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The Effect of Weather on Morphometric Traits of Juvenile Cliff Swallows

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ABSTRACT Episodes of food deprivation may change how nestling birds allocate energy to the growth of skeletal and feather morphological traits during development. Cliff swallows (*Petrochelidon pyrrhonota*) are colonial, insectivorous birds that regularly experience brief periods of severe weather-induced food deprivation during the nesting season which may affect offspring development. We investigated how annual variation in timing of rearing and weather were associated with length of wing and tail, skeletal traits, and body mass in juvenile cliff swallows reared in southwestern Nebraska during 2001–2006. As predicted under conditions of food deprivation, nestling skeletal and feather measurements were generally smaller in cooler years. However, variability explained by weather was small, suggesting that morphometric traits of juvenile cliff swallows were not highly sensitive to weather conditions experienced during this study. Measurements of juvenile morphological traits were positively correlated with measurements taken as adults, meaning that any variation among juveniles in response to rearing conditions showed evidence of persisting into a bird's first breeding season. Our results show that body size in this species is phenotypically plastic and influenced, in part, by weather variables.

KEY WORDS cliff swallow, morphology, *Petrochelidon pyrrhonota*, precipitation, temperature, weather

Inclement weather can reduce food abundance or curtail foraging activities, which may ultimately result in periods of food deprivation for breeding birds in temperate latitudes. Reductions in food availability occur regularly for aerial insectivorous species that depend on flying insects that are not active in cold or rainy weather (e.g., Löhrl 1971, Murphy 1983, Blancher and Robertson 1987, Brown and Brown 1996, McCarty and Winkler 1999). In response to periods of food deprivation, nestling birds might be expected to allocate energy differently among skeletal traits, wing and tail feathers, and fat deposition (e.g., Congdon 1990, Ashton and Armstrong 2002, Dahdul and Horn 2003, Bize et al. 2006). The nature of these tradeoffs among morphological traits varies across species, presumably reflecting differences in ecology and life histories (Dow and Gill 1984, Boag 1987, van Heezik 1990, Negro et al. 1994, Lepczyk and Karasov 2000).

Swallows are aerial insectivores that exhibit relatively long nestling periods and are particularly sensitive to periodic disruptions in food availability caused by unfavorable weather conditions (e.g., Stewart 1972*a,* Bryant 1975, Brown 1976, Hoogland and Sherman 1976, Brown and Brown 1996). This species nests synchronously in colonies, with most egg-laying at a given colony site occurring within a 10–14 day period, even at the largest colonies (Brown and Brown 1996). Birds arrive in the study area in late April and lay eggs primarily from mid-May to early June. Most birds fledge between late June and mid-July, and birds have mostly departed on migration by late July. The sexes do not differ in body size, and juvenile cliff swallows (*Petrochelidon pyrrhonota*) are easily distinguished from adults (Stoddard and Beecher 1983, Brown and Brown 1995, Johnson and Freedberg 2013). Upon fledging, many juvenile cliff swallows spend several days near their natal colony site, often entering other nests in the colony in apparent attempts to steal food from parents of smaller nestlings (Brown and Brown 1996).

Unusually cold or rainy weather can lead to widespread mortality of both adult and nestling birds, but less dramatic climatic variation also can influence many aspects of these birds' reproductive biology, likely through daily fluctuations in flying insect abundance (Bryant 1975, 1978, Turner 1983, Brown and Brown 1999*a*, *b*). We examined how annual variation in juvenile cliff swallow morphological traits is related to annual weather conditions. The same traits in adults were previously shown to be targets of intense natural selection during periods of food deprivation (Brown and Brown 1998, 2011).

We assumed that annual variation in temperature and precipitation affected flying insect prey upon which cliff swallows rely (e.g., Williams 1961, Taylor 1963, Johnson 1969). Summers with lower mean temperatures and higher precipitation reflect more days with conditions marginal for cliff swallow foraging, and thus in those years we assumed less food was available during brood rearing (Brown and Brown 1999*a*, *b*). Our objective was to evaluate whether foraging conditions experienced during brood rearing are reflected in juvenile morphology. We examined how patterns in skeletal trait measurements, wing and tail length, and body mass for juveniles varied with regard to measures of weather.

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STUDY AREA

Data collection occurred in June and July, 2001–2006 near the Cedar Point Biological Station (41º 13' N, 101º 39' W). Our study area was situated along the North and South Platte rivers in southwestern Nebraska and includes parts of Keith, Deuel, Garden, Lincoln, and Morrill counties (Fig. 1). Historically, cliff swallows built their nests on the sides of cliffs, but most birds in the study area now place their nests underneath road bridges or inside box-shaped highway or railroad culverts (Brown and Brown 1996). The size of nesting colonies varied within and between years; the mean colony size was 405 nests (SE ± 14; N = 2,209 colonies, over 30 years), with some colonies as large as 6,000 nests and other birds nesting as solitary pairs (Brown et al. 2013). Our study area is described in greater detail by Brown and Brown (1996).

