INTENSE NATURAL SELECTION ON BODY SIZE AND WING AND TAIL ASYMMETRY IN CLIFF SWALLOWS DURING SEVERE WEATHER

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Abstract.—Extreme climatic disturbances provide excellent opportunities to study natural selection in wild populations because they may cause measurable directional shifts in character traits. Insectivorous cliff swallows (*Petrochelidon pyrrhonota*) in the northern Great Plains must often endure periods of cold weather in late spring that reduce food availability, and if cold spells last four or more days, mortality due to starvation may result. We analyzed morphological shifts associated with viability selection, and how patterns of bilateral symmetry were affected by survival selection, during a four-day period of cold weather in 1992 and a six-day period in 1996 in southwestern Nebraska. Birds that died during the cold were compared to those still alive when the severe weather ended. The event in 1992 killed relatively few birds, but the cold spell in 1996 killed thousands of cliff swallows and reduced their population by about 53%. Climatological records suggest that mortality events comparable to that of 1996 have occurred in only one other year since 1875. Larger birds were favored in the 1996 event. Selection was more intense in 1996 than in 1992 because of more stressful conditions in 1996. Directional selection gradient analysis showed that measures of skeletal body size (tarsus length, culmen width and length) and wing length were targets of selection in 1996. Survivors had lower wing and outer tail asymmetry, and wing and tail asymmetry were targets of selection in both events. Mortality patterns did not differ by sex, but older birds suffered heavier mortality; morphological traits generally did not vary with age. Nonsurvivors were not in poorer apparent condition prior to the weather event than survivors, suggesting that selection acted directly on morphology independent of condition. Selection on body size in cliff swallows was more intense than in studies of body size evolution in other bird species. Larger swallows were probably favored in cold weather due to the thermal advantages of large size and the ability to store more fat. Swallows with low asymmetry were favored probably because low asymmetry in wing and tail made foraging more efficient and less costly, conferring survival advantages during cold weather. This population of cliff swallows may have undergone relatively recent body size evolution.

Key words.—Climate, life history, morphology, mortality, Nebraska, *Petrochelidon pyrrhonota*, survival.

Extreme environmental perturbations provide excellent opportunities to witness natural selection in contemporary populations (Endler 1986; Hairston and Walton 1986). Events that are short in duration, well-defined spatially, and far beyond normal environmental extremes, are the most useful for documenting selection and may also represent a large part of the total natural selection imposed on a species (O'Donald 1973). Intense episodic evolution may be the norm for many populations (Wiens 1977), and climatic events are likely causal agents (Grant and Grant 1993). However, surprisingly few demonstrations exist of selection in response to short-term climatic perturbations (Endler 1986). The best examples, now classics, are Bumpus's much analyzed study of body size selection in sparrows during a winter storm (Bumpus 1899; Grant 1972; Johnston et al. 1972; O'Donald 1973; Buttemer 1992; Pugesek and Tomer 1996) and the discovery of directional selection for bill size and shape in Darwin's finches of the Galapagos during unusually dry years (Boag and Grant 1981; Price et al. 1984; Gibbs and Grant 1987; Grant and Grant 1989, 1993, 1995).

Selection in response to climatic extremes might be most frequent in populations that inhabit unpredictable, climatically variable environments. Migratory insectivorous birds of northern temperate latitudes regularly experience climatic variability upon their arrival on the breeding grounds, with spring or early summer cold spells temporarily reducing or eliminating their food supply for periods of several days. These short-term episodes, if severe enough, can potentially cause microevolutionary change, analogous to droughts that affect food supply or predation pressure over longer periods of time (e.g., Boag and Grant 1981; Hairston and Walton 1986; Grant and Grant 1993). Species that have traditionally experienced short-term periods of food scarcity in spring exhibit various adaptations associated with these events: arrival with high levels of body fat (Odum and Connell 1956; Odum et al. 1961; King et al. 1963; Ward 1963; Johnston 1966) that can be used in lieu of food for brief periods; torpor (Jaeger 1949; Calder 1974; Prinzinger and Siedle 1988; Heller 1989); deferment of arrival until after the risk of spring storms for younger individuals (Rohwer and Niles 1977); and behavior such as huddling (Prinzinger and Siedle 1988; Robertson et al. 1992; Brown 1997). When climatic perturbations are unusually severe, observable directional selection can occur, and adaptation to more extreme environmental conditions may result. These events are usually so rare and unpredictable, however, that field studies—especially ones that are not long term—can seldom take advantage of what climatic disturbances may tell us (Hairston and Walton 1986).

We examined natural selection in cliff swallows (*Petrochelidon pyrrhonota*) during two rare, short-term climatic events of different severities. Events equivalent to the more severe of these apparently have occurred only twice in the last 123 years. These episodes thus represent conditions far beyond normal environmental extremes and provide opportunity for selection. We investigated morphological shifts associated with viability selection during these events and how patterns of bilateral symmetry were affected by survival selection. Degree of asymmetry is considered by some to be a

TABLE 1. Average daily maximum and minimum temperatures and total daily precipitation for weather events that led to swallow mortality in southwestern Nebraska, 1875–1997, compared to 123-yr average maximum and minimum temperatures for each period.*

Starting date	Duration (days)	Average maximum temperature (°C)	Average minimum temperature (°C)	No. days with measurable precipitation	Average precipitation per day (cm)
24 May 1996	6	11.1	6.4	3	1.7
123-yr average		24.0	9.0		
26 May 1992	4	9.2	0.9	1	0.1
123-yr average		24.1	9.1		
20 May 1988	4	11.1	7.1	4	2.4
123-yr average		23.0	8.0		
23 May 1976	4	11.0	6.5	3	2.3
123-yr average		23.6	8.6		
27 May 1967	7	12.1	6.6	6	0.9
123-yr average		24.6	9.6		
12 May 1943	6	10.4	2.9	3	0.3
123-yr average		21.7	6.7		
12 May 1935	9	10.3	6.7	7	1.1
123-yr average		22.0	7.0		
15 May 1930	4	8.6	2.8	3	1.4
123-yr average		22.1	7.1		
12 May 1920	5	10.0	4.2	3	0.7
123-yr average		21.6	6.7		
12 May 1916	4	10.4	5.2	2	0.3
123-yr average		21.5	6.5		
7 May 1892	8	9.9	3.4	6	0.9
123-yr average		21.1	6.0		

* Average values taken exclusively from North Platte reporting station, 1875–1997. Further details of these data can be obtained from the authors.

useful measure of developmental stability (Leamy and Atchley 1985; Clarke et al. 1986; Palmer and Strobeck 1986; Parsons 1990; Rowe et al. 1997) and therefore an indicator of individual quality useful in mate choice (e.g., Møller and Hoglund 1991; Møller and Pomiankowski 1993; Gangestad et al. 1994; Watson and Thornhill 1994), although others have urged caution in such interpretations (Palmer and Strobeck 1992; Balmford et al. 1993; Markow 1995; Palmer 1996). The episodic selection events we observed enabled us to examine whether observed levels of asymmetry were associated with viability in these species and thus whether asymmetry is a reliable predictor of individual fitness. Our results provide one of the few demonstrations of intense selection on body size in response to short-term environmental perturbations and perhaps the first direct demonstration of selection for low asymmetry in the wild. Our study is primarily of selection on phenotypic characteristics within generations, but we present limited information on the response to selection between generations.

