. Specifically, we investigate whether the directional selection observed during the climatic event has continued and whether the form or magnitude of selection has fluctuated with varying climatic conditions over the subsequent decade and a half.

Materials and Methods

Study site

We have studied cliff swallows since 1982 near the Cedar Point Biological Station (41°13'N, 101°39'W) in

Keith County, southwestern Nebraska, along the North and South Platte rivers; the study area also includes portions of Deuel, Garden and Lincoln counties. Cliff swallows construct gourd-shaped mud nests, often in dense, synchronously breeding colonies. In our study area, the birds nest mostly on the sides of bridges, in box-shaped road culverts or underneath overhangs on the sides of cliffs. The study area contains about 220 colony sites, with about a third not used in a given year. Colony size varies widely; in our study area it ranges from 2 to 6000 nests (mean \pm SE, 404 ± 13 , $n = 2318$ colonies), with some birds nesting solitarily. The study site is described in detail by Brown & Brown (1996). Cliff swallows spend the winter in southern South America (Brown & Brown, 1995), although the wintering range of our specific population is unknown.

Morphological measurements

Beginning in 1997 (the year following the climatic event) and continuing through 2006, birds were systematically measured during the course of a long-term mark-recapture project (Brown & Brown, 2004, 2009; Brown *et al.*, 2007, 2008a,b). All morphological measurements were taken by one person only (MBB), who also measured all birds in the 1996 weather event (Brown & Brown, 1998). For all individuals, the length of each un-flattened, closed wing (from the anterior most part of the wrist joint to the tip of the outermost primary) was measured to the nearest 1 mm with a stoppered wing ruler; the length of the middle-tail feather (from its emergence from the skin to the distal most point) was measured to the nearest 1 mm with a ruler; the length of each tarsus (from the proximate end of the tarso-metatarsus to the hallux) was measured to the nearest 0.1 mm with calipers; 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) was measured to the nearest 0.1 mm with calipers. Right and left wing lengths, and right and left tarsus lengths, were averaged for each bird on each measurement occasion. Repeatabilities of morphological measurements by this measurer (MBB) are given in Brown & Brown (1998) and, in general, were high and statistically significant.

The same birds were often measured on multiple occasions within a year and in different years. Morphological measurements for each trait of an individual were averaged over the occasions on which the bird was captured and measured, and a single value for each trait was used per individual. A total of 26 320 individuals were included in this analysis with annual cohorts (birds first measured that year) of 1289, 1759, 2346, 2519, 2319, 2447, 3621, 4233, 3042 and 2745 in the years 1997–2006 respectively.

Mark-Recapture

Cliff swallows were mist-netted at 27–40 colonies each year of the study. No birds were measured after 2006 but all of those measured from 1997–2006 were followed by recapture through 2010. Most of those measured had completed their lifespan by 2010; of the total birds measured, only 266 (1.0%) were recaptured in 2010. Recaptures from throughout the study area, including at colony sites where birds were not measured, were used in estimating survival, because cliff swallows often move to different colony sites between years. Mist nets were erected across the entrances to culverts or along the sides of bridges; at some sites, we dropped nets from the top of the bridge, catching residents when they flushed from their nests. Netting is described more fully in Brown & Brown (1996, 2004), Brown (1998) and Roche *et al.* (2013). The number of days on which we mist-netted birds at a colony site in a given year varied from 1 to 37, depending on the ease of netting there, the colony size, colony phenology or other considerations. All birds caught were banded with a USGS numbered aluminium leg band (upon first capture) and sexed by the presence of a cloacal protuberance and/or brood patch (Brown & Brown, 1996).

Estimating survival

We made the explicit assumption that annual survival is a reliable surrogate for fitness. This seemed justified for small passerines such as cliff swallows, given that various studies have shown that annual survival is the best single predictor of lifetime reproductive success for birds with lifespans typical of swallows (Clutton-Brock, 1988; Newton, 1989). As in any mark-recapture study of an open population (Lebreton *et al.*, 1992), our survival analyses measured local apparent survival only; permanent emigration from the study area was confounded with mortality. We make the assumption here that the morphological traits measured did not influence permanent emigration in ways that would lead to biased survival estimates for individuals from different parts of a trait's distribution.

Survival analyses were performed with the 14 years of cliff swallow mark-recapture data (1997–2010) using a Cormack-Jolly-Seber recaptures-only model in program RMark (White & Burnham, 1999; Laake *et al.*, 2012). We treated each year as an occasion, for a total of 14 occasions with equal intervals; we represented cliff swallow sex with two groups ($n = 14\ 606$ males, $n = 11\ 714$ females). Our fully parameterized global model consisted of 366 parameters and was structured such that there was a unique parameter for each sex (two sexes) by age (13 ages) by year (13 years) for apparent survival (ϕ) and detection probability (P). We used this model and the median \hat{c} test to calculate the over-dispersion parameter (\hat{c}) for these data ($\hat{c} = 1.19$) and adjusted the Akaike

information criterion values (AIC_c), yielding quasi- AIC_c values corrected for over-dispersion ($QAIC_c$).

We first fit simplified models for detection probability while keeping apparent survival fully parameterized. These models included parameterizations where detection probability (1) was constant across all years, (2) was constant across years and varied by sex, (3) varied by year, (4) followed a log-linear function of age and (5) varied according to an additive parameterization of year with a log-linear function of age. In this analysis, "age" was a relative measure of cliff swallow age, as it represents the number of years that elapsed since a cliff swallow had first entered the capture history (i.e. was initially measured). These sorts of relative measures of age are reliable indicators of actual age (Roche *et al.*, 2013). We compared these models to the global model and used the parameterization of detection probability associated with the lowest $QAIC_c$ to build models with simplified parameterizations of apparent survival. The simplified models for survival included ones where apparent survival (1) was constant across years, (2) was constant across years and varied by sex, (3) varied by year, (4) varied by year and sex, (5) varied by a log-linear function of age and (6) varied according to an additive parameterization of year with a log-linear function of age. We compared these models via $QAIC_c$ and used the best-ranked model to test the relationship of apparent survival to each morphological trait.