This study took place over years that exhibited May–July temperatures representative of the 30-year average. Overall, the years of the study were relatively similar in terms of temperature and precipitation levels, with only 2004 containing enough "severe weather days" (Table 1) that adult and nestling mortality was observed in the field (C. Brown and M. Brown, unpublished data). To put this in context, a major adult mortality event in 1996 consisted of 6 consecutive severe weather days (Brown and Brown 1998), while the greatest number of consecutive severe weather days observed in this study was 4 during the 2004 season.

METHODS

Capture and Banding

We captured and banded juvenile cliff swallows as part of a long term mark-recapture project, in which we rotated among different colony sites throughout the nesting season (Brown and Brown 1996, 2004, 2009). We placed mist nets across the entrances of culverts or along the sides of bridges to catch birds as they flew through the culverts or underneath the bridges. We considered birds juveniles if they had hatched earlier that summer but were capable of sustained flight, and displayed plumage patterns specific to young of the year (Johnson and Freedberg 2013). We banded all juveniles caught in nets with numbered U. S. Geological Survey leg bands. Juvenile swallows included in our analysis were banded and measured at three colony sites during 2001–2006 (sites 05, 90, and 97); measurements and banding occurred in all years for colony sites 05 and 97 but only 2001–2003 at colony site 90. Site 05 varied in size from 1,100–1,800 active nests, site 90 from 200–365 nests, and site 97 from 955–1,810 nests. For comparisons that used birds banded as nestlings or juveniles in the study area, and recaptured and measured as

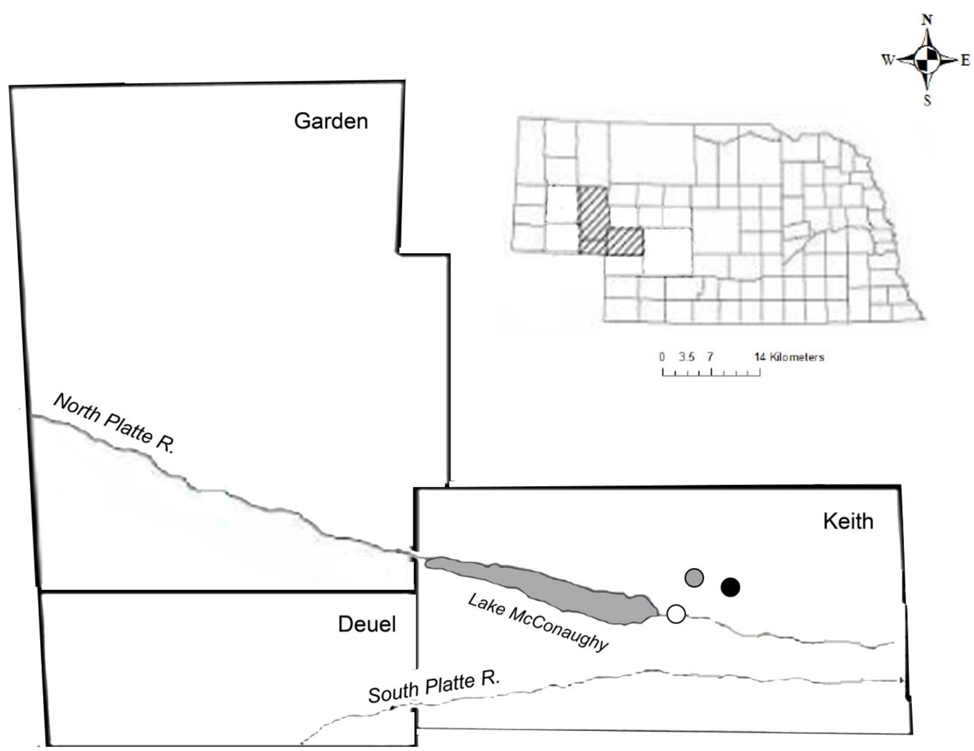

Figure 1. Cliff swallow colonies 05 (white circle), 97 (gray circle), and 90 (black circle) at which juvenile cliff swallow morphological traits were measured within the southwestern Nebraska study area, 2001–2006.

breeding adults during their first nesting season, we collected data as described in Brown and Brown (2011). Our research was approved by the Institutional Animal Care and Use Committee at the University of Tulsa (protocol no. TU-0020).