METHODS

Study Organism and Study Site

Cliff swallows are 20–28-g neotropical migrants that breed throughout most of western North America and winter in southern South America (Brown and Brown 1995). They feed exclusively on aerial insects and can forage only when weather conditions allow flying insects to be active. The birds' gourd-shaped, mud nests are placed beneath overhanging rock ledges on the sides of steep cliffs or underneath the protected eaves of artificial structures such as bridges and buildings. Cliff swallows often breed in dense colonies, and

colony size within a population varies widely. In southwestern Nebraska, mean (± SE) colony size is 393.0 (± 24.3) nests, ranging from birds that nest solitarily to colonies of 3700 nests (Brown and Brown 1996). In southwestern Nebraska, most cliff swallows arrive in early and mid-May, and breeding is largely completed by the end of July.

Our research is conducted along the North and South Platte Rivers, centered near Ogallala, and includes all or part of Keith, Garden, Lincoln, and Deuel Counties, southwestern Nebraska. Our study area is approximately 150 × 50 km and contains about 165 separate colony sites where cliff swallows breed, about 100 of which are active in any given year. The research site is described in detail by Brown and Brown (1996).

Weather Events and Field Collections

Cliff swallows are affected by periods of cold, rainy weather that reduce the availability of the flying insects on which they feed. Mortality may result if these conditions extend over several days (Anderson 1965; DuBowy and Moore 1985; Littrell 1992; Brown and Brown 1996). Weather events that led to swallow mortality occurred during 1992 and 1996 (Table 1). A third event in 1988 killed small numbers of birds (Brown and Brown 1996), but is not included in this study because the few dead birds found were not saved as specimens.

After each period of bad weather ended (as soon as the swallows resumed foraging), we surveyed colony sites for dead birds. In 1992 we visited a subset of 15 sites; in the more severe event of 1996, we visited all active colony sites in the study area. All dead birds found were placed in plastic

bags and frozen immediately. In most cases these were lying on the ground or floating in water underneath nests, although at some sites we removed dead birds from inside nests. Only dead birds found in the one to three days immediately after the cold weather were used in morphometric analyses. Mummified or decayed specimens found in nests later in the summer and dating from the cold weather, if banded, were used in analyses involving age or prior condition but were not saved or measured.

For the 1996 event, birds designated as survivors were those captured in mist nets at colony sites during the nine days immediately following the cold weather. Confining our sample to this time period minimized the probability of including as survivors any immigrants that might have arrived after the cold weather and that had not experienced selection. Although we could not entirely rule out possible pollution of our "survivors" by recent immigrants, the geographical scope of the 1996 weather event was extensive enough (see Results) that even immigrants likely experienced the same conditions elsewhere. For the less severe 1992 weather event, we used specimens of birds collected after the cold weather (net casualties, road kills, or ones killed due to other non-weather causes) as survivors for comparison.

In 1997, we mist-netted and measured 193 cliff swallows that had been banded as either nestlings or fledglings in the study area in 1996. These birds represented the first generation after selection; their parents had to have been survivors of the 1996 event by virtue of their having produced offspring in the study area. Our sample of yearlings in 1997 was obtained by systematically netting at colonies in the course of a mark-recapture project.

Measurements

For all birds, we measured length of each unflattened, closed wing (from the most anterior part of the wrist joint to the tip of the outermost primary) to the nearest 1 mm with a wing ruler; length of the middle tail feather (from its emergence from the skin to the most distal point) to the nearest 1 mm with a ruler; length of the left tarsus (from the proximate end of the tarso-metatarsus to the hallux) to the nearest 0.1 mm with calipers; and length and width of 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) to the nearest 0.1 mm with calipers. We elected not to measure the right tarsus and the outer tail feathers on surviving (living) cliff swallows in 1996 due to the length of processing time required per bird, although these measurements were taken on the 1997 sample of living birds. For birds associated with the 1992 mortality event, all of which were measured as museum skins, we took all of the above measurements including length of the outermost tail feather on each side plus length of both tarsi for both survivors and nonsurvivors. Wing and tail feathers that were broken or in any way damaged were not measured for any birds.

For 1996, survivors were measured while living and non-survivors three to four months after death. Nonsurvivors were completely thawed before measurement, and measurements were taken before the specimens were prepared as museum

TABLE 2. Morphological measurements of 29 cliff swallows measured alive and later as specimens in 1996–1997. Traits that showed significant differences (paired t-test after sequential Bonferroni correction) are shown in boldface.

	Alive		Dead		
	Mean	SE	Mean	SE	P
Wing length (mm)	106.48	0.45	106.29	0.51	0.49
Middle tail length (mm)	**46.69**	**0.35**	**45.79**	**0.31**	**0.007**
Tarsus length (mm)	11.60	0.12	11.73	0.10	0.20
Culmen length (mm)	7.09	0.08	7.21	0.08	0.04
Culmen width (mm)	6.20	0.05	6.27	0.06	0.18
Wing asymmetry*	0.76	0.19	0.38	0.14	0.07

* Unsigned R − L.

skins. Measurement of living birds and ones preserved as specimens sometimes introduces a measurement bias due to skin shrinkage or other artefacts of freezing or storage (Johnson et al. 1980). To legitimately compare morphology of 1996 survivors and nonsurvivors, we assume no such measurement bias. This assumption was met for cliff swallows (Table 2). For 29 birds first measured while alive in 1996–1997 and later found dead due to nonweather causes and measured again as thawed specimens, we found no systematic differences between measurements taken on living and dead birds (Table 2). Only middle tail length differed significantly, being smaller when birds were measured dead. However, this difference was *opposite* that seen among survivors and nonsurvivors (see Table 3), indicating that measurement bias cannot explain the observed morphological differences among survivors and nonsurvivors. This conclusion was further supported by the direction of the differences in the measurements for all other traits (Table 2), which although nonsignificant, also tended to be in an opposite direction from that seen among survivors and nonsurvivors (Table 3). Thus, our tests for selection on these morphological traits in 1996 were conservative.

All measurements of both living and dead birds were made by one person only (MBB). Thus, no correction factors (e.g., Price and Grant 1984; Bryant and Jones 1995; Grant and Grant 1995) for multiple measurers were necessary. Repeatabilities of our body size measures were estimated using intraclass correlation (r_I; Zar 1974) from a sample of 163 birds that were measured twice. This sample included 52 living birds measured twice in the field (survivors) and 111 birds measured twice as specimens (nonsurvivors), all from 1996. The field sample was chosen randomly by virtue of the double measures being done on birds by mistake; the rest were chosen blind from preserved specimens.

In the analyses that follow, wing length and, for the 1992 birds, outermost tail length and tarsus length represent the average of the right and left values per bird. The reliability of univariate measures of avian body size (e.g., wing length) has been debated (Rising and Somers 1989; Freeman and Jackson 1990; Wiklund 1996), and multivariate measures may provide a more realistic index. Following Via and Shaw (1996), we used the mean of the log-transformed p original variables, $[\Sigma \ln (X_i)]/p$, where X_i is the value of the ith variable for a given observation, as our overall measure of body size. To make our mean body size measures for 1996 and 1992

TABLE 3. Morphological characteristics and age of cliff swallows that survived and did not survive periods of severe weather in southwestern Nebraska and tests of significance of differences (those significant after sequential Bonferroni correction in boldface).