We built models for wing length (wing), middle-tail feather length (midtail), tarsus length (tarsus), bill length (billlength) and bill width (billwidth) to test the relationship of these covariates to annual apparent survival. We standardized all covariates to a mean of zero and standard deviation of 1 for all analyses. To infer the potential effect of a morphological trait, we added the morphological trait of interest to a model composed of our top-ranked models for detection (Table 1, model 1) and apparent survival (Table 2, model 34). We built covariate models in which apparent survival followed a linear function, two sex-specific linear functions, a quadratic function and two sex-specific quadratic functions of each covariate. We considered the model with the lowest $QAIC_c$ as best representing the relationship of that morphological measurement to apparent survival.

Estimating selection gradients and differentials

To estimate selection gradients across all years, we built a model with a parameterization for survival in which all potential interactions of morphological measurements were included [$\phi(\text{year} + \text{sex} + \text{wing} + \text{wing}^2 + \text{midtail} + \text{midtail}^2 + \text{billlength} + \text{billlength}^2 + \text{billwidth} + \text{billwidth}^2 + \text{tarsus} + \text{tarsus}^2 + \text{wing}*\text{midtail} + \text{wing}*\text{billlength} + \text{wing}*\text{billwidth} + \text{wing}*\text{tarsus} + \text{midtail}*\text{billlength} + \text{midtail}*\text{billwidth} + \text{midtail}*\text{tarsus} + \text{billlength}*\text{billwidth} + \text{billlength}*\text{tarsus} + \text{billwidth}*\text{tarsus})$, $P(\text{age} + \text{year})$]. However, this model was over-fit, and we used a process of backward model

Table 1 Set of Cormack-Jolly-Seber recaptures-only models for parameterizations of detection probability for cliff swallows in southwestern Nebraska, USA, 1997–2010. For all models, apparent survival was parameterized as ϕ (age*sex*year).

Model: P^*	ΔQAIC_c	w_i	k	QDev.
(1) age + year (QAIC _c = 90943.32)	0.00	0.58	197	2779.89
(2) age + year + sex	0.65	0.42	198	2778.52
(3) age	85.69	0.00	185	2889.77
(4) age*year*sex	147.01	0.00	366	2584.97
(5) sex	298.43	0.00	185	3102.52
(6) .	298.57	0.00	184	3104.67

Parameters with interactions are joined by ''; those having parallel (additive) relationships are joined by '+'; the designation '.' represents a time-constant model; Akaike's Information Criterion (AIC) values were corrected for over-dispersion, yielding quasi-AIC (QAIC_c) values ($\hat{c} = 1.19$). ΔQAIC_c values (the difference between the top-ranked model and all other models in the Table) and model weights (w_i) were used to rank models.

selection to eliminate the unsupported covariates. We began by removing each quadratic term one by one and comparing the resulting models (via QAIC_c) with the original, fully crossed model. If the QAIC_c values resulting from the removal of a quadratic term were lower than the fully crossed model, we interpreted this as evidence that the quadratic term did not explain significant variation and should be permanently eliminated from our parameterization of survival. We created a new model in which only the quadratic terms supported by QAIC_c were included and repeated the same process for the correlational covariates (i.e. covariate₁*covariate₂). From this, we created our finalized selection gradient model by including only the linear, quadratic and correlational (and associated linear) terms supported by QAIC_c. Each of the partial regression coefficients included in the top model were interpreted as selection gradients, a measure of the intensity of selection on a trait of interest while simultaneously controlling for the effect of other traits (Lande & Arnold, 1983). To obtain nonlinear selection gradients, we doubled the estimates of quadratic coefficients and their standard errors (Stinchcombe *et al.*, 2008).

We used an information theoretical approach to ensure that the models whose results we report were fully supported. Thus, we do not present selection coefficients derived from any model if that model was not supported by QAIC_c ranking. When such a model is not supported, the appropriate inference is that the additional covariate terms do not detectably influence survival and thus are equivalent to being "not significant" in the classical frequentist paradigm (Burnham & Anderson, 2002). We did not calculate separate gradients by year, because to do so for a regression model of this size (model 2, Table 2) would have increased the number of starting parameters by approximately 130 and, despite our relatively large sample sizes, would have led to a grossly over-fit model.

Linear (i.e. directional) and nonlinear selection differentials were derived from regression coefficients using the top individual covariate model that included supported linear and quadratic terms for each trait (e.g. for wing, model 3, Table 2). We calculated differentials both for the entire data set and for each year separately. For the yearly calculations, we used the top individual covariate model with a year*trait interaction termed added (these models not shown or ranked in Table 2). Only tarsus had a nonlinear term supported in the top individual model (model 15, Table 2), and thus a nonlinear differential was calculated only for that trait. Because yearly climatic variables (see below) co-varied with year, we removed any climatic variables from the top individual covariate model for calculating a year*trait interaction.

Estimating effects of annual climate

Summer weather conditions in southwestern Nebraska are highly variable; a season that is hot and dry can immediately follow a wet and cold one (Brown & Brown, 1996). Cliff swallows are most affected by temperature and rainfall, with cold and wet conditions reducing the birds' food supply to a level that can impair adult and nestling survival and delay egg-laying, and hot and dry weather leading to explosive population growth of haematophagous ectoparasites that also reduce nesting success (Brown & Brown, 1996, 1999a, b). In assessing whether the relationship between a morphological trait and survival varied depending on climate in given year, we used the US Palmer Drought Severity Index (PDSI) to describe annual climatic conditions. The PDSI is a measure of dryness used by the National Oceanic and Atmospheric Administration (NOAA), and it integrates both local temperature and rainfall data (and other variables) into a single index (e.g. Palmer, 1965; Dai *et al.*, 2004). We used PDSI values calculated by NOAA for Climate Division 7 of Nebraska (corresponding to southwestern Nebraska), averaged for the months of May to July each year, 1997–2010 (available at <http://www.ncdc.noaa.gov/temp-and-precip/time-series/>). We used a single measure for these 3 months as that was the inclusive time period that most cliff swallows were present in our study area. PDSI indices varied from -3.87 (very warm and dry, in 2006) to 7.46 (very cold and wet, in 2010) with 7 years exhibiting a negative PDSI and 7 years a positive PDSI. We make the assumption that climatic conditions in year t , as measured by the PDSI, may affect survival as measured to year $t + 1$.