Morphometric Measurements

A single individual collected all measurements of wing, tail, and skeletal traits, and consequently no corrections to the data for multiple measurers were required (e.g., Price and Grant 1984, Bryant and Jones 1995, Grant and Grant 1995). We recorded the following measurements: the length of the unflattened, closed wing on each side; length of the middle tail feather on each side; tarsus length; and length and width of the exposed bill. Wing and tail feathers that were damaged were not measured; likewise, no tarsi or bill were measured if they appeared damaged or malformed. We measured wing and tail lengths to the nearest millimeter with a stoppered wing ruler (Avinet Inc., Dryden, NY). Similarly, we measured tarsus and bill lengths to the nearest 0.1 millimeter with Mitutoyo dial calipers (Mitutoyo America Corporation, Aurora, IL; see Brown and Brown 1998, 2011), and body mass to the nearest 0.5 g using a Pesola scale (Pesola AG, Baar, Switzerland).

Fumigation

We removed the confounding effects of ectoparasites on nestling growth by using only fumigated, parasite-free nests (Brown and Brown 1986, 1996). To remove the deleterious effects of blood-feeding swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*) on cliff swallow growth and development, we regularly fumigated the nests in the colonies used in this study by spraying them with a dilute solution of Dibrom®. The nest fumigation protocol is described in greater detail by Brown and Brown (1986, 1996).

Weather

Previous studies have suggested that weather variables such as air temperature and precipitation have the greatest effect on availability of flying insects that cliff swallows depend on (Williams 1961, Taylor 1963, Johnson 1969) and that consequently are most likely to affect the development of nestling birds (Bryant 1975, Turner 1983, Dow and Gill 1984, Murphy 1985, Blancher and Robertson 1987). We used daily precipitation and temperature values calculated for climate division 7 of Nebraska averaged for the months of May to July each year (available at http://www.ncdc.noaa.gov/temp-and-precip/time-series/), a span of time corresponding to the nesting and development period for juvenile cliff swallows (Table 1). The number of days that were considered "severe weather days," were defined as days occurring after 15 May that were mostly cloudy (i.e. >75% cloud cover) with high temperatures less than 16.7° C (Table 1). These conditions likely restricted or prevented cliff swallow foraging (Brown and Brown 2000*b*).

Table 1. Numbers of juvenile cliff swallows caught and measured at three colony sites (05, 90, 97), presented along with average May-July precipitation (cm), average May-July temperature (° C), the number of severe weather days (days < 16.7° C and mostly cloudy), and the inclusive dates of capture in southwestern Nebraska, 2001–2006.

Year	Site 05	Site 90	Site 97	Precipitation* (cm)	Temperature** (° C)	No. severe weather days***	Inclusive dates of capture
2001	192	22	118	19.5	20.8	4	05, 22 Jun–17 Jul 90, 29 Jun–22 Jul 97, 2 Jul–5 Aug
2002	199	18	101	11.6	21.6	3	05, 22 Jun–17 Jul 90, 29 Jun–24 Jul 97, 3 Jul–22 Jul
2003	291	8	462	17.3	20.0	2	05, 20 Jun–9 Jul 90, 1 Jul only 97, 24 Jun–12 Jul
2004	117	0	253	29.1	19.4	7	05, 22 Jun–22 Jul 97, 29 Jun–20 Jul
2005	331	0	527	23.7	20.3	4	05, 22 Jun–18 Jul 97, 24 Jun–18 Jul
2006	98	0	183	17.6	21.8	0	05, 23 Jun–14 Jul 97, 24 Jun–16 Jul

*Average May-July precipitation during 1977–2006 was 23.4 centimeters; **Average May-July temperature during 1977–2006 was 20.0° C; ***Days greatly restricting cliff swallow foraging; see text.

Statistical Analyses

We estimated the repeatability (r_i) of morphological measurements using intraclass correlation (Zar 1974, Kuehl 2000, Soper 2009) from a total of 1,525 adult birds that were measured twice while alive during the same breeding season. Repeatabilities for all traits were statistically significantly different from 0 ($P < 0.001$ on all morphological traits).

We used package "lme4" (Bates et al. 2011) in Program R (R Development Core Team 2013) to build linear mixed-effects models for each morphometric measurement using annual covariates and weather-related covariates in a multi-step process. First, we constructed a null model in which each morphometric variable was regressed against an intercept-only model; we included colony site by year (e.g., site 05, 90, or 97 in years 2001–2006) as a random effect intended to account for any otherwise unmodeled sources of heterogeneity attributable to site-by-year combinations. We added banding date, a fixed effect and individual-specific covariate indicating the date on which each juvenile cliff swallow was first caught and measured, which correlated with hatching dates of individual birds. Although exact hatching dates for these birds were unknown, fledged juveniles are generally caught only during the first 1–5 days after they leave the nest (Brown and Brown 1996). Thus, juvenile banding date is a relative index of hatching date within the season, and we statistically controlled for variation in morphological measurements potentially due to seasonal date effects unrelated to weather. We added our indices of weather conditions (e.g., precipitation and temperature covariates; see Table 1 to our model. We ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c), and we calculated model weights using package "AICcmodavg" (Mazerolle 2013). We considered the model with the lowest AIC_c value the best at explaining variation in the morphometric response variable, but those differing by ≤ 2 AIC_c units from the highest ranked model also were considered competitive (Burnham and Anderson 2002).