	Survivors			Nonsurvivors			
	Mean	SE	n	Mean	SE	n	P*
1996							
Wing length (mm)	106.87	0.07	1028	107.53	0.06	1843	**< 0.0001**
Middle tail length (mm)	46.13	0.06	1027	46.65	0.05	1838	**< 0.0001**
Tarsus length (mm)	11.52	0.02	1027	10.00	0.01	1853	**< 0.0001**
Culmen length (mm)	6.94	0.01	1027	6.33	0.01	1795	**< 0.0001**
Culmen width (mm)	6.27	0.01	1027	5.54	0.01	1795	**< 0.0001**
Mean body size	2.94	0.00	1027	2.87	0.00	1781	**< 0.0001**
Wing asymmetry*	0.49	0.02	891	1.20	0.05	1832	**< 0.0001**
Age (yrs)	1.96	0.11	163	2.59	0.16	131	**0.002**
Body mass prior to cold weather (g)	25.19	0.23	96	24.50	0.37	45	0.14
Condition index*	1.31	0.01	30	1.38	0.01	31	**< 0.0001**
1992							
Wing length (mm)	108.53	0.26	62	108.74	0.36	41	0.74
Middle tail length (mm)	45.43	0.26	62	44.58	0.62	41	0.25
Outer tail length (mm)	48.68	0.19	62	47.07	0.76	41	0.005
Tarsus length (mm)	10.50	0.08	62	10.38	0.09	41	0.33
Culmen length (mm)	6.44	0.04	62	6.36	0.07	41	0.44
Culmen width (mm)	5.54	0.04	62	5.51	0.06	41	0.88
Mean body size	2.88	0.00	62	2.87	0.01	41	0.29
Wing asymmetry*	0.42	0.08	62	1.58	0.17	41	**< 0.0001**
Outer tail asymmetry*	0.55	0.09	62	2.05	0.24	41	**< 0.0001**
Tarsus asymmetry*	0.25	0.03	62	0.34	0.04	41	0.06

* Based on nonparametric Wilcoxon rank sum test.
** Unsigned R − L.
*** log(body mass)/log(tarsus length).

comparable, we did not use outer tail length in calculating the mean body size for 1992, because this measurement was unavailable for the 1996 sample.

Cliff swallows are sexually monochromatic, presenting difficulties in determining sex even among breeding birds. Sexes were determined by dissection for 1992 birds and by field methods—presence or absence of a cloacal protuberance or brood patch (Brown and Brown 1996)—for those in 1996. However, sexes were not known for many of the nonsurvivors in 1996. Only nonsurviving birds that had been banded and sexed in an earlier year while alive could be included in analyses involving sex. Field methods for sexing were unreliable for birds once dead, especially emaciated ones that had been frozen. Unbanded nonsurvivors could be accurately sexed only by dissection when prepared as museum skins. Due to the length of time required for preparing and dissecting the sample of nonsurviving birds from 1996 (n = 1856), we elected to defer most analyses based on sex. Use of only banded, previously sexed nonsurvivors in analyses involving sex introduced potential biases because of possible associations between age and sex and the fact that the nonsurvivors of known sex were, for the most part, older birds (see Results). Overall sample sizes in 1992 were too small to allow rigorous analysis by sex for that event. Ages were assigned for all birds that had been banded in an earlier year as a nestling or recently fledged juvenile (Brown and Brown 1996).

In 1996, condition of cliff swallows before the cold weather was inferred from body masses taken on birds netted at colony sites during the six days before the cold spell, beginning on 18 May. During this time, we captured 515 birds and weighed them with a Pesola scale to the nearest 0.5 g. Of

this sample we found 45 individuals dead after the cold weather; 96 were known to have survived by virtue of having been recaptured later in the summer. These mass data were taken from several colonies, and a colony-by-colony analysis would have been most appropriate. However, we were forced to combine birds from all colonies due to the small sample size. Not all birds weighed before the cold weather and known to have survived or died were later measured. To separate the effect of body size on mass, we computed log(mass)/log(tarsus length) as a measure of body condition. We did not include body mass (or age) in our analyses of selection differentials and gradients, because sample sizes for these variables were so small compared to those for the other morphological traits studied in 1996 (see Table 3).

Our measure of asymmetry in most analyses was the absolute (unsigned) difference between right and left sides. Because our wing and tail measurements were taken only to the nearest 1 mm (more precise measures were impractical on living birds), we underestimated true levels of asymmetry for these traits. When asymmetry varies inversely with the size of a character (Møller and Pomiankowski 1993; Rowe et al. 1997), measures of asymmetry are sometimes standardized by dividing the absolute difference between right and left sides by character size (e.g., Palmer and Strobeck 1986). Although outer tail asymmetry declined with trait size in cliff swallows (see Results), we did not use standardized values of asymmetry because doing so in our selection gradient analyses would have included measures of the same variable (character size) twice in the multiple regression. Furthermore, the selection gradients control for correlations between traits. The extent to which estimated asymmetry could be distinguished from measurement error was assessed with

a mixed-model ANOVA following the method of Swaddle et al. (1994). For this we used the sample of 163 birds that had been measured twice (above).

Weather Data

Climatological data for 1948–1997 were taken from a long-term monitoring site in Arthur County, Nebraska, about 48 km directly north of the center of the study area (Brown and Brown 1996). This site was part of the University of Nebraska's Automated Weather Data Network and recorded daily high and low temperatures and amount of precipitation. Similar temperature and rainfall data for 1875–1947, before the Arthur station was established, came from a National Weather Service site at North Platte on the eastern edge of the study area.

Estimating Population Size

We estimated relative population size of cliff swallows in the study area by summing the total number of active nests at 150 colony sites from 1990–1996. These sites were those that were surveyed for size and use each year and included most of the colony sites in the study area. Active nests were counted in late June or early July several weeks after any mortality events had occurred. Methods of estimating colony size at a site are described in detail by Brown and Brown (1996).

Statistical Analyses of Selection

Standardized directional (i) and variance (j) selection differentials (Endler 1986) were calculated using the combined set of survivors and nonsurvivors as the before-selection group and the survivors as the after-selection group. Significance tests for i and j were done following Endler (1986, pp. 172–173) where nonsurvivors represented the unselected group and survivors the selected group, yielding two independent samples. Directional (β) and variance (γ) selection gradients (Lande and Arnold 1983; Arnold and Wade 1984) were estimated from linear and from quadratic standardized partial-regression coefficients of relative fitness (survival) on each trait (e.g., Grant and Grant 1993, 1995). γ coefficients were those obtained from a quadratic regression when the linear terms were excluded, as recommended by Brodie et al. (1995). Survivors were assigned a relative fitness of one and nonsurvivors zero. Because mean body size was a multivariate measure, it was not included in the selection gradient analyses. Regressions, correlation coefficients, and summary statistics were performed with SAS (SAS Institute 1990). We applied sequential Bonferroni corrections (see Rice 1989) to tables containing multiple statistical tests. P-values shown in tables are uncorrected ones; those comparisons significant at $P \leq 0.05$ after the Bonferroni correction are generally indicated in boldface.

RESULTS

Characteristics and History of Weather Events

Cold spells of two to three days are regular in April, May, and early to mid-June in southwestern Nebraska (Brown and

Brown 1996), but in the 16-year duration of our study no cliff swallow mortality attributed to weather ever occurred during two- to three-day cold spells. Cold and rainy weather had to last four or more days to kill birds, and three such periods occurred during the study (Table 1). These weather events were characterized by four to six days of maximum temperatures usually $\leq 15°C$ (generally 7–18° below normal maximums), minimum temperatures $< 8°C$, and precipitation on some or all of the days (Table 1). Days preceding and following the periods shown in Table 1 had maximum temperatures mostly $\geq 23°C$ and little or no precipitation, conditions sufficient for swallows to find food without any known mortality. Rain seems to have the largest effect on insectivorous birds such as cliff swallows, because these birds do not feed in extended periods of rain regardless of temperature (C. Brown and M. Brown, pers. obs.). The severe weather of 1996 was unusual in lasting for six days.