Each yearly PDSI represented an annual covariate that was added as an interaction term with the morphological trait to the top model in each individual analysis. We standardized all annual PDSI measurements to a mean of zero and standard deviation of 1. Relative to models without PDSI as a covariate, we interpreted a

Table 2 Set of Cormack-Jolly-Seber recaptures-only models used to explore the relationship between apparent survival (ϕ) and morphological traits for cliff swallows banded in southwestern Nebraska, USA, 1997–2010. See text for covariate abbreviations. Model structure refers to that for apparent survival.

	Model: ϕ^*	$\Delta\text{QAIC}_c^\dagger$	w_i^\dagger	k	QDev ‡
	<i>All traits</i>				
(1)	year + sex + wing + midtail + billlength + billwidth + tarsus + tarsus ² + wing*billwidth + midtail*billwidth + billlength*billwidth + billwidth*tarsus + billlength*PDSI + billwidth*PDSI + tarsus*PDSI + tarsus ² *PDSI (QAIC _c = 90025.41)	0.00	1.00	43	89939.33
(2)	year + sex + wing + midtail + billlength + billwidth + tarsus + tarsus ² + wing*billwidth + midtail*billwidth + billlength*billwidth + billwidth*tarsus	323.44	0.00	39	90268.95
	<i>Wing length</i>				
(3)	year + sex + wing (QAIC _c = 90852.99)	0.00	0.43	29	90794.96
(4)	year + sex + wing + wing ²	1.72	0.18	30	90794.68
(5)	year + sex + sex*wing	1.74	0.18	30	90794.70
(6)	year + sex + wing + wing*PDSI	1.98	0.16	30	90794.96
(7)	year + sex + sex*wing + sex*wing ²	4.07	0.05	32	90793.02
(8)	year + sex	19.27	0.00	28	3048.41
	<i>Middle-tail length</i>				
(9)	year + sex + midtail (QAIC _c = 90787.60)	0.00	0.38	29	90729.56
(10)	year + sex + midtail + sex*midtail	0.99	0.23	30	90728.56
(11)	year + sex + midtail + midtail*PDSI	1.16	0.22	30	90728.77
(12)	year + sex + midtail + midtail ²	2.04	0.14	30	90729.60
(13)	year + sex + sex*midtail + sex*midtail ²	5.07	0.03	32	90728.63
(14)	year + sex	84.67	0.00	28	3048.41
	<i>Tarsus length</i>				
(15)	year + sex + tarsus + tarsus ² + tarsus*PDSI + tarsus ² *PDSI (QAIC _c = 90676.09)	0.00	1.00	32	90612.03
(16)	year + sex + tarsus + tarsus ²	41.94	0.00	30	90657.98
(17)	year + sex + sex*tarsus + sex*tarsus ²	43.86	0.00	32	90655.89
(18)	year + sex + sex*tarsus	190.81	0.00	30	90806.84
(19)	year + sex + tarsus	195.94	0.00	29	90813.98
(20)	year + sex	196.20	0.00	28	3048.41
	<i>Bill length</i>				
(21)	year + sex + billlength + billlength*PDSI (QAIC _c = 90445.01)	0.00	1.00	30	90384.97
(22)	year + sex + billlength	208.55	0.00	29	90595.53
(23)	year + sex + sex*billlength	208.76	0.00	30	90593.74
(24)	year + sex + billlength + billlength ²	210.54	0.00	30	90595.52
(25)	year + sex + sex*billlength + sex*billlength ²	212.78	0.00	32	90593.75
(26)	year + sex	427.26	0.00	28	3048.41
	<i>Bill width</i>				
(27)	year + sex + billwidth + billwidth*PDSI (QAIC _c = 90772.90)	0.00	0.87	30	90712.86
(28)	year + sex + billwidth	5.42	0.06	29	90720.28
(29)	year + sex + sex*billwidth	6.12	0.04	30	90718.98
(30)	year + sex + billwidth + billwidth ²	7.48	0.02	30	90720.34
(31)	year + sex + sex*billwidth + sex*billwidth ²	10.11	0.01	32	90718.97
(32)	year + sex	99.37	0.00	28	3048.41
(33)	.	260.68	0.00	15	3335.11

Table 2 (Continued)

	Model: ϕ^*	$\Delta\text{QAIC}_c^\dagger$	w_i^\dagger	k	QDev [‡]
	<i>Basic survival</i> [‡]				
(34)	year + sex (QAIC _c = 90872.27)	0.00	1.00	28	3048.41
(35)	year	25.77	0.00	27	3076.18
(36)	year + age	27.74	0.00	28	3076.15
(37)	age*year*sex	71.05	0.00	197	2779.89
(38)	sex	232.75	0.00	16	3305.19
(39)	age	255.32	0.00	16	3327.76
(40)	.	260.68	0.00	15	3335.11

Parameters with interactions are joined by ''; those having parallel (additive) relationships are joined by '+'; the designation '.' represents a time-constant model; Akaike's Information Criterion (AIC) values were corrected for over-dispersion, yielding quasi-AIC (QAIC_c) values. ΔQAIC_c values (the difference between the top-ranked model and all other models in a subgroup) and model weights (w_i) were used to rank models. For all models other than the fully parameterized global model [$\phi(\text{age}*\text{sex}*\text{year})$, $P(\text{age}*\text{sex}*\text{year})$], detection probability was parameterized as $P(\text{age} + \text{year})$.

[†] ΔQAIC_c , w_i and QDev are presented relative to the top model in each subgroup.

[‡]Used to determine best survival parameterization for models with covariates.

