



INTENSE NATURAL SELECTION ON MORPHOLOGY OF CLIFF SWALLOWS (*PETROCHELIDON PYRRHONOTA*) A DECADE LATER: DID THE POPULATION MOVE BETWEEN ADAPTIVE PEAKS?

MARY BOMBERGER BROWN^{1,3} AND CHARLES R. BROWN²

¹Tern and Plover Conservation Partnership, University of Nebraska, 3310 Holdrege Street, Lincoln, Nebraska 68583, USA; and

²Department of Biological Sciences, University of Tulsa, 800 South Tucker Drive, Tulsa, Oklahoma 74104, USA

ABSTRACT.—Unusual climatic events often lead to intense natural selection on organisms. Whether episodic selection events result in permanent microevolutionary changes or are reversed by opposing selection pressures at a later time is rarely known, because most studies do not last long enough to witness rare events and document their aftermath. In 1996, unusually cold and wet weather in southwestern Nebraska led to the deaths of thousands of Cliff Swallows (*Petrochelidon pyrrhonota*) over a 6-day period. Survivors were skeletally larger, with shorter wings and tails, and had less asymmetry in wing length than those that died. We determined trajectories of morphological traits in the decade following this event by measuring yearling birds each year from 1997 to 2006. Wing and middle tail-feather lengths continued to decrease, bill length and width continued to increase, tarsus length was unchanged, and levels of asymmetry in wing length increased. Cumulative directional change in wing, tail, and bill length was greater in the decade after selection than during the selection event itself. Morphological variation could not be explained by phenotypic plasticity resulting from better environmental conditions during growth, because weather variables (that influence food supply and ectoparasitism) were not significantly different before and after selection. There was no evidence that opposing selection restored skeletal size or wing or tail length to that before the selection event. The reasons for continued change in morphology in this population are unclear but may represent a population shift to a different fitness peak in the adaptive landscape as a consequence of the intense selection in 1996. Received 21 September 2010, accepted 29 October 2010.

Key words: body size, Cliff Swallow, episodic selection, fluctuating asymmetry, morphological evolution, *Petrochelidon pyrrhonota*.

Sélection naturelle intensive sur la morphologie de *Petrochelidon pyrrhonota* une décennie plus tard: la population s'est-elle déplacée entre deux pics adaptatifs?

RÉSUMÉ.—Des événements climatiques inhabituels conduisent souvent à une sélection naturelle intensive sur des organismes. On sait rarement si les événements de sélection épisodiques résultent en des changements micro-évolutionnaires permanents ou s'ils sont inversés ultérieurement par des pressions de sélection contraires, car la plupart des études ne durent pas assez longtemps pour témoigner des événements rares et documenter leurs effets. En 1996, le temps inhabituellement froid et humide dans le sud-ouest du Nebraska a causé la mort de milliers d'individus de *Petrochelidon pyrrhonota* sur une période de 6 jours. Les survivants possédaient un squelette plus imposant, une queue et des ailes plus petites et une asymétrie de la longueur des ailes moins marquée que les individus qui sont morts. Nous avons déterminé des trajectoires des traits morphologiques au cours de la décennie suivant cet événement en mesurant annuellement les oiseaux d'un an entre 1997 et 2006. La longueur des ailes et des plumes centrales de la queue a continué à décliner, la longueur et la largeur du bec a continué d'augmenter, la longueur du tarse est demeurée inchangée et les niveaux d'asymétrie de la longueur des ailes ont augmenté. Un changement directionnel cumulatif de la longueur des ailes, de la queue et du bec était plus marqué dans la décennie suivant l'événement de sélection qu'au cours de l'événement lui-même. Les variations morphologiques ne peuvent être expliquées par la plasticité phénotypique résultant de meilleures conditions environnementales au cours de la croissance, car les variables météorologiques (qui influencent l'approvisionnement alimentaire et l'ectoparasitisme) n'étaient pas significativement différentes avant et après la sélection. Aucune preuve n'a pu être établie quant à la restauration par une sélection inverse de la taille squelettique ou de la longueur des ailes ou de la queue. Les raisons expliquant un changement continu de la morphologie dans cette population sont obscures mais peuvent être associées à un déplacement de la population vers un différent pic de valeur adaptative conséquemment à la sélection intensive en 1996.

³E-mail: mbrown9@unl.edu

INTENSE EPISODIC SELECTION events often provide opportunities for observing significant evolutionary change over short time frames (Bumpus 1899, Endler 1986, Grant and Grant 2002, Siepielski et al. 2009). Most often, unusual climatic conditions are the drivers for rapid selection, but other events, such as epidemics, drastic habitat modification, introduction of new predators, or colonization of vacant island habitats, may also cause short-term microevolutionary shifts in particular traits (e.g., Hairston and Walton 1986, Grant and Grant 1993, Benkman and Miller 1996, Clegg et al. 2008, Mathys and Lockwood 2009, Wilcoxon et al. 2010; reviewed in Carroll et al. 2007). However, the extent to which rare selective episodes result in relatively permanent microevolutionary change is less well documented. Although many studies have measured the intensity of natural selection in the wild (Siepielski et al. 2009), most field studies are not conducted over long enough periods to both witness rare selection events and determine the long-term trajectories of any trait changes. A notable exception is Grant and Grant's (2002) 30-year study of evolution in body size and bill dimensions in two species of Darwin's finches in the Galápagos Islands. They documented several periods of intense selection on morphology brought about by rare climatic events, and as they followed these populations after selection, unpredictable patterns of change were revealed (Grant and Grant 2002). In most cases, intense selection during unusual climatic conditions tended to be reversed in the years immediately after these events by opposing selection pressures, yet both species showed long-term changes in morphology apparently brought about by recurring bouts of directional selection in response to environmental changes (Price et al. 1984; Grant and Grant 1989, 1993, 1995, 2002). The Darwin's finch study suggests that rare selection events can serve as catalysts to the evolution of some traits, yet the generality of this conclusion is difficult to evaluate because so few comparable long-term studies of natural populations exist.