Climatological records for the study area dating to 1875 suggest that weather events severe enough to cause mortality are infrequent, especially ones lasting more than four days. We searched the records for past periods of four or more days in length with climatological characteristics similar to those that led to swallow mortality during the study. Because few cliff swallows arrive in the study area before 7 May, we restricted our search to 8–31 May and all of June and July. Three other four-day events (in 1976, 1930, and 1916) and five additional periods of more than four days (in 1967, 1943, 1935, 1920, and 1892) occurred (Table 1). However, probably only the event in 1967 was comparable to the 1996 mortality. This is because the cold spells of 1943, 1935, 1920, and 1892 occurred earlier in May, all prior to 20 May, when fewer birds would have been present and those there would not have been as far into the breeding cycle. In years with cold weather occurring as early as 12 May, cliff swallows' arrival in the study area is typically delayed (C. Brown and M. Brown, pers. obs.). The 1967 event, in contrast, which extended for seven days (Table 1), may have had an even greater impact than that in 1996 due to its longer duration and greater rainfall. Thus, during the 123-year period from 1875 through 1997, probably only two catastrophic climatic events have impacted cliff swallow populations in the study area.

Impact of Weather Events

So few cliff swallows died during the 1988 cold spell (we found only 11 dead birds; Brown and Brown 1996) that its overall effect was negligible, and it is not considered further in this paper. In 1992, mortality at some colony sites reached 90 birds (Brown and Brown 1996) and extended at least into southwestern Kansas (Jaramillo and Rising 1995), but population size was unaffected. Population size in the study area from 1990–1995 was stable: Total active nests counted in these years were 30,033; 32,101; 31,439; 30,612; 28,849; and 29,490, respectively. The six-day spell of cold weather in 1996, however, caused heavy mortality and reduced the population by about 53% (13,827 active nests in 1996). We salvaged 1856 dead cliff swallows, and thousands more dead ones were inaccessible to us: They fell into water beneath colony sites and were washed away or died in nests that we could not reach. The geographical scope of the 1996 mortality

TABLE 4. Repeatability (r_I) of morphological measurements in cliff swallows, taken from 52 birds measured twice while alive during the same breeding season (1996) and 111 dead birds measured twice as specimens. Missing repeatabilities were due to these measurements not being taken on live birds in 1996. All repeatabilities were highly significant ($P < 0.0001$, sequential Bonferroni corrections).

	Alive		Dead	
	r_I	SE	r_I	SE
Right wing length	0.921	0.056	0.955	0.029
Left wing length	0.873	0.085	0.968	0.024
Middle tail length	0.724	0.095	0.943	0.032
Right outer tail length	—	—	0.988	0.015
Left outer tail length	—	—	0.965	0.025
Right tarsus length	—	—	0.910	0.039
Left tarsus length	0.755	0.093	0.938	0.033
Culmen length	0.657	0.107	0.921	0.038
Culmen width	0.615	0.111	0.899	0.043
Wing asymmetry*	0.771	0.058	0.891	0.020
Outer tail asymmetry*	—	—	0.851	0.004
Tarsus asymmetry*	—	—	0.682	0.051

* Unsigned R − L.

event was extensive. We received reports of dead cliff swallows from north-central Iowa westward to eastern Wyoming, and weather records suggested that mortality extended north into South Dakota and possibly south into northern Kansas.

Repeatability and Measurement Error

The repeatabilities of our body size measures for cliff swallows were all statistically significant (Table 4). These were similar in magnitude to those in other studies of morphological variation (e.g., Balmford et al. 1993; Møller 1994). Dividing our sample of doubly measured birds into ones measured while alive and those done as specimens or carcasses, we found that repeatabilities tended to be lower for living birds (Table 4). This reflected both the fact that cliff swallows struggle while being handled and the less controlled physical conditions (e.g., lighting, wind) under which field samples are taken. Culmen width was the least repeatable measure, although still significant (Table 4). These data show that measurements of morphology in cliff swallows had a relatively high precision.

Wing asymmetry was significantly higher than expected based on measurement error ($F_{162,304} = 6.60$, $P < 0.0001$). Thus, measures of wing asymmetry had a relatively high degree of precision (see also Table 4) and do not represent "noise" in the measurement process. In contrast, outer tail asymmetry and tarsus asymmetry were not higher than expected based on measurement error (tail: $F_{110,220} = 0.07$, $P = .99$; tarsus: $F_{162,272} = 0.66$, $P = 0.99$). This is perhaps not surprising given that tail and tarsus were harder to measure. The inability to distinguish asymmetry from measurement error within a sample does not necessarily invalidate a comparison between populations (e.g., survivors vs. nonsurvivors), especially if a biologically significant difference is found (Swaddle et al. 1994; Møller 1997), but it does require caution in concluding that there is no difference in tail asymmetry or tarsus asymmetry between groups.
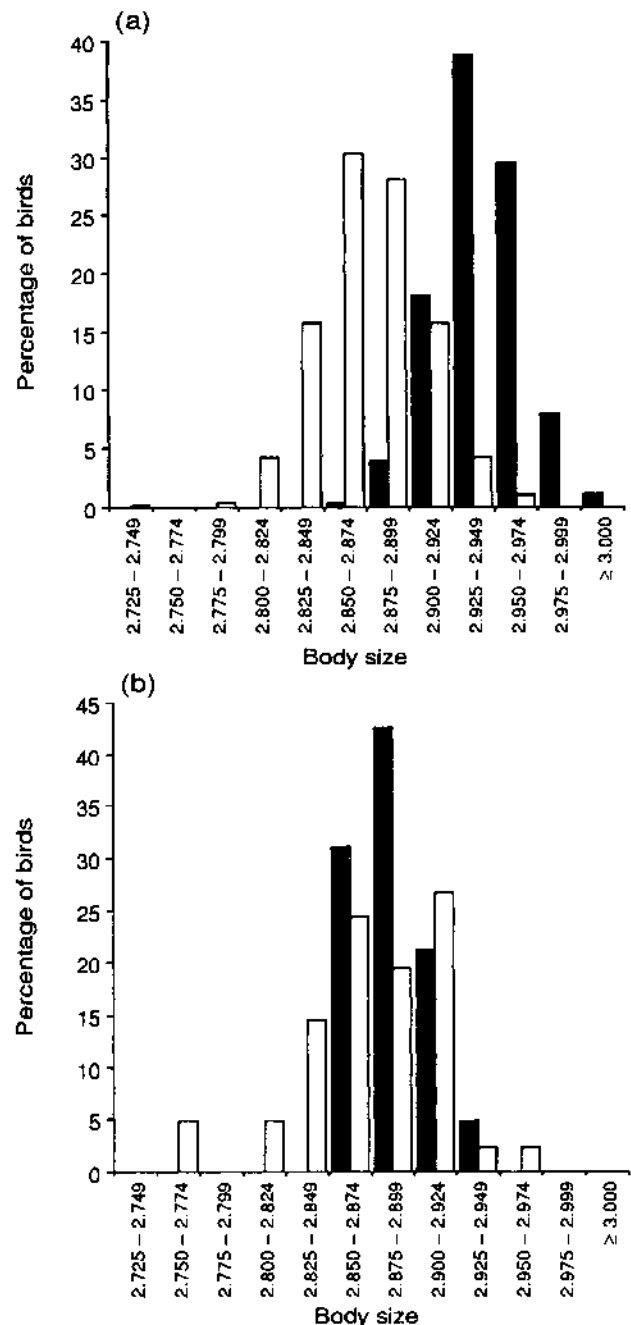

FIG. 1. Percentage distributions of mean body size for cliff swallows that survived (solid bars) and did not survive (open bars) a period of cold weather in 1996 (a) and 1992 (b). Sample sizes are shown in Table 3. The distributions of survivors and nonsurvivors differed significantly in 1996 ($\chi^2_{11} = 1802.1$, $P < 0.0001$) and in 1992 ($\chi^2_7 = 21.4$, $P = 0.003$).