RESULTS

We measured 2,920 juvenile cliff swallows over six years and at three colony sites (Table 1); these were distributed across the entire portion of the breeding season when juveniles were expected to be present (Table 1). Mean wing length of juvenile cliff swallows across all years and colony sites was 103.75 mm (SD = 2.55). Cliff swallows reared later in the breeding season and under relatively dry conditions (Fig. 2, Table 2a: model 1 vs. 8) had longer wings, but wing length was unrelated to temperature (Table 2a). A delay in banding date by 1 SD (approximately 8 days) was associated with an increase in wing length of 1.0 mm, representing a 40% SD change in size. An increase in precipitation by 1 SD (approximately 5 cm) was associated with a decrease in wing length of 0.04 mm, a 14% SD change in size.

Mean middle tail length of juvenile cliff swallows across

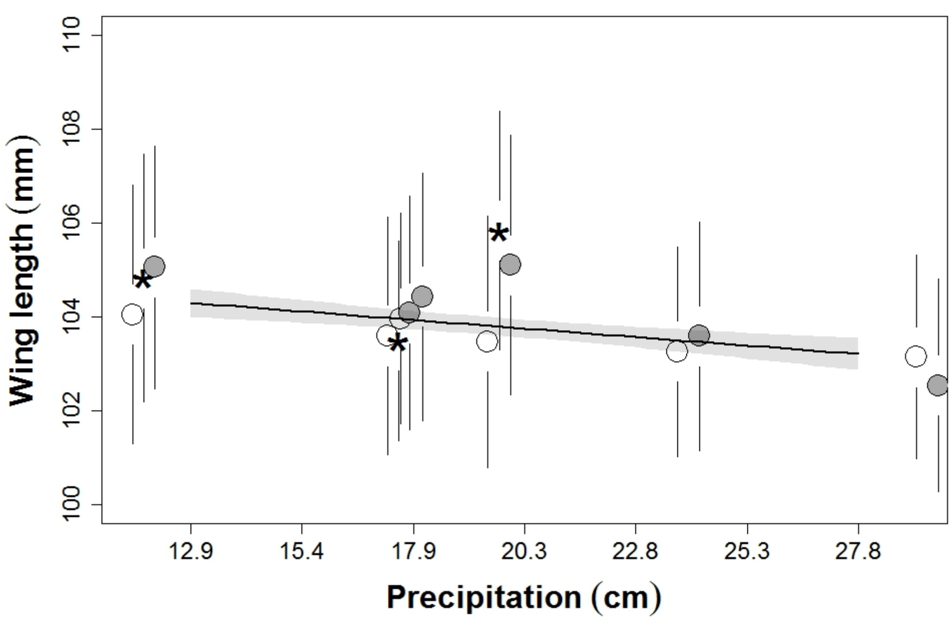

Figure 2. Juvenile cliff swallow wing length in relation to average May–July precipitation in southwestern Nebraska, 2001–2006. Mean trait values for each colony site (05, open circles; 90, asterisks; 97, closed circles) each year are plotted along with standard deviations (vertical bars) against annual average May–July precipitation values. The regression line (± 95% CI) was generated by using the top mixed-model to project measurement values for independent variable values ranging from two standard deviations above and below the mean (Table 2).

Table 2. Mixed models used to investigate covariates associated with morphological traits in juvenile cliff swallows. Models were ranked using Akaike's Information Criterion adjusted for small sample size (AIC_c); here we present the change in AIC_c relative to the top model (ΔAIC_c), the number of model parameters (k), and the model weight (w_i).

Model	AIC_c[1]	k	ΔAIC_c	w_i
a. *Wing length*				
banding.date + precip	13,198.13	5	0.00	0.69
banding.date + precip + temp		6	1.76	0.28
banding.date + temp		5	7.14	0.02
banding.date		4	9.00	0.01
precip		4	418.07	0.00
precip + temp		5	418.82	0.00
temp		4	418.98	0.00
intercept		3	424.77	0.00
b. *Middle tail length*				
banding.date + precip + temp	11,248.54	6	0.00	0.63
banding.date + temp		5	1.28	0.33
banding.date		4	7.10	0.02
banding.date + precip		5	8.07	0.01
precip + temp		5	11.46	0.00
temp		4	12.38	0.00
intercept		3	17.98	0.00
precip		4	18.81	0.00
c. *Tarsus length*				
banding.date + precip	1,741.65	5	0.00	0.39
banding.date + precip + temp		6	0.14	0.36
precip		4	2.86	0.09
precip + temp		5	3.43	0.07
banding.date		4	4.30	0.04
banding.date + temp		5	5.22	0.03
intercept		3	7.07	0.01
temp		4	7.83	0.01
d. *Bill length*				
banding.date	1,313.88	4	0.00	0.46
banding.date + precip		5	1.97	0.17
banding.date + temp		5	1.99	0.17
intercept		3	3.86	0.07
banding.date + precip + temp		6	3.98	0.06
precip		4	5.86	0.02
temp		4	5.87	0.02
precip + temp		5	7.85	0.01