In late May 1996, unusually cold and wet weather extending over a 6-day period resulted in the deaths of thousands of Cliff Swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska, reducing the breeding population by at least half (Brown and Brown 1998). The cold and wet weather depressed the abundance of the flying insects that Cliff Swallows feed on to the extent that a portion of the population starved to death. The comparison of morphological measurements of those that died and birds that survived the event revealed strong selection on tarsus, wing and bill length, and bill width; in addition, those with lower levels of fluctuating asymmetry in wing length tended to survive. We hypothesized that the skeletally larger birds were favored because they had been able to store more fat before the inclement weather commenced and that low levels of wing asymmetry may have promoted more efficient foraging in cold weather (Brown and Brown 1998). These morphological characteristics were retained in the first-generation offspring of the survivors.

Here, we report how morphology of Cliff Swallows in the Nebraska study area changed in the 10 years subsequent to the 1996 selection event. Measuring the same traits of birds known to be born in the study area and taking the measurements at identical ages (1 year old) in each year over a decade allowed us to investigate long-term changes in morphology. Specifically, we asked whether the directional selection on morphology documented in 1996 had

been reversed by opposing selection pressures in response to potential environmental change in subsequent years; whether there is evidence of continuing directional selection on any of the traits, perhaps as a result of the population crossing to a different adaptive peak (Feare and Price 1998, Arnold et al. 2001); whether the morphological changes over time are consistent with possible responses to global climate change (e.g., Yom-Tov 2001, Van Buskirk et al. 2010); and whether the microevolutionary changes documented in the episodic selection event resulted in a relatively permanent shift in body size in this population of Cliff Swallows.

METHODS

Study site.—Cliff Swallows have been studied since 1982 near the Cedar Point Biological Station (41°13'N, 101°39'W) in Keith County, southwestern Nebraska, along the North Platte 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 170 colony sites, of which about a third are not used in a given year. Colony size varies widely; in our study area it ranges from 2 to 6,000 nests (mean \pm SE = 393 \pm 15, n = 1,812 colonies), with some birds nesting solitarily. The study site is described in detail in Brown and Brown (1996).

Measurements.—Beginning in 1997 and continuing through 2006, birds were measured during the course of a long-term mark-recapture project in which we rotated among 25–40 colonies in the study area on a regular basis each year, mist netting birds for studies of survival and movement (Brown and Brown 2004, 2009; Brown et al. 2007, 2008a, b). At smaller colonies, we measured most birds captured on a given occasion; at larger sites, processing time allowed us to measure only a subset of those netted. At the latter sites, we generally tried to include as many previously banded birds as possible, because more information on those individuals was potentially available (e.g., age, prior colony-site use). In the field at the time of measurement, however, we knew only a previously marked bird's band prefix and thus the approximate year it was banded. Birds were sexed by the presence of a cloacal protuberance, brood patch, or both.

M.B.B. measured all birds in all years of the present study and in the 1996 weather event (Brown and Brown 1998), and thus no corrections to the data for multiple measurers were necessary. For all birds, the length of each unflattened, 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; and the length and width of the exposed culmen (length from the proximate end of the exposed culmen to the bill tip along the upper mandible and width of the exposed mandibles at the nostrils) were measured to the nearest 0.1 mm with calipers. Asymmetry in wing length was expressed by the unsigned difference between the right and left wing measurements (Palmer 1994).

Repeatabilities of morphometric measurements by M.B.B. are given in Brown and Brown (1998); repeatabilities, in general, were high and statistically significant. We also found that wing asymmetry was higher than expected given the measuring error, which means that asymmetry could be distinguished from random noise (Brown and Brown 1998). We found evidence for directional asymmetry in wing measurements, as indicated by signed asymmetry values that differed significantly from zero (Brown and Brown 2002). This asymmetry likely reflected a handedness bias by the measurer (Brown and Brown 1998, 2002). To correct for directional asymmetry (Palmer 1994), we divided the mean signed asymmetry by 2 and subtracted the result from the wing measurement of the larger average side and added the latter value to the measurement of the smaller average side for each observation. The corrected unsigned asymmetry values are those presented and analyzed here. Statistical analyses were performed with SAS (SAS Institute 2004).

Individuals included in analyses.—For the period 1997–2006, our analyses used only birds known by banding to have been born in the Nebraska study area the previous summer and that were thus 1 year old at the time of measurement. These birds had been banded as nestlings or recently fledged juveniles; those measured in 1998 and 1999 included some that were part of a cross-fostering experiment the previous year (Brown and Brown 2000) in which 5-day-old nestlings were moved between nearby colonies and reared in colonies of different sizes. Although many individuals were measured in multiple years, for the present study we used a bird's measurements only from the season in which it was 1 year old; thus, all measurements were from birds of identical life stage, and data from each year were statistically independent. The number of 1-year-old birds measured varied between 113 and 314 per season, reflecting differences in the number of nestlings and juveniles banded, recapture effort, and population size in a given year. If a 1-year-old bird was measured multiple times that season, average within-year values for its respective measurements were used.

For comparison, we used measurement data from the birds that did or did not survive the 1996 event, as described in Brown and Brown (1998). The principal difference between the data reported in the earlier publication and in these analyses is that here we separated the survivors and nonsurvivors from 1996 by sex. Sex had not been determined for the initial analyses (Brown and Brown 1998), but subsequently all nonsurviving birds were prepared as skins and dissected, so the sexes were known. Briefly, nonsurvivors were dead birds collected on the ground below nests or found inside nests on the day after the cold and rainy weather ended, and survivors were live birds (at least 1 year old) measured in 1996 in the immediate aftermath of the event. See Brown and Brown (1998) for additional details. The trait distributions prior to the 1996 selection event were unknown (Price et al. 2000).

Weather data.—To evaluate potential weather changes in the study area that could have influenced growth and development of nestlings before and after the selection event, we compared total June rainfall and average June high temperature in the 10 years prior to the selection event (1986–1995), during which time most of the birds that experienced the event hatched, with the same measures for the 10 years after the selection event (1996–2005), during which time the descendants of the survivors would have hatched. June was used because that is when most brood-rearing

by Cliff Swallows occurs in the study area and their reproductive traits depend heavily on climatic conditions such as temperature and rainfall (Brown and Brown 1999a, b). Climatological data were taken from a long-term monitoring site in Arthur County, Nebraska, about 48 km directly north of the study area (Brown and Brown 1996). This site, part of the University of Nebraska's Automated Weather Data Network, recorded daily high and low temperatures and total precipitation.