Selection on Body Size

Surviving cliff swallows tended to have shorter wings, longer tarsi, and longer and wider culmens than nonsurvivors (Table 3). These differences led to a pronounced shift toward larger body size among survivors of the more severe 1996 event (Fig. 1a). Directional selection differentials, showing the net effect of selection on trait means (Table 5), were

TABLE 5. Standardized directional (i) and variance (j) selection differentials, directional selection gradients estimated from linear partial-regression coefficients (β), variance selection gradients estimated from quadratic partial-regression coefficients (γ), and significance levels of each (those significant after sequential Bonferroni correction in boldface), for episodes of selection on cliff swallows in southwestern Nebraska.

	i	P	j	P	β	P	γ	P
1996								
Wing length	−0.183	<0.0001	−0.211	<0.0001	−0.0268	<0.0001	−0.00004	0.82
Middle tail length	−0.172	<0.0001	−0.106	0.004	−0.00156	0.55	−0.00072	0.002
Tarsus length	1.0956	<0.0001	−0.560	<0.0001	0.325	<0.0001	0.00956	0.11
Culmen length	0.837	<0.0001	−0.553	<0.0001	0.0835	<0.0001	−0.0153	0.40
Culmen width	0.906	<0.0001	−0.484	0.24	0.221	<0.0001	0.0622	0.022
Mean body size	0.995	<0.0001	−0.680	<0.0001				
Wing asymmetry*	−0.262	<0.0001	−0.850	<0.0001	−0.0218	<0.0001	0.00144	0.031
Model r^2					0.74		0.84	
1992								
Wing length	−0.0181	0.62	−0.102	0.17	0.0135	0.50	−0.00198	0.35
Middle tail length	0.0376	0.16	−0.527	<0.0001	−0.0205	0.40	−0.00950	0.24
Outer tail length	0.0566	0.017	−0.802	<0.0001	0.0247	0.27	−0.00494	0.59
Tarsus length	0.131	0.34	0.0507	0.33	−0.0097	0.88	−0.0414	0.46
Culmen length	0.247	0.25	−0.390	<0.001	0.210	0.13	−0.0321	0.90
Culmen width	0.128	0.60	−0.223	0.023	−0.127	0.42	0.0401	0.88
Mean body size	0.127	0.73	−0.419	<0.0001				
Wing asymmetry*	−0.444	<0.0001	−0.607	<0.0001	−0.202	<0.0001	−0.0192	0.35
Outer tail asymmetry*	−0.344	<0.0001	−0.741	<0.0001	−0.141	<0.0001	−0.00427	0.79
Tarsus asymmetry*	−0.579	0.075	−0.0412	0.42	−0.269	0.08	−0.00678	0.90
Model r^2					0.50		0.62	

* Unsigned R − L.

highly significant for all morphological traits in 1996. The directional selection differentials (i) show that selection favored birds with shorter wings and tails but larger skeletal size as measured by tarsus and culmen. Fewer of the directional selection differentials for 1992 were significant (Table 5), although the trends generally matched those of 1996. The large directional selection differentials in 1996 suggest intense directional viability selection on morphological traits during the more severe cold spell.

Directional selection gradients, measuring the effect of selection on each trait's mean independent of selection on correlated traits (Lande and Arnold 1983; Arnold and Wade 1984), reveal strong selection on skeletal measures of size (culmen dimensions and tarsus length) in 1996 (Table 5). Wing length was also a target of selection, with shorter wings being favored independent of selection for larger culmen and tarsi. Middle tail length was not a target of selection in 1996 (Table 5). In the 1992 event, none of the body size measurements were significant in the directional selection gradient analysis (Table 5).

Variance selection differentials (j), a measure of the net change in variance (Lande and Arnold 1983; Endler 1986), were predominantly negative (Table 5), indicating reduced phenotypic variance in most traits after selection. All of those that were significant were negative. However, despite the reduction in overall phenotypic variance, the variance selection gradient (Table 5) indicated little evidence for strong stabilizing selection during these events. The partial regression coefficients (γ), a measure of univariate nonlinear selection (Brodie et al. 1995), were all nonsignificant in 1992, and in 1996 only one was significant (Table 5). Only middle tail length was an apparent target of stabilizing selection when the effects of directional selection were removed.

We also looked for bivariate nonlinear selection using the

cross-product terms of the quadratic regression (Brodie et al. 1995). In the variance selection gradient for both 1996 and 1992, none of the cross-product terms were significant after sequential Bonferroni corrections were applied. Thus, there was no strong evidence for nonlinear correlational selection on combinations of wing, tail, and tarsus. Correlational selection is best explored graphically (Schluter and Nychka 1994), however, which is beyond the scope of this paper.

Nature of Asymmetry Variation

Statistical measures of asymmetry in wing, tail, and tarsus in cliff swallows departed from those expected in ideal fluctuating asymmetry (Table 6). Signed values of R − L should be normally distributed with mean zero if fluctuating asymmetry is present (Palmer and Strobeck 1986). In cliff swallows we found that mean signed asymmetry often differed significantly from zero (Table 6), indicating directional asymmetry. All mean signed asymmetry values in our study were negative (Table 6). Rather than reflecting a real biological result, however, these negative values probably indicate only a measurement bias stemming from the "handedness" of the measurer. Left-sided traits tended to be measured as larger than right sided ones, and this held both for birds measured alive (survivors) and those measured dead (nonsurvivors; Table 6). Because the handedness bias applied to all classes of birds and repeatabilities were high (Table 4), this "directional" asymmetry does not affect our conclusions about relative differences among survivors and nonsurvivors.