Table 3 Across-years selection differentials and selection gradients (± 1 SE) of morphological traits on annual apparent survival for cliff swallows in southwestern Nebraska, USA, 1997–2010.

Trait	Selection differential (\pm SE)		Selection gradient (\pm SE)		Correlational selection coefficient (\pm SE)		
	Directional	Nonlinear	Directional	Nonlinear	*tarsus	*bill length	*bill width
Wing length	0.047 \pm 0.010						–0.015 \pm 0.012
Tail length	0.094 \pm 0.010		0.085 \pm 0.012				0.015 \pm 0.012
Tarsus length	0.024 \pm 0.010	–0.157 \pm 0.012	–0.022 \pm 0.010	–0.176 \pm 0.012		0.073 \pm 0.011	–0.018 \pm 0.011
Bill length	0.161 \pm 0.011		0.149 \pm 0.012				0.022 \pm 0.011
Bill width	0.105 \pm 0.011		0.067 \pm 0.011				

Selection differentials are taken from regression coefficients for each trait from its top-supported individual covariate model that did not include climate (PDSI; Table 2). The selection gradients are the regression coefficients of the top-supported model using all morphological traits (Table 2, model 2). Significant values ($P < 0.05$) are bolded. Blank entries are for terms not supported in the top models and thus considered nonsignificant.

drop in QAIC_c as evidence that annual weather conditions influence the magnitude and direction of a morphological trait's association with annual survival. To control for the influence of all morphological measurements when interpreting the effect of PDSI, we built a final model with all supported covariates that also included all morphological traits-by-PDSI interactions that were supported in the individual analyses and used this to interpret the overall influence of PDSI on morphology-related survival.

Results

In agreement with previous analyses of this population, the probability of detecting a cliff swallow (effective sample size = 48899) decreased with swallow age following a log-linear relationship ($\beta_{p-\text{Age}} = -0.09$; 95% CI, –0.11 to –0.07) and was variable depending on the year (Table 1, model 1). The mean probability of annual detection was 0.50 (95% CI, 0.48–0.52) for birds after 1 year (i.e. year first measured), 0.46 (95% CI, 0.44–0.48) for birds after 3 years and 0.41 (95% CI,

0.38–0.44) for birds after 5 years. Annual apparent survival of cliff swallows was also variable by year, but on average, male survival (0.69; 95% CI, 0.62 to 0.75) was slightly higher than that for females (0.67; 95% CI, 0.61 to 0.74; $\beta\phi_{\text{-Male}} = 0.06$; 95% CI, 0.02–0.09; Table 2, model 34).

Overall patterns of selection

Annual apparent survival was related to all morphological traits both when these traits were added to models of apparent survival individually and in a combined analysis (Table 2). In general, skeletally larger cliff swallows experienced the highest annual apparent survival rates. Across all years, annual survival of cliff swallows varied little with wing length (Fig. 1a) and increased slightly with increasing mid-tail length (Fig. 1b). Survival varied with tarsus length following a quadratic relationship (Fig. 2a), and increased with increasing bill length (Fig. 2b) and with increasing bill width (Fig. 2c). All five traits exhibited approximately normal distributions when the proportions of birds with

each measurement value were plotted (Figs 1 and 2), although some distributions (bill width, tarsus length) were more leptokurtic, and one (bill length) exhibited platykurtosis. All patterns were the same for males and females, although because trait means tended to differ by sex, an additive effect of sex was supported in all top models. In all survival curves and calculations, we present average values and 95% confidence intervals calculated for both sexes and across all years.

Calculated across all years, linear (directional) selection differentials were significant for all morphological traits and in all cases were positive (Table 3). Nonlinear selection differentials, however, were significant only for tarsus length, again consistent with the observed survival curve (Table 3, Fig. 2a). When taking into account the effect of other morphological traits, all traits except wing length were independently targets of linear (directional) selection, as indicated by these traits' significance in the across-years selection gradient (Table 3). Tarsus length was the only significant target of nonlinear (stabilizing) selection once accounting for the simultaneous effects of other morphological traits (Table 3).

Although several correlational selection coefficients were included in the top-supported gradient model across all years, only two did not overlap zero (Table 3; Fig. 3). Survival was lowest for birds with long tarsi and short bills, while those with short bills and short tarsi were comparatively less disadvantaged. Birds with the shortest tarsi realized essentially no improvement in survival as bill length increased (Fig. 3a). In contrast, birds with the longest tarsi exhibited a 48% increase in annual survival probability (from 0.512 to 0.757) between those with the shortest vs. longest bills (Fig. 3a). Birds with intermediate tarsus lengths, which appeared to have highest survival in the univariate analysis (Fig. 2a), showed a 17% increase in annual survival probability between those with the shortest vs. longest bills (Fig. 3a). Bill length and bill width also exhibited correlational selection (Table 3). As might be expected from the univariate analyses (Fig. 2b, c), those with the longest and widest bills had the highest survival, but short-billed birds realized comparatively little gain as bill widths went from smallest to largest (a 3% increase in annual survival probability), while long-billed birds showed a greater improvement in annual survival (a 10.5% increase) as bill widths went from smallest to largest (Fig. 3b). The correlational selection depicted (Fig. 3) was that for the observed data space of the population, as shown by comparison of actual trait values corresponding with the standardized traits (Fig. 3) to the cumulative distribution of trait values in the population (Fig. 2).