Quantitative changes in traits during selection.—As a measure of relative changes in trait means during the 1996 selection event versus in the subsequent 10 years, we computed the directional change among trait means expressed as a fraction of the before-selection standard deviation (SD) using the following formula: (trait mean after selection – trait mean before selection)/trait SD before selection.

For the 1996 event, we used survivors and nonsurvivors combined as the before-selection population and survivors as the after-selection population. For the decade following selection, we used the 1996 survivors as the before-selection population and those measured in 2006 as the after-selection population.

RESULTS

Body-size variation over time.—For skeletal measures of body size, the strong differences documented between survivors and nonsurvivors of the 1996 selection event were maintained in the 10 years afterward (Fig. 1). Tarsus length remained essentially unchanged in later years, with mean values for both sexes mostly within the 95% confidence interval of the 1996 survivors' tarsus length (Fig. 1A). Mean tarsus length per year did not vary over time in the 1996–2006 interval for either males ($r_s = -0.16$, $P = 0.64$, $n = 11$ years) or females ($r_s = -0.21$, $P = 0.53$). By contrast, both bill length (Fig. 1B) and width (Fig. 1C) continued to increase in the years after the kill. Bill length of both sexes by 2003 was well outside the 95% confidence interval for that of the 1996 survivors (Fig. 1B), and bill width in males also tended to track to larger values than in 1996 (Fig. 1C). Bill length in both males ($r_s = 0.61$, $P = 0.046$) and females ($r_s = 0.68$, $P = 0.022$) increased significantly across the 11 years from 1996 to 2006, as did bill width ($r_s = 0.72$, $P = 0.012$ for both sexes). There was no evidence that any of the skeletal measures drifted back toward those of the nonsurvivors in 1996 (Fig. 1).

Wing length showed a continuing decline in the years following the 1996 kill, with yearly means for both sexes generally outside the 95% confidence interval for the survivors (Fig. 2A). Male mean wing length per year declined significantly after 1996 ($r_s = -0.87$, $P = 0.005$, $n = 11$ years), with females showing the same trend, though it was not significant ($r_s = -0.55$, $P = 0.078$). Wing length did not exhibit a directional increase in size toward that of the nonsurvivors from 1996 (Fig. 2A). Length of middle tail feathers showed a less consistent pattern, with some yearly values near the 95% confidence interval of the 1996 survivors, but the trend was for smaller middle tail feathers and generally away from that of the nonsurvivors (Fig. 2B). Neither males ($r_s = -0.46$, $P = 0.15$, $n = 11$) nor females ($r_s = -0.38$, $P = 0.25$) showed a significant change in middle tail feather length over the 11-year interval.

Average wing asymmetry increased in the years after the 1996 event, although by 2006 wing asymmetry was still below that of the nonsurvivors (Fig. 3). Both males ($r_s = 0.82$, $P = 0.002$, $n = 11$ years)

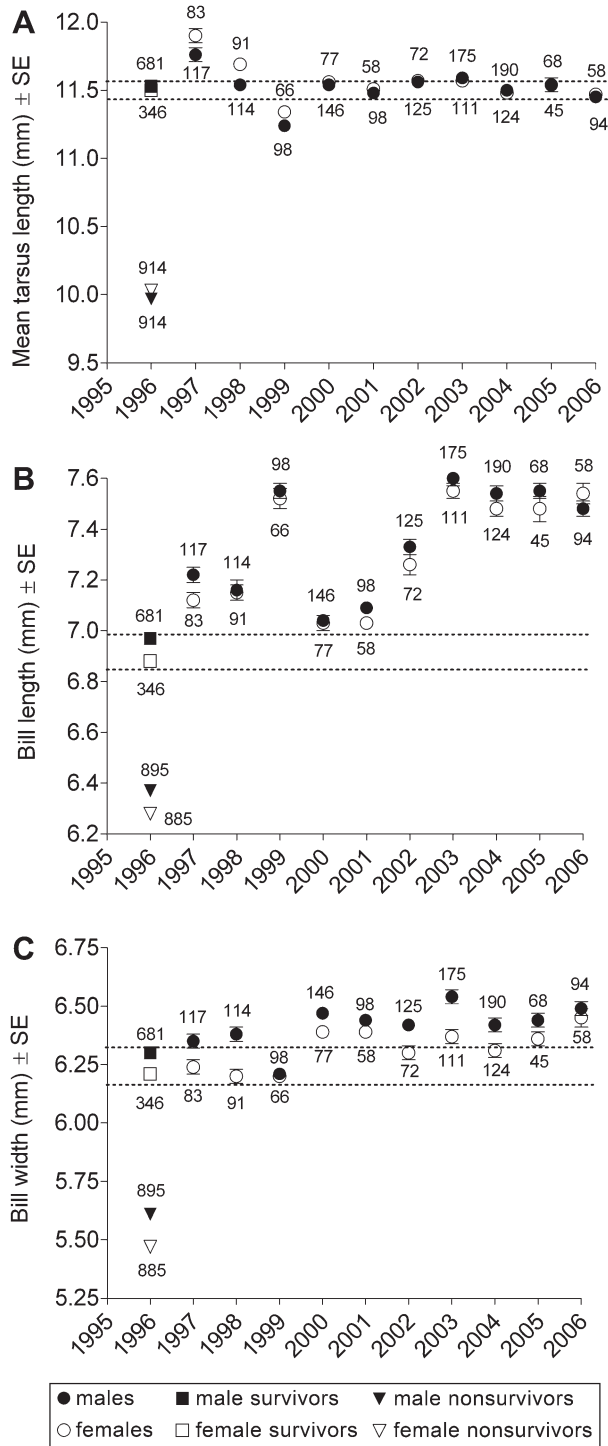


FIG. 1. Average (A) mean tarsus length, (B) bill length, and (C) bill width for male and female Cliff Swallows each year following a 1996 selection event in southwestern Nebraska. Birds in 1997–2006 were 1 year old and born in the study area the previous summer. Sample sizes (number of birds measured) are shown next to symbols; error bars indicate SE. For comparison, survivors and nonsurvivors of the 1996 event (Brown and Brown 1998) are also shown, and the dotted line indicates 95% confidence interval for the 1996 survivors.