Skewness and kurtosis values also suggested a departure from ideal fluctuating asymmetry (Table 6). Measures of wing asymmetry in both years were not normally distributed, whereas outer tail and tarsus asymmetry varied in the degree to which they conformed to a normal distribution. Skewness

TABLE 6. Statistical descriptors of asymmetry in cliff swallows that survived and did not survive periods of severe weather in southwestern Nebraska (sample sizes given in Table 3).

| | Survivors | | | | | | Nonsurvivors | | | | | |
| | Mean unsigned asymmetry (± SE) | Signed R − L asymmetry | | | | | Mean unsigned asymmetry (± SE) | Signed R − L asymmetry | | | | |
		Mean (± SE)	$P(t)^*$	Skewness	Kurtosis	$P(W)^{**}$		Mean (± SE)	$P(t)^*$	Skewness	Kurtosis	$P(W)^{**}$
1996												
Wing	0.49 (± 0.02)	−0.27 (± 0.03)	<0.0001	−1.16	5.90	<0.0001	1.20 (± 0.05)	−0.12 (± 0.06)	0.036	20.70	695.6	<0.0001
1992												
Wing	0.42 (± 0.08)	−0.03 (± 0.10)	0.74	0.28	1.89	<0.0001	1.58 (± 0.17)	−0.76 (± 0.28)	0.010	1.63	4.21	<0.0001
Tail	0.55 (± 0.09)	−0.29 (± 0.10)	0.007	−0.53	−0.03	<0.0001	2.05 (± 0.24)	−0.73 (± 0.39)	0.065	−0.03	0.07	0.43
Tarsus	0.25 (± 0.03)	−0.06 (± 0.04)	0.15	0.24	0.77	0.08	0.34 (± 0.04)	−0.20 (± 0.06)	0.001	0.27	−0.37	0.41

* Probability that mean signed asymmetry = 0 (one-sample t-test).
** Probability that signed asymmetry is normally distributed (W test; SAS Institute 1990).

and kurtosis values for wing asymmetry among nonsurvivors were much larger than comparable values for survivors (Table 6), reflecting a pronounced leptokurtic distribution among nonsurvivors (likely caused by the selective mortality of the highly asymmetric individuals; see next section). These patterns of asymmetry variation reflect differential growth and not feather breakage, because no birds with damaged feathers were included in asymmetry calculations.

Unsigned R − L asymmetry did not vary significantly with mean trait size for wing but declined significantly for outer tail (Fig. 2). Visual inspection of these scatterplots suggests that outer tail asymmetry resembles antisymmetry, which Rowe et al. (1997) argue may be common even among datasets thought to represent fluctuating asymmetry. However, for both wing asymmetry and outer tail asymmetry, the lower bound (fifth percentile) of each half of the trait distribution equalled zero, a result more consistent with fluctuating asymmetry (Rowe et al. 1997).

Selection on Asymmetry

Surviving birds had lower unsigned asymmetry during both selection events (Table 3). Differences were most obvious in wing asymmetry and outer tail asymmetry (Fig. 3a,b); the frequency distributions of asymmetry values for survivors and nonsurvivors differed significantly. These differences between groups were detectable even though we underestimated the true extent of asymmetry in wing and tail (see Methods). The same general pattern, although nonsignificant, held for tarsus asymmetry (Fig. 3c). Directional selection differentials for wing asymmetry and outer tail asymmetry showed that birds with smaller asymmetry were favored in both weather events, and variance selection differentials showed that phenotypic variance in wing asymmetry and outer tail asymmetry was reduced after selection (Table 5). The lack of a difference in tarsus asymmetry between survivors and nonsurvivors (Fig. 3c) should be qualified by the difficulty in separating tarsus asymmetry from measurement error (see Repeatability and Measurement Error).

Selection gradient analysis suggested that asymmetry in wing and outer tail were targets of directional selection, in-

dependent of other traits, in both weather events (Table 5). Tarsus asymmetry approached significance in the directional selection gradient for the 1992 cliff swallows (tarsus asymmetry was unavailable for the 1996 birds).

As with measures of body size (above), the variance selection gradient showed no evidence of stabilizing (univariate nonlinear) selection on measures of asymmetry (Table 5). With the effect of directional selection removed, we found no significant regression coefficients (γ) for wing asymmetry in either year. Outer tail and tarsus asymmetry were not targets of univariate nonlinear selection in 1992 (Table 5), although again the difficulty in resolving asymmetry from measurement error for these two traits should be kept in mind.

Selection by Sex, Age, and Prior Condition

For two reasons, we could not determine whether cliff swallow mortality differed between the sexes in the 1996 event: Many of the nonsurvivors cannot be sexed until they are prepared as museum skins (see Methods), which will take several years, and survivors were identified by catching them in nets, and net captures tend to be male-biased (Brown and Brown 1996). However, for the 1992 event, for which we did not rely on net captures and used only birds sexed by dissection ($n = 90$), we found no significant difference in sex ratio between survivors and nonsurvivors ($\chi^2_1 = 0.01$, $P = 0.92$). Among the nonsurvivors in 1996 that had been sexed in a previous year while alive ($n = 712$), the sex ratio did not depart significantly from 1:1 ($\chi^2_1 = 1.01$, $P = 0.31$). These analyses suggest that mortality did not differ between the sexes. Exploratory analyses of selection differentials and gradients using the sample of known-sex nonsurvivors in 1996 (although possibly a biased sample) showed the same patterns for each sex separately that we report for the entire sample (Tables 3, 5). After we complete the dissection and preparation of the nonsurvivors from 1996, we will search further for potential sex differences.

In 1996, survivors and nonsurvivors differed significantly in age (Table 3, Fig. 4). Survivors tended to be younger birds, averaging about 0.6 yrs younger than nonsurvivors. Given this age effect, we examined whether any of the morpholog-
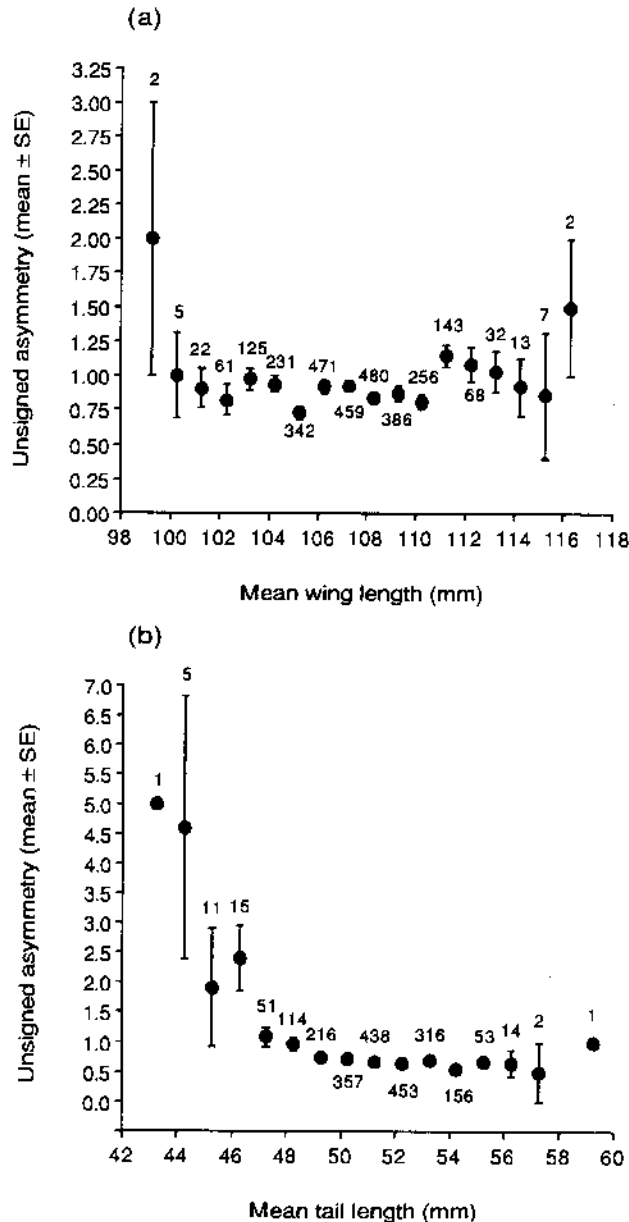
(a)

Mean wing length (mm)

(b)

Mean tail length (mm)