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e. *Bill width*				
banding.date + precip + temp	1,296.02	8	0.00	0.21
precip + temp		5	0.39	0.17
banding.date		4	0.52	0.16
intercept		3	0.87	0.13
banding.date + precip		5	0.95	0.13
precip		4	1.45	0.10
banding.date + temp		5	2.52	0.06
temp		4	2.86	0.05
f. *Body mass*				
intercept	10,126.11	3	0.00	0.24
precip		4	0.29	0.21
banding.date		4	1.26	0.13
banding.date + precip		5	1.65	0.11
temp		4	1.71	0.10
precip + temp		5	1.75	0.10
banding.date + precip + temp		6	3.02	0.05
banding.date + temp		5	3.04	0.05

[1]AIC_c shown for top ranked model; all others had this $AIC_c + \Delta AIC_c$ as shown.

all years and colony sites was 42.98 mm (SD = 1.68). Middle tail length was longer for cliff swallows reared later in the breeding season under wetter (Fig. 3a) and warmer (Fig. 3b) conditions (Table 2b). A delay in banding date by 1 SD was associated with an increase in middle tail length of 0.12 mm, representing a 7% SD change in size. An increase in precipitation by 1 SD was also associated with an increase in middle tail length of 0.12 mm, a 7% SD change in size. An increase in temperature by 1 SD (approximately 0.7° C) was also associated with an increase in wing length of 0.25 mm, a 15% SD change in size.

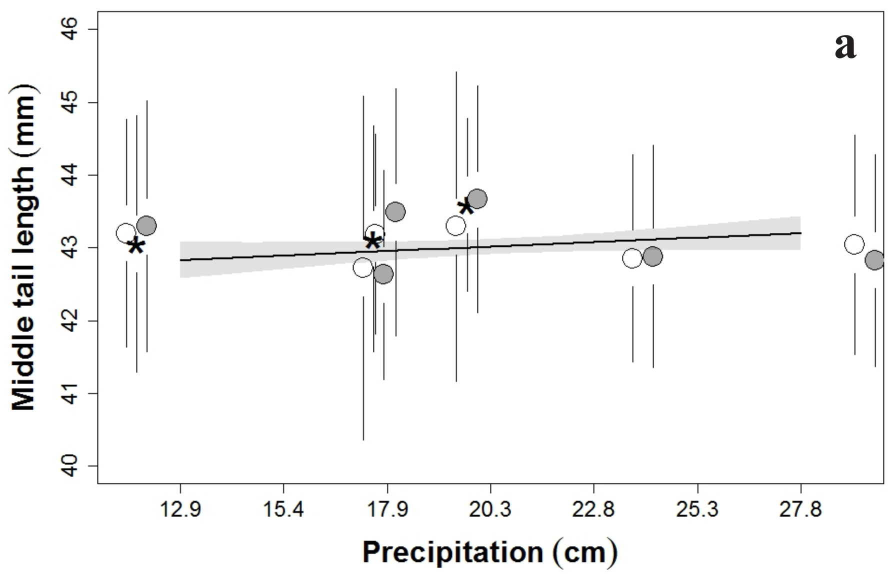
The mean tarsus length of juvenile cliff swallows across all years and colony sites was 42.98 mm (SD = 1.68). Tarsus length was longer for swallows reared later in the season and under drier conditions (Fig. 4, Table 2c) but was unrelated to temperature (Table 2c). A delay in banding date by 1 SD was associated with an increase in tarsus length of 0.02 mm, representing a 4% SD change in size. An increase in precipitation by 1 SD was associated with a decrease in tarsus length of 0.08 mm, a 23% SD change in size.

Mean bill length of juvenile cliff swallows across all years and colony sites was 7.04 mm (SD = 0.31), and the mean bill width was 6.06 mm (SD = 0.32). Bills were longer later in the season, but their length was unrelated to both precipitation and temperature (Table 2d). A delay in banding date by 1 SD was associated with an increase in bill length of 0.01 mm, representing a 5% SD change in size. Bills were wider later in the season and under wet (Fig. 5a) and warm conditions (Fig. 5b, Table 2e). A delay in banding date by 1 SD was associated with an increase in bill width of 0.01 mm, representing a 3% SD change in size. An increase in precipitation by 1 SD was also associated with an increase bill width of 0.11 mm, a 34% SD change in size. An increase in temperature by 1 SD was also associated with an increase in bill width of 0.09 mm, a 26% SD change in size.