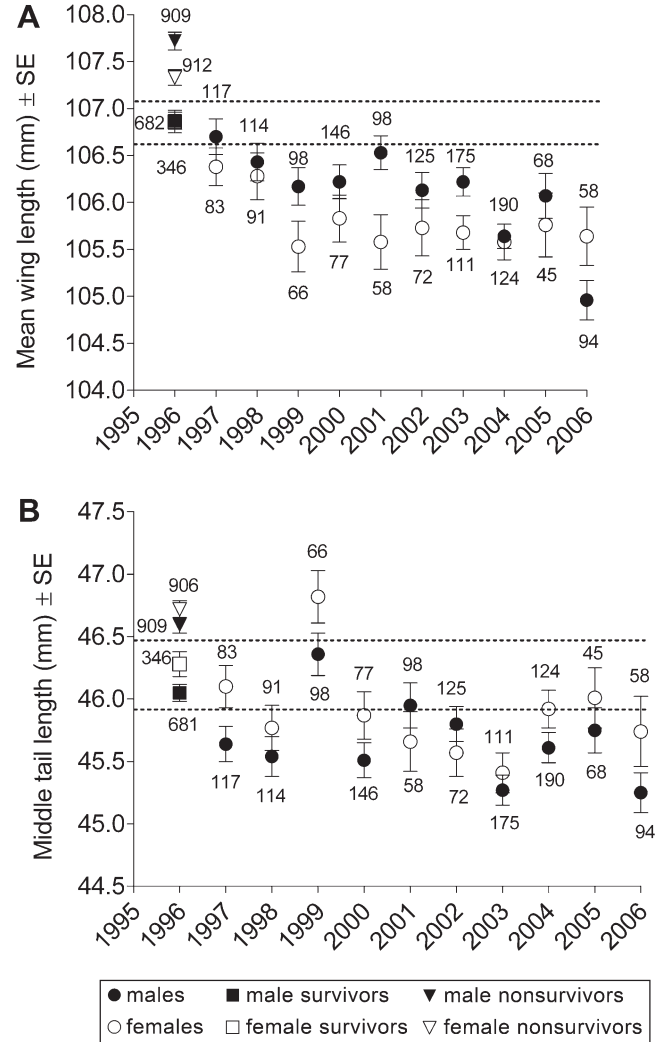


FIG. 2. Average (A) mean wing length and (B) middle-tail-feather length for male and female Cliff Swallows each year following a 1996 selection event in southwestern Nebraska. Birds in 1997–2006 were 1 year old and born in the study area the previous summer. Sample sizes (number of birds measured) are shown next to symbols; error bars indicate SE. For comparison, survivors and nonsurvivors of the 1996 event (Brown and Brown 1998) are also shown, and the dotted line indicates 95% confidence interval for the 1996 survivors.

and females ($r_s = 0.66$, $P = 0.026$) showed significant yearly increases in wing asymmetry with time over the 11-year period.

Quantitative changes in traits.—Wing, middle tail, and bill lengths exhibited greater change (and in the same direction) in the subsequent 10 years than during the selection event (Table 1). Bill width showed about the same level of change, and tarsus length showed much less change in the subsequent period, compared with the selection event (Table 1). Wing asymmetry showed opposite patterns of change during the two periods (Table 1).

Weather before and after selection.—Total June rainfall in the years prior to the selection event (mean = 6.8 cm year⁻¹; range: 3.0–13.9 cm) did not differ significantly from that in the years after the

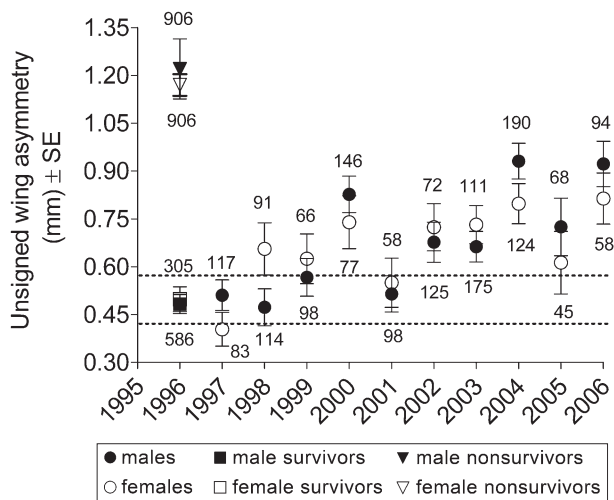


FIG. 3. Average unsigned fluctuating asymmetry in wing length for male and female Cliff Swallows each year following a 1996 selection event in southwestern Nebraska. Birds in 1997–2006 were 1 year old and born in the study area the previous summer. Sample sizes (number of birds measured) are shown next to symbols; error bars indicate SE. For comparison, survivors and nonsurvivors of the 1996 event (Brown and Brown 1998) are also shown, and the dotted line indicates 95% confidence interval for the 1996 survivors.

selection event (mean = 6.3; range: 2.3–9.9 cm; Wilcoxon test, $Z = 0.00$, $P = 0.98$). Average June high temperature in the years prior to the selection event (mean = 26.3°C year⁻¹; range: 23.1–30.2°C) did not differ significantly from that in the years after the selection event (mean 25.5°C year⁻¹; range: 22.9–29.5°C; Wilcoxon test,

TABLE 1. Intensity of selection, as indicated by change in trait mean expressed as the fraction of the before-selection standard deviation (ΔSD), for morphology of Cliff Swallows during an intense selection event in 1996 (Brown and Brown 1998), compared with that during the period from 1996 to 2006. ΔSD for the 1996 event was calculated using combined survivors and nonsurvivors (before selection) and survivors (after selection), and ΔSD for 1996–2006 used 1996 survivors (before selection) and birds measured in 2006 (after selection). Negative values indicate that trait mean decreased in size during the respective selection event; positive values indicate that the trait mean increased in size.