Annual fluctuation in selection

Yearly selection differentials exhibited variation among years (Fig. 4). Wing length showed the least annual var-

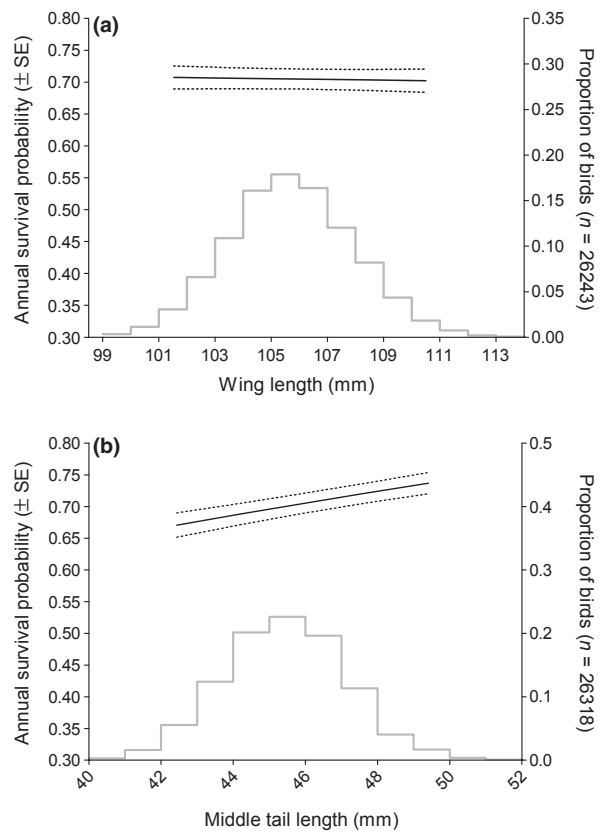


Fig. 1 Annual apparent survival in relation to (a) wing length and (b) middle-tail length for cliff swallows marked and recaptured in southwestern Nebraska, 1997–2010. Survival estimates are from model 2 (Table 2). Dashed lines represent 95% confidence intervals calculated with the delta method using all sex-specific annual estimates from model 2 (Table 2). Histogram represents the proportional distribution of measurements across all birds in the sample. When projecting annual survival estimates for a particular trait size, all other covariates were held at their mean value. Differences in sample sizes reflect individuals that had missing values for some traits.

iation and the least evidence for selection, with the linear differential for only 1 year being significant (as determined by the 95% CI not overlapping zero; Fig. 4a). Middle-tail length, tarsus length and bill length all showed significant linear differentials that were either positive or negative in different years (Fig. 4). Only bill width did not have at least one significant linear differential of each sign (Fig. 4f). The nonlinear selection differentials for tarsus length exhibited both significantly positive and negative values in different years (Fig. 4d). In general, the differentials for the later years of the study (2006 on) were less likely to be significant and exhibited greater sampling variance (Fig. 4), likely because new cohorts of measured birds did not enter the data set after 2006 and patterns for the later years were based on a declining number of surviving

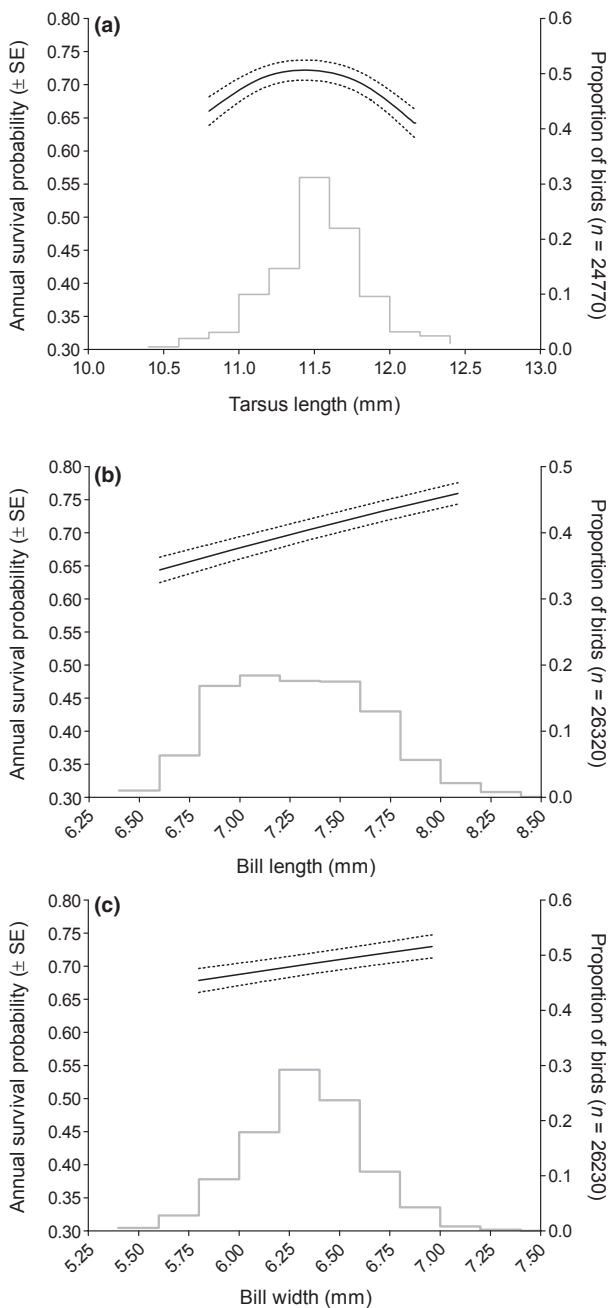


Fig. 2 Annual apparent survival in relation to (a) tarsus length, (b) bill length and (c) bill width for cliff swallows marked and recaptured in southwestern Nebraska, 1997–2010. Survival estimates are from model 2 (Table 2). Dashed lines represent 95% confidence intervals calculated with the delta method using all sex-specific annual estimates from model 2 (Table 2). Histogram represents the proportional distribution of measurements across all birds in the sample. When projecting annual survival estimates for a particular trait size, all other covariates were held at their mean value. Differences in sample sizes reflect individuals that had missing values for some traits.

birds. Differentials were not shown for 2009, because of the confounding of survival and recapture parameters in the final year (2010) of the study.