Fig. 2. Unsigned R − L asymmetry (mean ± SE) in wing (a) and outer tail (b) in cliff swallows in relation to trait size. Sample sizes (number of birds) shown by each dot. All birds from 1992 and 1996 (survivors and nonsurvivors) were combined; (b) includes nonsurvivors from 1996 in which tail asymmetry was measured. Asymmetry values for full-integer (e.g., 100.0) and half-integer (e.g., 100.5) mean trait sizes were pooled and are plotted at the midpoint of each interval (e.g., 100.25). Unsigned asymmetry did not vary significantly with trait size for wing ($r = -0.10$, $P = 0.69$, $n = 18$ trait sizes) but decreased significantly for outer tail ($r = -0.72$, $P = 0.002$, $n = 16$ trait sizes). In (a) and (b), the fifth percentile for each half of the distribution equalled zero (see Rowe et al. 1997).

ical traits we identified as being targets of selection (Table 5) varied significantly with age. Only middle tail length varied significantly with age (ANOVA with age classes 1–8 yrs, $F_{7,231} = 3.57$, $P = 0.001$; all other variables, $P \geq 0.16$). In particular, the variables we identified as most influenced by selection showed no relationship with age (mean body size,

$F_{7,227} = 0.83$, $P = 0.56$; wing asymmetry, $F_{7,217} = 1.51$, $P = 0.16$; tail asymmetry, $F_{7,127} = 1.29$, $P = 0.26$). Because middle tail length had less effect in the selection gradient than measures of skeletal body size and our sample of known-age birds was relatively small (Table 3), we did not attempt a more fine-grained analysis of selection by age. We had no information on age for the 1992 sample.

Body mass of cliff swallows prior to the cold weather did not seem to affect whether they survived the selection event in 1996 (Table 3). Mass of survivors, while greater, did not differ significantly from that of nonsurvivors. To the degree that our condition index (log[mass]/log[tarsus length]) reflects body condition independent of overall size, there was no evidence that survivors had been in better condition prior to the weather event. Nonsurvivors had a significantly higher condition index (Table 3), suggesting that they were heavier for their size than survivors.

Response to Selection

Cliff swallow body size and wing asymmetry changed between generations. For each trait, the mean of the generation after selection (the mature offspring of the 1996 survivors measured in 1997) differed significantly from that of the whole population before selection (Table 7). These differences between generations match closely those between survivors and nonsurvivors within 1996, reflected in similar distributions of body size and wing asymmetry among 1997 yearlings and the 1996 survivors (Fig. 5). Overall body size increased significantly among the mature offspring, compared to the parental generation (Fig. 5a). The shifts toward larger body size and decreased wing asymmetry as a consequence of the 1996 selection event were thus maintained in the first generation after selection.

Discussion

Selective mortality resulting from unusual climatic events provides one of the best means of demonstrating natural selection and microevolutionary change in contemporary populations (Bumpus 1899; Boag and Grant 1981; Endler 1986; Hairston and Walton 1986; Gibbs and Grant 1987; Grant and Grant 1993, 1995), particularly where surviving (alive) and nonsurviving (dead) individuals may be observed. These cases do not require making assumptions about survival, death, and dispersal among individuals not seen again in a study area (sensu Lebreton et al. 1992). The natural experiment that we observed and document here thus provides strong evidence for directional selection on morphological characteristics in cliff swallows.

Character response to strong directional selection is rarely seen in natural populations (Hairston and Walton 1986). In the few previous reports of viability selection in response to weather, directional selection on skeletal body size or bill shape has been intense: In house sparrows (*Passer domesticus*; Bumpus 1899; Johnston and Selander 1971; Pugesek and Tomer 1996), brown-headed cowbirds (*Molothrus ater*; Johnson et al. 1980), red-winged blackbirds (*Agelaius phoeniceus*; Johnson et al. 1980), large cactus finches (*Geospiza conirostris*; Grant and Grant 1989), medium ground finches (*G. fortis*; Gibbs and Grant 1987; Grant and Grant 1993,
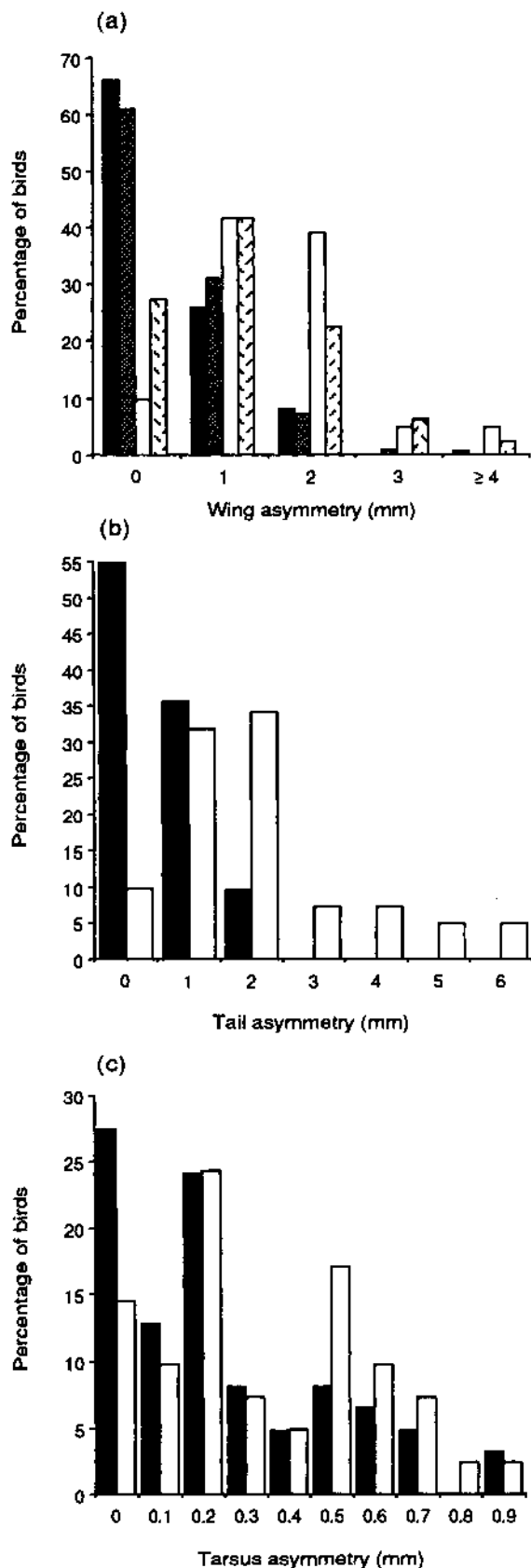
(a)

Wing asymmetry (mm)

(b)

Tail asymmetry (mm)

(c)

Tarsus asymmetry (mm)

FIG. 3. Percentage distributions of extent of unsigned R − L asymmetry in wing (a), outer tail (b), and tarsus (c) for cliff swallows

1995), and bank swallows (*Riparia riparia*; Bryant and Jones 1995). Our data for cliff swallows fit this pattern and show even greater body size selection than reported for other avian taxa. The selection differentials in the 1996 event (Table 5) tend to be larger than comparable values reported for the medium ground finch in the Galapagos (Grant and Grant 1993, 1995) and much larger than those we calculated from Bumpus's data for house sparrows (C. Brown, unpubl.). In 1996, trait means for skeletal measures of body size (tarsus length, culmen length, culmen width) and mean body size in cliff swallows shifted from 0.85 to 1.1 standard deviations, compared to 0.5 to 0.75 standard deviations in medium ground finches (Grant and Grant 1995) and 0.05 to 0.08 for comparable measurements in Bumpus's house sparrows. In cliff swallows, selection seems to have acted directly on morphological traits and was not an artefact of poor-condition birds succumbing, because our condition index indicated that nonsurvivors were in as good and perhaps better condition than survivors prior to the cold weather. Body size in cliff swallows would thus appear to show unusual sensitivity to short-term climatic change.