Trait	1996 selection event ΔSD	1996:2006 ΔSD
Male mean wing length	-0.18	-0.82
Female mean wing length	-0.14	-0.46
Male middle-tail-feather length	-0.16	-0.44
Female middle-tail-feather length	-0.16	-0.29
Male mean tarsus length	+0.95	-0.12
Female mean tarsus length	+1.29	-0.04
Male bill length	+0.72	+1.58
Female bill length	+0.98	+2.72
Male bill width	+0.78	+0.64
Female bill width	+1.12	+1.08
Male wing asymmetry	-0.20	+0.61
Female wing asymmetry	-0.50	+0.46

$Z = 0.49$, $P = 0.62$). In 2004, however, cold and wet weather in late June resulted in the mean high temperature for the second half of the month being at least 6°C colder than that for the comparable period in any other year either before or after the selection event. Many nestling Cliff Swallows in the study area, and some adults, starved to death during the period 17–20 June 2004, although overall population size was unaffected.

DISCUSSION

The most striking result of our study is that none of the measures of Cliff Swallow body size showed evidence of opposing selection in the years after the unusual climatic event, and the patterns of directional selection that occurred during that event have been maintained for most traits. The trend toward evolution of birds of larger skeletal size (especially bill size) with shorter wings and tail has continued even in the apparent absence of similar selection events in subsequent years. Hypotheses to explain these results include (1) relaxation of opposing selection pressure for smaller body size due to recent environmental changes; (2) undetected continuing episodic selection events similar to that of 1996; and (3) as a consequence of the intense selection in 1996, the population may have crossed to another fitness peak on the adaptive landscape, leading to further directional selection on body size. In contrast to what we observed for body size, levels of fluctuating asymmetry in wing length moved in the opposite direction in the subsequent decade, likely indicating relaxed selection for high levels of symmetry in the apparent absence of extreme climatic events. All patterns seemed roughly similar between the sexes, with no sex-specific differences in any of the results.

Body size in Bank Swallows (*Riparia riparia*) in Great Britain in the 1980s showed evidence of oscillating selection, believed to be related in part to climatic conditions. Populations crashed in 1983–1984, with smaller birds being favored, presumably because of unusual drought conditions on the African wintering grounds (Jones 1987, Bryant and Jones 1995). Larger birds have reproductive advantages on the breeding grounds, however, and by 1990 countervailing selection for large size had restored the population to a body-size morphology largely characteristic of that before the drought (Bryant and Jones 1995). Similar reversals of selection were documented for Darwin’s finches in response to short-term changes in rainfall that affected seed availability (Price and Grant 1984; Gibbs and Grant 1987; Grant and Grant 1989, 1995). Because we observed little shift in any morphological trait (except wing asymmetry; see below) back toward that before the severe weather event, opposing selection based on advantages associated with smaller skeletal size and longer wings and tail did not apparently occur in the decade following selection in this Cliff Swallow population. We have not identified any obvious ecological or social benefit of small body size per se during the course of our long-term research on Cliff Swallow coloniality. Furthermore, the fact that the Nebraska population has retained its morphological characteristics in the aftermath of the selection event suggests that there have been no environmental changes or episodic disturbances (e.g., drought on the wintering range; Bryant and Jones 1995) that favored smaller body size or longer wings and tail during other times or stages of the annual life cycle, at least during the past decade. Not finding evidence of directional selection for smaller size is not

surprising, given the lack of empirical evidence for advantages of being small in animals generally (Blanckenhorn 2000).

Long-term change in body morphology can occur through recurring bouts of directional selection, as documented in Darwin's finches (Price et al. 1984, Grant and Grant 2002). This requires environmental conditions that favor continued directional changes. Climatological records (Brown and Brown 1998) show that the 1996 weather event in our study area was one of only two such events of this magnitude in southwestern Nebraska since 1875. Cold and rainy weather of shorter duration occurs more frequently, which can result in limited Cliff Swallow mortality. These events also lead to viability selection for birds of larger skeletal size, lower asymmetry, and shorter wings (Brown and Brown 1998). One such selection event occurred in June 2004. The extent of mortality that resulted from the severe weather of 2004 was limited, but it was second only to the major mortality event of 1996 in severity of mortality. The 2004 event was also the latest in the summer that weather-related mortality is known to have occurred in our study area. We detected apparent selection for lower wing asymmetry in 2004, with a corresponding drop in levels of wing asymmetry among yearlings the following summer (Fig. 3). Other morphological traits seemed unaffected by the 2004 event. Although another drop in wing asymmetry in 2001 (Fig. 3) might suggest another selection event of some kind in 2000, if so, it was not cold-weather-related and we did not detect it. The summer of 2000 was unusually dry, perhaps exerting selection on asymmetric individuals if drought affected foraging conditions. Although drought in 2000 and the cold weather event in 2004 may have produced patterns of selection similar to that of 1996, on balance it seems unlikely that directional selection in response to unusual environmental events has recurred frequently enough or has been intensive enough since the 1996 selection event to account, in general, for the morphological trajectories that we observed (Figs. 1, 2).

The continued evolution of Cliff Swallow morphology in the same direction as that following the 1996 selection event suggests that this population may have crossed to another fitness peak in the adaptive landscape (Wright 1931, Arnold et al. 2001, Benkman et al. 2005). With the virtual elimination of the smaller and longer-winged birds in 1996 (Brown and Brown 1998, Price et al. 2000), any ecological or social niche occupied by individuals of this phenotype would have been permanently vacated. In addition, and in the absence of appreciable immigration from populations not exposed to the 1996 selection event, presumably most of the additive genetic variation for small skeletal size and longer wings and tail would have been eliminated from the study population, given that avian morphology is highly heritable (Alatalo and Lundberg 1986, van Noordwijk et al. 1988, Wiggins 1989, Grant and Grant 1995). Consequently, the population may now experience a different fitness function in which larger birds with shorter wings continue to be favored. In support of this, we found some evidence that at least the distribution of tarsus length may have been bimodal before the selection event (Price et al. 2000). With the smaller mode now eliminated, the population as a whole cannot cross the adaptive "valley" of intermediate size because larger birds are continually favored over ones that drift back toward the deleterious intermediate size on the population's way to becoming smaller. The adaptive landscape model has been criticized, and few empirical studies support it (Coyne et al. 1997), but it seems consistent with

the patterns reported here. Linking size to fitness measures such as annual survival and nesting success would be necessary to better determine the applicability of the adaptive landscape concept to Cliff Swallow morphological evolution.