Selection in relation to climate

We found support for an interaction between PDSI and the three skeletal traits in their effects on survival (tarsus length, bill length and bill width; Table 2, models 15, 21, 27), and when the PDSI interactions were added to the top-supported model (Table 2, model 1 vs model 2), QAIC_c dropped by an additional 323.44. The magnitude of the quadratic relationship between tarsus length and apparent survival was most pronounced in wet years and almost negligible in drought years (Fig. 5a; examples of wet, dry and average years are plotted for comparison; $\beta_{\text{linear}} = 0.06$, 95% CI, 0.00–0.12; $\beta_{\text{nonlinear}} = -0.10$, 95% CI, 0.06–0.14). In wet years increasing bill length was associated with decreasing apparent survival, while in drought years increased bill length was related to increased annual survival (Fig. 5b; $\beta = -0.72$, 95% CI, -0.82 to -0.62). Increasing bill width was associated with increased survival during wet years but decreased annual survival during drought years (Fig. 5c; $\beta = 0.31$, 95% CI, 0.23–0.39). In each case, there was a much weaker relationship between bill morphology and annual survival in climatically normal years (Fig. 5b,c).

Discussion

The most striking result of this study is that cliff swallow annual survival varied with skeletal traits (tarsus, bill) in different ways in different years depending on climatic factors (drought conditions experienced on the breeding grounds), while feather traits (wing, tail length) showed either no or a weak relationship with annual survival regardless of climatic conditions. Despite the fact that viability selection on some traits fluctuated in different directions in some years, bill dimensions and tail length generally showed net positive directional selection overall. Only one trait (tarsus length) seemed to be subject to stabilizing selection across years. All patterns detected here were the same for both sexes, even though trait means tended to differ slightly between males and females (see Brown & Brown, 2011).

Annual climatic effects on morphology-based selection

Climatic events such as the unusual weather experienced in 1996 clearly can have major effects on cliff swallow morphology (Brown & Brown, 1998) and behaviour (Brown & Brown, 2000). However, the analyses here reveal that annual variation in summer climate exclusive of catastrophic mortality events also may affect the pattern of natural selection on morphological

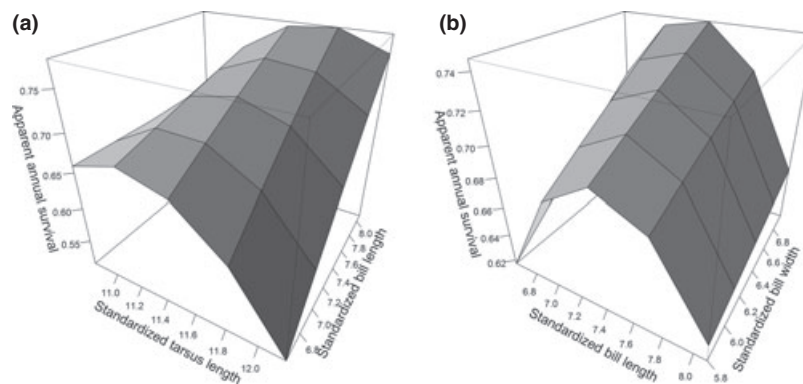


Fig. 3 Correlational plot of annual apparent survival in relation to standardized measures of (a) tarsus length and bill length and (b) bill length and bill width for cliff swallows marked and recaptured in southwestern Nebraska, 1997–2010. Measurements were standardized by subtracting the mean from each and dividing by the standard deviation, with, for example, a standardized measure of -1 being an individual bird with a measurement one standard deviation below the mean. The actual trait values that correspond to standardized values of -2 , -1 , 0 , 1 and 2 are depicted on the axes. When projecting annual survival estimates for a particular trait size, all other covariates were held at their mean value, and all survival estimates were generated from model 2 (Table 2).

traits and in some cases lead to fluctuating selection. We used the annual PDSI as an integrative measure of precipitation and temperature during the breeding season to model how yearly weather conditions may have affected morphology-associated survival. Summer temperature and rainfall exhibit extensive variation across years in our study area (Brown & Brown, 1996) and influence key parameters associated with cliff swallow fitness: time of nesting, ectoparasite load, food supply and eventual nesting success (Brown & Brown, 1999a,b).

Summer climate had a clear effect on survival associated with all three skeletal traits in this study and in unexpected ways. The curvilinear survival function associated with tarsus held in wet years but was weaker in more normal years and virtually vanished in dry years. Bill length and width showed essentially opposite patterns, with survival of long- and narrow-billed birds declining in wet years and that of short- and wide-billed birds declining in dry years. The survival differences both between years and for birds of different morphology within years were in many cases quite extreme and greater than all of the average values estimated for the data set as a whole. Scenarios to explain these patterns are all highly speculative, especially in the absence of data on how flying insect availability varies with seasonal climatic conditions, but the overall conclusion is that morphology-based survival is widely variable from year to year. The representative years depicted in Fig. 5 occurred successively (2005–2007), illustrating dramatic change from year to year in the fitness function associated with these traits. The variation in annual selection differentials (Fig. 4) is also consistent with frequent reversals in the pattern of selection between years.

We do not know why selection favoured bill length and bill width in opposite patterns in wet vs. dry years. The negative directional selection on bill length in wet and cool years was not what was observed during the severe climatic event of 1996: in that intense selection episode, birds with longer bills survived better. Perhaps, the difference is that in unusually severe short-term storms, bill length is simply an index of body size, and bigger birds are favoured because they can store more fat to get through a few days of food scarcity (Brown & Brown, 1998). In contrast, when the entire summer is subject to cool and wet conditions, perhaps annual changes in insect availability favour shorter bills (and the reverse holds in dry summers). The annual differences that suggest fluctuating selection based on climate are consistent with the results on Darwin's finches in which selection was reversed between climatically different years (Grant & Grant, 1989, 1993, 1995, 2002). This sort of fluctuating selection may slow the long-term directional trajectories of these traits, and is the basis for the view that evolutionary stasis can be maintained by opposing patterns of selection (Siepielski *et al.*, 2009; Bell, 2010).