The mean body mass of juvenile cliff swallows across all years and colony sites was 20.98 g (SD = 1.43). Body mass was unrelated to timing of rearing and weather conditions (Table 2f). For 323 birds measured both as a juvenile and the next year as an adult, significant positive relationships between the two times existed for wing (r = 0.37), tail (r = 0.36), tarsus (r = 0.24), and bill measurements ($r \geq 0.43$); correlations were significant ($P < 0.001$) in all cases.

DISCUSSION

Using weather variables as an index of food availability during brood rearing, our results showed that body mass, skeletal traits, and wing and tail length in juvenile cliff swallows did not change in a consistent way with cooler and wetter conditions. Date of first banding often explained the most variation in morphological measures, with wing length



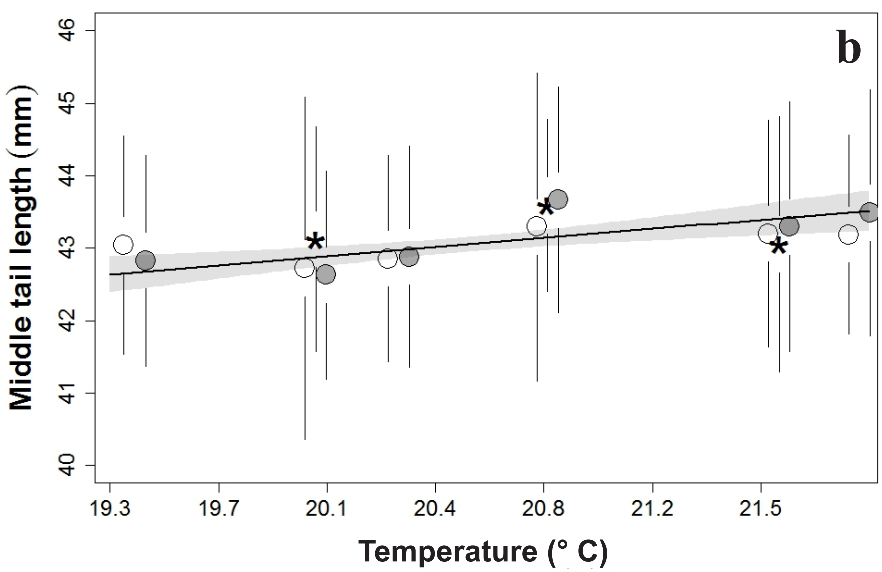


Figure 3. Juvenile cliff swallow middle tail length in relation to a) average May–July precipitation, and b) average May–July temperature in southwestern Nebraska, 2001–2006. Mean trait values for each colony site (05, open circles; 90, asterisks; 97, closed circles) each year are plotted along with standard deviations (vertical bars) against annual average May–July precipitation and temperature values. The regression line (± 95% CI) was generated by using the top mixed-model to project measurement values for independent variable values ranging from two standard deviations above and below the mean (Table 2).

specifically being demonstrably longer later in the breeding season. Although the proportion of variability attributable to weather was small, annual changes in juvenile skeletal and feather growth in response to rearing conditions appeared to be permanent, as juveniles tended to maintain their relative size into adulthood. While some bird species exhibit reductions in skeletal traits such as tarsus or bill length and width during food deprivation (e.g., Rodway 1997, Bize et al. 2006, Sears and Hatch 2008), in most species skeletal measures seem the least sensitive to nutritional deficits (e.g., Dow and Gill 1984, Boag 1987, van Heezik 1990, Negro et al. 1994, Lepczyk and Karasov 2000). Cliff swallows were somewhat unusual, especially among small passerines, in that skeletal size varied with seasonal weather variables. The range of yearly variation observed in tarsus and bill measurements was in some cases equivalent to or greater than that seen in