Why might birds with larger bills and shorter wings continue to be favored in the aftermath of the 1996 climatic event and in the absence of continuing episodic selection of this nature? One possibility is that avian morphology is responding to global climate change. Studies on multiple species from both North America and Europe have documented directional changes in morphological measurements over the past 50 years that are interpreted as responses to warming global climate (Przybylo et al. 2000, Yom-Tov 2001, Kanuscak et al. 2004, Guillemain et al. 2005, Yom-Tov et al. 2006, Monahan 2008, Van Buskirk et al. 2010). For many of these species, the trend is for shorter wings, as we documented for Cliff Swallows. The rationale offered is that warming climate favors smaller body size, based on Bergmann's biogeographic rule that animals in colder, more northerly latitudes tend to be larger (Ashton 2002).

However, for several reasons the climate-change hypothesis seems an unlikely explanation for directional change in morphology of Cliff Swallows in particular, and probably of birds in general. Although the trend in wing length for Cliff Swallows matched the pattern seen in other species, our skeletal measures showed that the Nebraska population increased in bill size and did not change in tarsus length (an index of body size), despite exhibiting the decline in wing length. Thus, studies that use only wing length (or mass, which in Cliff Swallows, at least, varies enormously across a day, a season, and with colony size; Brown and Brown 1996) as a surrogate of body size may not reflect a true reduction in skeletal size in some species. In addition, global climate change may lead to an increased frequency of unusually severe weather events such as we saw in 1996 (Easterling et al. 2000, Greenough et al. 2001, Rosenzweig et al. 2001), and if so, larger (not smaller) body size should be favored to allow animals to better endure these unpredictable events (e. g., by retaining more body fat; Ashton 2002). Finally, there is little evidence for most species that recent changes in morphology (that are putatively linked to climate) reflect microevolutionary genetic change, and they more likely represent phenotypic plasticity (Gienapp et al. 2008, Teplitsky et al. 2008).

Developmental plasticity (Cooch et al. 1991, Larsson et al. 1998) could account for these patterns (Figs. 1 and 2) if conditions during brood rearing were routinely better in the decade after the selection event (1996–2005) than in the decade before (1986–1995). With more food available or smaller populations of ectoparasitic Swallow Bugs (*Oeciacus vicarius*) in the nests, both of which may be influenced by summer rainfall and temperature (Brown and Brown 1999a, b), birds may attain larger skeletal size simply as a result of favorable conditions for nestling growth. This might also be brought about by higher-quality parents being overrepresented in the population after the selection event (see below), which could lead to greater nestling-provisioning rates. However, we found no evidence that seasonal weather patterns in the study area were different before and after the selection event. Thus, phenotypic plasticity during growth, at least that attributable to weather-driven environmental conditions, can probably be ruled out.

The gradual increase in wing asymmetry (presumably a deleterious trait) in Cliff Swallows following the selection event (Fig. 3)

supports studies on other organisms that show that fluctuating asymmetry has low heritability (e.g., Palmer and Strobeck 1997, Bryden and Heath 2000, Campo et al. 2005); otherwise, we should have seen a trajectory of little change in the population following the intense selection event. The elimination of highly asymmetric individuals in this population in 1996 may have reflected simply a culling of low-quality individuals, with fluctuating asymmetry being a reliable index of phenotypic quality. With the relaxation of the episodic selection event in subsequent years (except in 2004; see above) and the population returning by 2001 to a size equal to that before the selection event, individuals of lower (non-genetically-based) phenotypic quality presumably increased and led to higher average levels of observed fluctuating asymmetry (Fig. 3).

Morphometric traits in many bird populations clearly are not static and often show directional change over time (e.g., Larsson et al. 1998; Nowakowski 2000, 2002; Acquarone et al. 2004; Guillemain et al. 2005; Yom-Tov et al. 2006; Monahan 2008; Van Buskirk et al. 2010). There may be no single general explanation for these patterns (e.g., climate change), and understanding each species' ecology may be necessary in interpreting why morphology is so temporally variable. However, even in a population as well studied as the Cliff Swallows of southwestern Nebraska, the causes of the continuing directional changes in bill size and wing length remain unknown. Possibilities (at least for bill size) could include an increase in competition for the best nesting sites within colonies, increased competition to settle in colonies of particular sizes or to exclude other individuals from settling, better nest defense against conspecifics, increased competition (among males) for access to extrapair matings or (for females) to place as many parasitic eggs in other nests as possible, or habitat modifications (e.g., conversion of native prairie to crops) that have changed the size distribution of the birds' insect prey. All of these could potentially favor birds with larger bills, but there is no direct evidence that these factors have intensified in the study area in the past decade to the extent that we would expect an evolutionary response. The 1996 selection event and the subsequent directional changes in morphology may be two relatively independent phenomena; lack of similar data prior to 1996 prevents us from knowing this with certainty. Nevertheless, the directional selection that occurred in the extreme climatic event has clearly not been reversed in the subsequent decade, leading apparently to a relatively permanent microevolutionary change in the morphology of this species. Whether opposing selection occurs in discrete bouts at even longer intervals (≥ 10 years) and results in directional change in the other direction can be determined only by continued long-term study of this population.

ACKNOWLEDGMENTS

We thank S. Aldridge, J. Blackwell, K. Brazeal, A. Briceno, K. Cornett, S. Huhta, J. Klaus, A. Johnson, E. Landay, J. Leonard, L. Libaridian, J. Malfait, S. Narotam, C. Ormston, G. Redwine, S. Robinson, K. Rodgers, A. Rundquist, R. Sethi, M. Shanahan, S. Strickler, P. Wallace, and E. Westerman for field assistance. The School of Biological Sciences at the University of Nebraska-Lincoln allowed use of the facilities of the Cedar Point Biological Station. The R. Clary, D. Dunwoody, D. Knight, and L. Soper families and the Union Pacific Railroad granted access to land. Financial support

was provided to C.R.B. by the National Science Foundation (DEB-9613638, DEB-0075199, IBN-9974733, DEB-0514824), the National Institutes of Health (AI057569), and the National Geographic Society, and to M.B.B. by the University of Nebraska-Lincoln's School of Natural Resources and Nebraska Environmental Trust. For helpful comments on the manuscript we thank E. Blankenship, T. J. Fontaine, J. Jorgensen, L. Powell, and C. Thody.