Temperature and rainfall have been shown to have effects on annual survival in other species of swallows (Szep, 1995; Cowley & Siriwardena, 2005; Stokke *et al.*, 2005; Robinson *et al.*, 2008). Generally, this seems to result from changes in insect availability brought on by climatic conditions on either the breeding or wintering grounds that directly influence food resources and thus whether birds can find enough food to survive. These results from other species are thus consistent with ours in showing strong annual differences in survival for aerial insectivores. Only rarely, however, has varying climate-dependent survival been related to morphological traits. In bank swallows, body size (as measured by

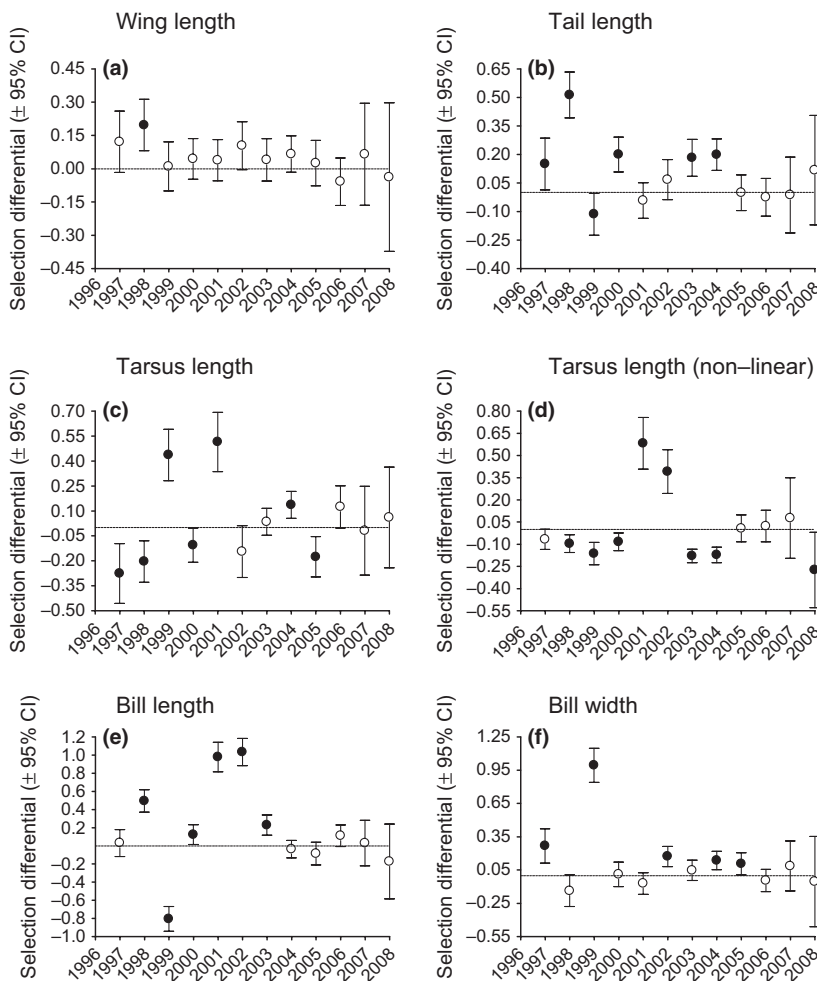


Fig. 4 Selection differentials by year for cliff swallow morphological traits. All those shown are linear differentials except for (d) that depicts the nonlinear selection differential for tarsus. Differentials were generated from the top-supported individual covariate model for each trait, as described in Methods. Differentials are shown with 95% CI; those considered significant ($P < 0.05$) by not overlapping zero (dashed line) are shown by closed circles, those nonsignificant by open circles. To facilitate future meta-analyses, the actual values used to construct this Figure are given in Table S1 (Supplementary Online Material).

keel length) fluctuated over time, with smaller birds favoured during years with extreme drought conditions in the winter (Bryant & Jones, 1995). During more normal years, larger body size was selected for, such that over time body size remained relatively stable. The bank swallow results (Bryant & Jones, 1995) thus support the hypothesis that climatically driven selection can fluctuate in direction between years (sometimes episodically) but maintains evolutionary stasis over the long term.

Net directional changes in morphology

Our analyses indicate that directional change in cliff swallow morphology still appears to be happening despite reversals in selection in some years. This conclusion is strengthened by comparison of trait values, taken each year from yearling birds raised in the study area 1997–2006, which reveal that wing length, bill length and (to a lesser extent) bill width have increased steadily over time to be significantly greater now than

that of the survivors from the 1996 climatic event (Brown & Brown, 2011). Thus, our results support the contention from across studies (Kingsolver & Diamond, 2011; Morrissey & Hadfield, 2012) that, despite occasional reversals, directional selection tends to be relatively consistent in sign over time.

The cause(s) of directional selection on morphology remain unclear. One possibility is that we are observing shifts in morphology that reflect relatively recent changes in the insect taxa on which cliff swallows feed in our study area. For example, changes in prey may now favoured larger billed birds. In insectivorous species, jaw force and the consequent speed of mandible movement increases with both increasing bill width and bill length, meaning that larger billed birds are more efficient at capturing larger and more fast-moving prey (Beecher, 1962; Bock, 1964; Lederer, 1975). Although we lack long-term data on the cliff swallow's diet in the study area, a relatively recent increase in larger insects could select for larger bill dimensions as we observed. Changes in insect populations are possible