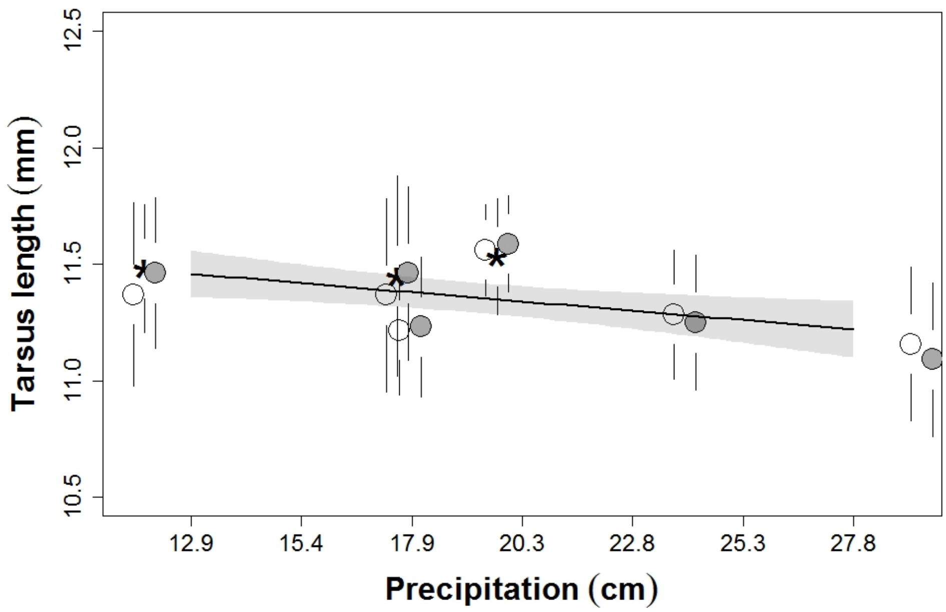


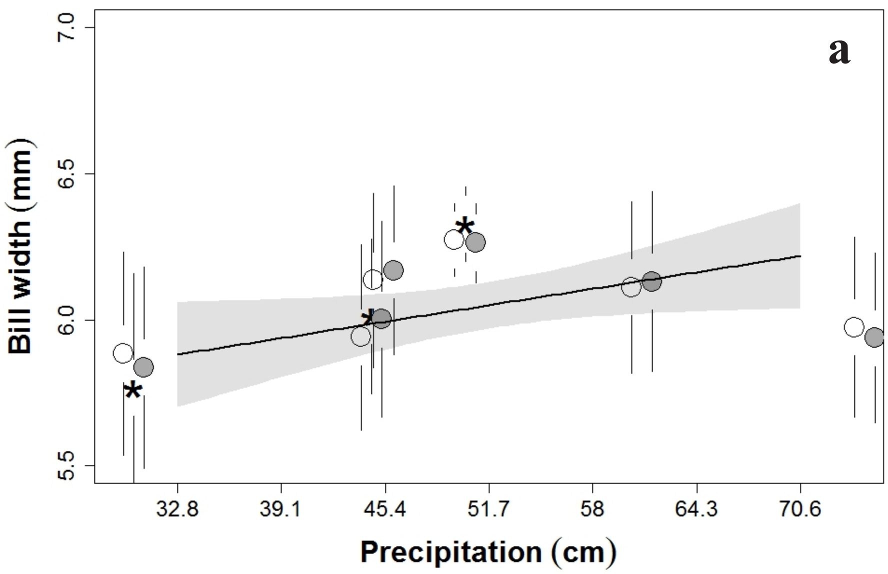
Figure 4. Juvenile cliff swallow tarsus length in relation to average May–July precipitation in southwestern Nebraska, 2001–2006. Mean trait values for each colony site (05, open circles; 90, asterisks; 97, closed circles) each year are plotted along with standard deviations (vertical bars) against annual average May-July precipitation values. The regression line (± 95% CI) was generated by using the top mixed-model to project measurement values for independent variable values ranging from two standard deviations above and below the mean (Table 2).

intense episodic survival selection in adult cliff swallows (Brown and Brown 1998, 2011), suggesting that differences in morphology (and their potential effects on survival) documented during our study are not trivial.

Like a variety of other species (including some swallows) in which wing growth is compromised under stressful rearing conditions (e.g., Murphy 1985, Quinney et al. 1986, Boag 1987, Johnston 1993, Negro et al. 1994), cliff swallows exhibited reduced wing growth in cool or wet summers when food was presumably less available. For a species that relies on flight for foraging, a reduction in wing feather development could have major survival consequences in the critical time after fledging, suggesting that post-fledging survival (and thus annual reproductive success) may be lower in cooler and wetter years. Brown and Brown (2004) observed lower juvenile survival in the days following fledging during an extremely cool season.

Although we were unable to account for the effects of variable clutch size and development times, both of which could have influenced the variation in morphological measurements documented by this study, we were able to rule out several non-weather related variables as affecting our results. These included time of nesting, temperature inside the nests, presence of blood-feeding ectoparasites in the nests, and foraging efficiency of parental birds due to social foraging opportunities. For instance, while date can affect reproductive success and potentially nestling condition in various birds (e.g., Hochachka 1990, Rowe et al. 1994, Brown and Brown 1999*b*), we controlled statistically for the effect of date in our analyses. Thus, any weather-associated variation in morphological measurements was detected while already accounting for any influence of seasonal date.