LITERATURE CITED

- ACQUARONE, C., M. CUCCO, G. MALACARNE, AND F. SILVANO. 2004. Temporary shift of body size in Hooded Crows *Corvus corone cornix* of NW Italy. *Folia Zoologica* 53:379–384.
- ALATALO, R. V., AND A. LUNDBERG. 1986. Heritability and selection on tarsus length in the Pied Flycatcher (*Ficedula hypoleuca*). *Evolution* 40:574–583.
- ARNOLD, S. J., M. E. PFRENDER, AND A. G. JONES. 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* 112–113:9–32.
- ASHTON, K. G. 2002. Patterns of within-species body size variation of birds: Strong evidence for Bergmann's rule. *Global Ecology and Biogeography* 11:505–523.
- BENKMAN, C. W., J. S. COLQUITT, W. R. GOULD, T. FETZ, P. C. KEENAN, AND L. SANTISTEBAN. 2005. Can selection by an ectoparasite drive a population of Red Crossbills from its adaptive peak? *Evolution* 59:2025–2032.
- BENKMAN, C. W., AND R. E. MILLER. 1996. Morphological evolution in response to fluctuating selection. *Evolution* 50:2499–2504.
- BLANCKENHORN, W. U. 2000. The evolution of body size: What keeps organisms small? *Quarterly Review of Biology* 75:385–407.
- BROWN, C. R., AND M. B. BROWN. 1996. Coloniality in the Cliff Swallow: The Effect of Group Size on Social Behavior. University of Chicago Press, Chicago, Illinois.
- BROWN, C. R., AND M. B. BROWN. 1998. Intense natural selection on body size and wing and tail asymmetry in Cliff Swallows during severe weather. *Evolution* 52:1461–1475.
- BROWN, C. R., AND M. B. BROWN. 1999a. Fitness components associated with clutch size in Cliff Swallows. *Auk* 116:467–486.
- BROWN, C. R., AND M. B. BROWN. 1999b. Fitness components associated with laying date in the Cliff Swallow. *Condor* 101:230–245.
- BROWN, C. R., AND M. B. BROWN. 2000. Heritable basis for choice of group size in a colonial bird. *Proceedings of the National Academy of Sciences USA* 97:14825–14830.
- BROWN, C. R., AND M. B. BROWN. 2002. Ectoparasites cause increased bilateral asymmetry of naturally selected traits in a colonial bird. *Journal of Evolutionary Biology* 15:1067–1075.
- BROWN, C. R., AND M. B. BROWN. 2004. Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behavioral Ecology and Sociobiology* 56:498–511.
- BROWN, C. R., M. B. BROWN, AND K. R. BRAZEAL. 2008a. Familiarity with breeding habitat improves daily survival in colonial Cliff Swallows. *Animal Behaviour* 76:1201–1210.
- BROWN, C. R., M. B. BROWN, A. MOORE, AND N. KOMAR. 2007. Bird movement predicts Buggy Creek virus infection in insect vectors. *Vector-Borne and Zoonotic Diseases* 7:304–314.
- BROWN, C. R., M. B. BROWN, A. PADHI, J. E. FOSTER, A. T. MOORE, M. PFEFFER, AND N. KOMAR. 2008b. Host and vector movement