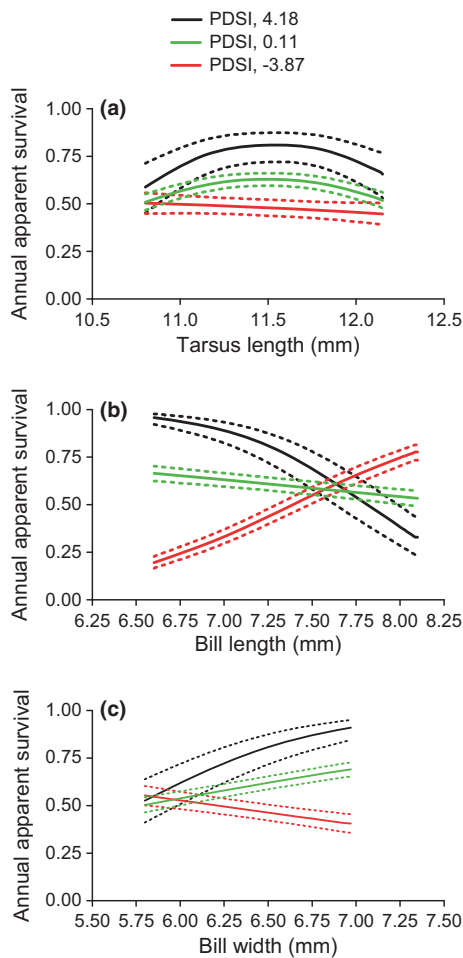


Fig. 5 Annual apparent survival in relation to (a) tarsus length, (b) bill length and (c) bill width for cliff swallows marked and recaptured in southwestern Nebraska under variable annual weather conditions as measured by the Palmer Drought Severity Index (PDSI). A representative wet year (2007) had a PDSI of 4.18, a normal year (2005), 0.11 and a dry year (2006), -3.87 . Survival estimates are from model 1 (Table 2). When projecting annual survival estimates for a particular trait size, all other covariates were held at their mean value. Dashed lines represent 95% confidence intervals calculated with the delta method using all sex-specific estimates from model 1 (Table 2).

in response to recent modifications in land use in southwestern Nebraska, which involve primarily the conversion of grasslands to corn (*Zea mays*) cultivation. Many different insect taxa are associated with corn (Steffey *et al.*, 1999), and at least some of these have likely increased (and others that occur in grasslands, have decreased) as potential cliff swallow prey in recent years.

Another possibility is that larger bills afford competitive advantages to cliff swallows in their efforts to take over existing nests or settle in the best places early in the spring. These birds fight extensively for old nests

and for certain sites within a colony (Brown & Brown, 1996), and gaining access to a nest for shelter from periodic spells of poor weather (Brown & Brown, 2000) could be reflected in annual survival. Increases in cliff swallow population size in the study area that began in the 1980s (Brown & Brown, unpublished data) may be favouring larger billed birds via advantages in competing for nesting sites within colonies.

Some evidence indicated correlational viability selection on combinations of bill length and width. Birds with shorter bills realized comparatively little advantage with increases in bill width, while selection was stronger on bill width among those with longer bills. In the absence of a longer bill, increased width may not improve jaw force or mandible mobility to the extent that it confers an advantage in prey capture. On the other hand, although not necessarily reflected in annual survival, wider bills should increase the ability to transfer parasitic eggs among nests (Brown & Brown, 1988), and if wider billed birds are more successful brood parasites, we might expect to see wider billed birds increase in the population (Brown & Brown, 2011). Whatever the advantages of wider gape, apparently these are less for shorter billed birds.

Nonlinear selection on tarsus

Across years, we detected evidence for relatively strong stabilizing selection on tarsus length, with the selection differential and selection gradient for tarsus being the only ones where the nonlinear component was supported by QAIC_c. However, only in some years was there evidence for strong stabilizing selection on tarsus; the nonlinear selection differential did not differ significantly from zero in some years and was positive in 2 years (Fig. 4). Selection on tarsus seems to move in opposite directions in different years but seems to stay generally in what Estes & Arnold (2007) term “an adaptive zone with stable boundaries.” The two consecutive years with positive nonlinear selection on tarsus (Fig. 4d) may have reflected correlational selection between tarsus and bill length (see below), as the 2 years with the increased phenotypic variance (2001, 2002) were the same year where positive directional selection on bill length was most intense (Fig. 4e).

Overall, our analyses here show the average tarsus length of the cliff swallow population following the 1996 climatic event, about 11.5 mm, has remained the value where associated survival is the highest and continues to be the most common tarsus size in the population. Trait trajectories based on yearling birds born in the study area have shown virtually no change in the years following the climatic event (Brown & Brown, 2011). Thus, the rapid evolution of longer tarsi for the population, as precipitated by the weather event, has not been reversed in the subsequent years. Our guess is that the tarsus itself is an index of skeletal size and that

selection works primarily on total size (e.g. ability to store body mass; Covas *et al.*, 2002); why a given leg length *per se* should be subject to such strong stabilizing selection in cliff swallows remains unclear. In general, overall body size seems to be the life-history trait most often subject to stabilizing selection (Kingsolver & Diamond, 2011).

The significant correlational selection on tarsus length and bill length suggests an asymmetric relationship between these traits in how they affect cliff swallows' annual survival. The longest-legged birds with short bills fared the worst by far, whereas the shorter legged birds (that did better than the longest-legged birds) realized little advantage associated with longer bills. Thus, the curvilinear fitness function of tarsus length is skewed towards longer tarsi for birds with longer bills and towards shorter tarsi for birds with shorter bills. If bill length *per se* continues to be subject to directional selection, we might predict that longer bills will "pull" the optimal tarsus length larger and lead to observed increases in tarsus length in the future. Selection may have worked in this way during the climatic event, although the change in tarsus length was so extreme that any correlational selection with bill length is probably not the only explanation (Price *et al.*, 2000). That tarsus length has not increased since the weather event, despite continued directional selection on bill length, suggests that other factors are also in play. There may be allometric consequences of having mismatched appendage sizes that are worse in one direction (long legs, short bill) than the other (short legs, long bill).

Conclusions

Patterns of morphology-based viability selection in this population of cliff swallows showed annual variation, fluctuating largely in response to climatic conditions. Despite these changes among years, however, overall there was a trend over time for most traits to increase in size. The patterns of selection for some traits were consistent with those documented during the rare climatic event (Brown & Brown, 1998). In no case has any trait moved back towards its mean before the episodic selection event. In particular, the continued directional selection on bill dimensions documented here suggests that cliff swallow morphology in the population may continue to shift and could be exacerbated by global climate change, particularly if the magnitude of annual climatic variation increases. Our study indicates that net directional selection on morphology has occurred despite fluctuating climate-related reversals in some years.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Values of yearly selection differentials and their standard errors (SE) for morphological traits in a study of viability selection in cliff swallows.

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