Colonial bird species often exhibit wide variation in the size of a colony that forms at a given site (Brown and Brown 2001). In cliff swallows, colony size can both positively and negatively affect nestling growth: opportunities to transfer information about food locations may enhance nestling growth (e.g., body mass), competition for food can increase the likelihood of nestling starvation in larger broods at the largest colonies, and colonies of different sizes may be settled by birds of different phenotypic characteristics (Brown and Brown 1996, 2000*a*). Potential effects on reproduction were controlled in this study by restricting our comparison to juveniles that were captured at colonies of approximately similar size. For example, most of the birds sampled came from sites 05 and 97 (Table 1), and these sites were perennially among the largest in the study area. Because these birds were raised in large colonies without ectoparasites, they may have been subject to less physiological stress (as measured by corticosterone levels; Raouf et al. 2006). Though uncertain, it is possible that growth tradeoffs in response to changes in resource availability would be different for birds raised under more stressful conditions that included ectoparasitism or variation in colony size (with its associated variation in parental foraging success; Brown and Brown 1996).



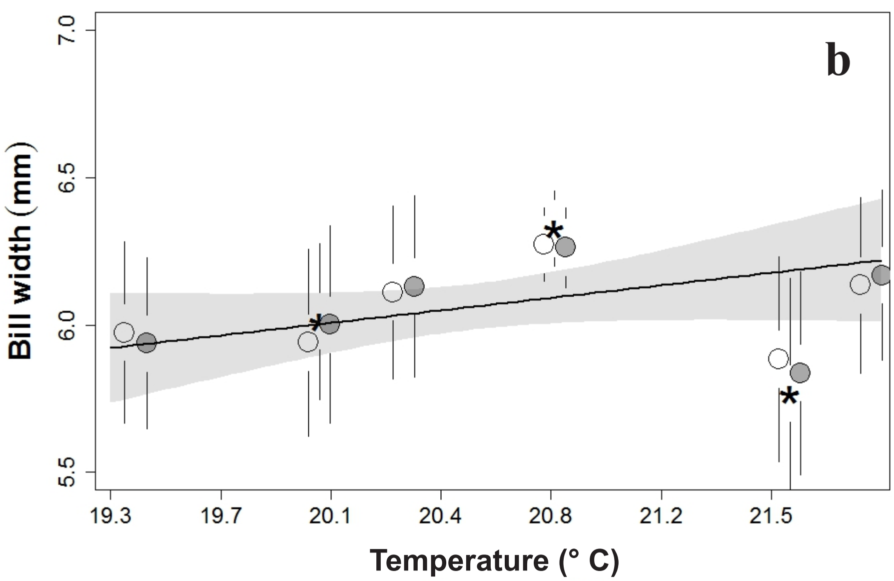


Figure 5. Juvenile cliff swallow bill width in relation to a) average May–July precipitation and b) average May–July temperature in southwestern Nebraska, 2001–2006. Mean trait values for each colony site (05, open circles; 90, asterisks; 97, closed circles) each year are plotted along with standard deviations (vertical bars) against annual average May–July precipitation and temperature values. The regression line (± 95% CI) was generated by using the top mixed-model to project measurement values for independent variable values ranging from two standard deviations above and below the mean (Table 2).

Numerous studies have shown that flying insect activity varies positively with temperature and negatively with precipitation (e.g., Williams 1961, Taylor 1963, Johnson 1969). Our results are consistent with those of previous studies in which we demonstrated strong relationships between annual weather variables and time of laying, clutch size, and fledging success, and in all cases the relationships were ones predicted if food availability varied systematically with seasonal weather conditions (Brown and Brown 1999*a, b*). Additionally, our results indicated that both skeletal and wing/tail size in cliff swallows are to some degree variable and that these relative effects may persist into adulthood. The plasticity of morphology in this species, even of skeletal traits that are thought to be under strong genetic control (e.g., Boag and Grant 1978, Smith and Zach 1979, Boag 1983, Alatalo and Lundberg 1986), indicates that interpretation of long-term morphological changes (e.g., Brown and Brown 2011) must account for yearly variation in weather-related food availability during the rearing of nestling cliff swallows.

MANAGEMENT IMPLICATIONS

These analyses indicate that both skeletal and wing/tail growth in cliff swallows are surprisingly plastic and that these relative effects persist into adulthood. The plasticity of morphology in this species, even of skeletal traits that are thought to be under strong genetic control, indicates that interpretation of long-term morphological changes must account for yearly variation in climatically driven food availability during nestling rearing. While cliff swallows are not a managed species, understanding how weather potentially affects morphology in songbirds could help us better predict how climate change may potentially mismatch morphological traits with food supply and thus better inform the management of declining North American aerial insectivore populations (Nebel et al. 2010).

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