- affects genetic diversity and spatial structure of Buggy Creek virus (Togaviridae). *Molecular Ecology* 17:2164–2173.
- BROWN, M. B., AND C. R. BROWN. 2009. Blood sampling reduces annual survival in Cliff Swallows. *Auk* 126:853–861.
- BRYANT, D. M., AND G. JONES. 1995. Morphological changes in a population of Sand Martins *Riparia riparia* associated with fluctuations in population size. *Bird Study* 42:57–65.
- BRYDEN, C. A., AND D. A. HEATH. 2000. Heritability of fluctuating asymmetry for multiple traits in chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:2186–2192.
- BUMPUS, H. C. 1899. The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesticus*. *Biological Lectures of the Woods Hole Marine Biology Station* 6:209–226.
- CAMPO, J. L., M. G. GIL, S. G. DAVILA, AND I. MUNOZ. 2005. Estimation of heritability for fluctuating asymmetry in chickens by restricted maximum likelihood: Effects of age and sex. *Poultry Science* 84:1689–1697.
- CARROLL, S. P., A. P. HENDRY, D. N. REZNICK, AND C. W. FOX. 2007. Evolution on ecological time-scales. *Functional Ecology* 21:387–393.
- CLEGG, S. M., F. D. FRENTIU, J. KIKKAWA, G. TAVECCHIA, AND I. P. F. OWENS. 2008. 4000 years of phenotypic change in an island bird: Heterogeneity of selection over three microevolutionary timescales. *Evolution* 62:2393–2410.
- COOCH, E. G., D. B. LANK, R. F. ROCKWELL, AND F. COOKE. 1991. Long-term decline in body size in a Snow Goose population: Evidence of environmental degradation? *Journal of Animal Ecology* 60:483–496.
- COYNE, J. A., N. H. BARTON, AND M. TURELLI. 1997. A critique of Sewall Wright's shifting balance theory of evolution. *Evolution* 51:643–671.
- EASTERLING, D. R., J. L. EVANS, P. Y. GROSIMAN, T. R. KARL, K. E. KUNKEL, AND P. AMBENJE. 2000. Observed variability and trends in extreme climate events: A brief review. *Bulletin of the American Meteorological Society* 81:417–425.
- ENDLER, J. A. 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton, New Jersey.
- FEARE, K. K., AND T. PRICE. 1998. The adaptive surface in ecology. *Oikos* 82:440–448.
- GIBBS, H. L., AND P. R. GRANT. 1987. Oscillating selection on Darwin's finches. *Nature* 327:511–513.
- GIENAPP, P., C. TEPLITSKY, J. S. ALHO, J. A. MILLS, AND J. MERILÄ. 2008. Climate change and evolution: Disentangling environmental and genetic responses. *Molecular Ecology* 17:167–178.
- GRANT, B. R., AND P. R. GRANT. 1989. Natural selection in a population of Darwin's finches. *American Naturalist* 133:377–393.
- GRANT, B. R., AND P. R. GRANT. 1993. Evolution of Darwin's finches caused by a rare climatic event. *Proceedings of the Royal Society of London, Series B* 251:111–117.
- GRANT, P. R., AND B. R. GRANT. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 44:1796–1805.
- GRANT, P. R., AND B. R. GRANT. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707–711.
- GREENOUGH, G., M. MCGEEHIN, S. M. BERNARD, J. TRTANJ, J. RIAD, AND D. ENGELBERG. 2001. The potential impacts of climate variability and change on health impacts of extreme weather events in the United States. *Environmental Health Perspectives* 109 Supplement 2:191–198.
- GUILLEMAIN, M., J.-Y. MONDAIN-MONVAL, A. R. JOHNSON, AND G. SIMON. 2005. Long-term climatic trend and body size variation in Teal *Anas crecca*. *Wildlife Biology* 11:81–88.
- HAIRSTON, N. G., JR., AND W. E. WALTON. 1986. Rapid evolution of a life history trait. *Proceedings of the National Academy of Sciences USA* 83:4831–4833.
- JONES, G. 1987. Selection against large size in the Sand Martin *Riparia riparia* during a dramatic population crash. *Ibis* 129:274–280.
- KANUSCAK, P., M. HROMADA, P. TRYJANOWSKI, AND T. SPARKS. 2004. Does climate at different scales influence the phenology and phenotype of the River Warbler *Locustella fluviatilis*? *Oecologia* 141:158–163.
- LARSSON, K., H. P. VAN DER JEUGD, I. T. VAN DER VEEN, AND P. FORSLUND. 1998. Body size declines despite positive directional selection on heritable size traits in a Barnacle Goose population. *Evolution* 52:1169–1184.
- MATHYS, B. A., AND J. L. LOCKWOOD. 2009. Rapid evolution of Great Kiskadees on Bermuda: An assessment of the ability of the island rule to predict the direction of contemporary evolution in exotic vertebrates. *Journal of Biogeography* 36:2204–2211.
- MONAHAN, W. B. 2008. Wing microevolution in the House Sparrow predicted by model of optimized wing loading. *Condor* 110:161–166.
- NOWAKOWSKI, J. J. 2000. Long-term variability of wing length in a population of the Reed Warbler *Acrocephalus scirpaceus*. *Acta Ornithologica* 35:173–182.
- NOWAKOWSKI, J. J. 2002. Variation of morphometric parameters within the Savi's Warbler (*Locustella luscinioides*) population in eastern Poland. *Ring* 24:49–67.
- PALMER, A. R. 1994. Fluctuating asymmetry analyses: A primer. Pages 335–364 in *Developmental Instability: Its Origins and Evolutionary Implications* (T. A. Markow, Ed.). Kluwer, Dordrecht, The Netherlands.
- PALMER, A. R., AND C. STROBECK. 1997. Fluctuating asymmetry and developmental stability: Heritability of observable variation vs. heritability of inferred cause. *Journal of Evolutionary Biology* 10:39–49.
- PRICE, T., C. R. BROWN, AND M. B. BROWN. 2000. Evaluation of selection on Cliff Swallows. *Evolution* 54:1824–1827.
- PRICE, T. D., AND P. R. GRANT. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. *Evolution* 38:483–494.
- PRICE, T. D., P. R. GRANT, H. L. GIBBS, AND P. T. BOAG. 1984. Recurrent patterns of natural selection in a population of Darwin's finches. *Nature* 309:787–789.
- PRZYBYLO, R., B. C. SHELDON, AND J. MERILÄ. 2000. Climatic effects on breeding and morphology: Evidence for phenotypic plasticity. *Journal of Animal Ecology* 69:395–403.
- ROSENZWEIG, C., A. IGLESIAS, X. B. YANG, P. R. EPSTEIN, AND E. CHIVIAN. 2001. Climate change and extreme weather events: Implications for food production, plant diseases, and pests. *Global Change and Human Health* 2:90–104.
- SAS INSTITUTE. 2004. *SAS/STAT User's Guide*, version 9.1. SAS Institute, Cary, North Carolina.
- STIEPIELSKI, A. M., J. D. DiBATTISTA, AND S. M. CARLSON. 2009. It's about time: The temporal dynamics of phenotypic selection in the wild. *Ecology Letters* 12:1261–1276.

- TEPLITSKY, C., J. A. MILLS, J. S. ALHO, J. W. YARRALL, AND J. MERILÄ. 2008. Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Sciences USA* 105:13492–13496.
- VAN BUSKIRK, J., R. S. MULVIHILL, AND R. C. LEBERMAN. 2010. Declining body size in North American birds associated with climate change. *Oikos* 119:1047–1055.
- VAN NOORDWIJK, A. J., J. H. VAN BALEN, AND W. SCHARLOO. 1988. Heritability of body size in a natural population of the Great Tit (*Parus major*) and its relation to age and environmental conditions during growth. *Genetical Research* 51:149–162.
- WIGGINS, D. A. 1989. Heritability of body size in cross-fostered Tree Swallow broods. *Evolution* 43:1808–1811.
- WILCOXEN, T. E., R. K. BOUGHTON, AND S. J. SCHOECH. 2010. Selection on innate immunity and body condition in Florida Scrub-jays throughout an epidemic. *Biology Letters* 6:552–554.
- WRIGHT, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.
- YOM-TOV, Y. 2001. Global warming and body mass decline in Israeli passerine birds. *Proceedings of the Royal Society of London, Series B* 268:947–952.
- YOM-TOV, Y., S. YOM-TOV, J. WRIGHT, C. J. R. THORNE, AND R. DU FEU. 2006. Recent changes in body weight and wing length among some British passerine birds. *Oikos* 112:91–101.

Associate Editor: L. Joseph