Advantages of Large Body Size

Natural selection experiments in other birds suggest that individuals of larger size, and in some cases with shorter wings, are favored during severe weather (Bumpus 1899; Johnson et al. 1980; Fleischer and Johnston 1984; Pugesek and Tomer 1996). In cliff swallows, individuals of larger skeletal size were favored in both weather events, and wing length was shorter in survivors.

Why might larger swallows be favored? During cold weather and times of food scarcity, large body size probably confers both thermal advantages in retaining heat and benefits of allowing more fat to be stored (Odum and Connell 1956; Kendeigh 1969, 1972; James 1970; Johnston and Selander 1971; Calder 1974; Ketterson and King 1977; Westerterp and Bryant 1984). Migratory insectivorous birds such as cliff swallows typically arrive on the breeding grounds with high levels of subcutaneous body fat; these reserves decline as the nesting season progresses (Brown and Brown 1996), often being used in lieu of food while fasting during cold spells. Larger birds may be able to survive without food longer because they were fatter to start with, and this advantage should be most pronounced whenever cold weather extends for an unusually long period such as in 1996. Although mass before the severe weather did not vary significantly among survivors and nonsurvivors and our condition index (Table 3) indicated that nonsurvivors may have weighed more for their size prior to the weather event, there was a trend for surviving birds to have had greater total mass. Survivors thus may have had greater total fat before the cold weather. Non-

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←

that survived a period of cold weather in 1992 (solid bars) and 1996 (gray bars), and that did not survive in 1992 (open bars) and 1996 (stippled bars). Sample sizes for each are shown in Table 3. The distributions differed significantly for wing (χ^2_{12} = 378.0, $P <$ 0.0001) and tail (χ^2_6 = 37.0, $P <$ 0.0001) but not for tarsus (χ^2_9 = 5.9, P = 0.75).
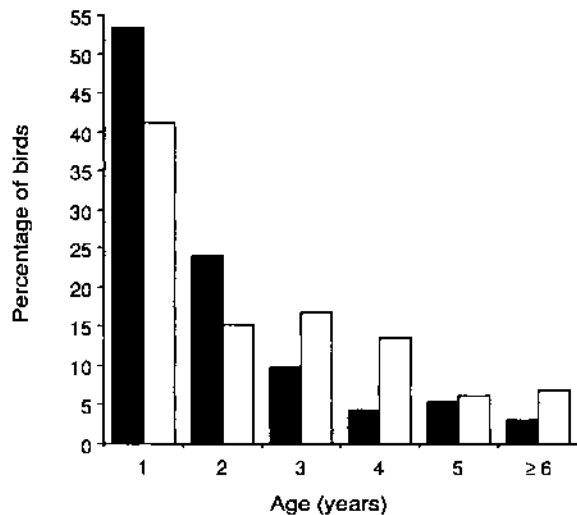
FIG. 4. Percentage distributions of age for cliff swallows that survived (solid bars) and did not survive (open bars) a period of cold weather in 1996. Sample sizes are shown in Table 3. The distributions differed significantly ($\chi^2{}_5 = 17.6$, $P = 0.004$).

survivors that have been skinned were extremely emaciated with no traces of body fat remaining, but we had no way to assess the remaining fat reserves on live individuals.

A less likely alternative interpretation for the greater survival of larger birds, suggested by Buttemer (1992) for Bumpus's house sparrows, is that larger birds were socially dominant and had secured the best nesting and roosting places prior to the severe weather. If so, mortality may have resulted more from exposure than from depletion of energy (fat) reserves (Buttemer 1992). Although the nonsurvivors being in possibly better condition prior to the cold weather is consistent with such an interpretation, it seems otherwise unlikely for cliff swallows. These weather events were unusual only in their length (number of consecutive days), and cliff swallows routinely endure similar weather conditions for shorter time periods without mortality. This suggests that starvation, not exposure per se, was primarily responsible for the mortality. The nature of the cliff swallow's aerial insect food supply seems to rule out differential resource use (sensu Gibbs and Grant 1987; Grant and Grant 1989, 1993, 1995) among survivors and nonsurvivors, as body size per se would not seem to obviously influence prey selection.

Directional selection on skeletal size in cliff swallows increased the mean overall body size in the population. If this occurs after each selection episode (Table 1), body size is undergoing microevolutionary change. However, the selection during these events may be reversed by directional selection in the opposite direction, either during another episode of unusual weather (Grant and Grant 1989, 1995) or at times in between these events (Gibbs and Grant 1987; Schluter et al. 1991; Bryant and Jones 1995). Observing selection in response to sudden cold spells is easier than seeing more gradual shifts (in perhaps the opposite direction) as a consequence of subtle behavioral or ecological differences among birds or due to environmental effects on expression of traits (Schluter et al. 1991). We do not know if directional selection favors smaller body size in cliff swallows during less extreme conditions or at other stages of the life cycle. Smaller and lighter swallows may be more maneuverable (Norberg 1981; Jones 1987; Witter and Cuthill 1993), but given the natural history of these animals, it is unclear how important that advantage might be. In cliff swallows, higher body mass confers survival advantages other than those associated with cold spells (Brown and Brown 1996), further suggesting little benefit to a smaller skeletal size. However, in bank swallows, Bryant and Jones (1995) found apparent selection for smaller body size following droughts on the birds' African wintering range. The reasons for such directional selection in bank swallows were unclear.

Furthermore, we saw no evidence for smaller size in the first generation after selection; if anything, body size continued to increase (Fig. 5a). We have no information on heritability of body size in cliff swallows, but it is likely to be high given work on other species (van Noordwijk et al. 1988; Grant and Grant 1995) including other swallows (Wiggins 1989). Environmental effects such as nestling diet (James 1983; Boag 1987; Richner et al. 1989) may, of course, have affected body size in the generation after selection, perhaps through lowered food competition (Brown and Brown 1996) during rearing in the smaller breeding colonies of 1996. This could have resulted in the continued shift toward larger size observed in the 1997 yearlings (Fig. 5a). Nevertheless, the overall response to selection would imply that countervailing directional selection for smaller size did not exist, at least in the first generation. Perhaps the principal constraint on evolution of larger body size in swallows is the rarity of the

TABLE 7. Evolutionary response of cliff swallows to the 1996 selection event. All differences between generations (Δ) are significant ($P < 0.001$, Wilcoxon rank sum tests with sequential Bonferroni correction).

	Before selection, 1996*			After selection, 1997**			
	Mean	SE	n	Mean	SE	n	Δ
Wing length (mm)	107.29	0.05	2871	106.60	0.15	193	−0.69
Middle tail length (mm)	46.47	0.04	2865	45.80	0.11	193	−0.67
Tarsus length (mm)	10.54	0.02	2880	11.83	0.04	193	+1.29
Culmen length (mm)	6.55	0.01	2822	7.14	0.02	192	+0.59
Culmen width (mm)	5.81	0.01	2822	6.30	0.02	192	+0.49
Mean body size	2.90	0.00	2808	2.95	0.00	192	+0.05
Wing asymmetry***	0.97	0.03	2723	0.42	0.05	193	−0.55

* All birds (survivors + nonsurvivors).
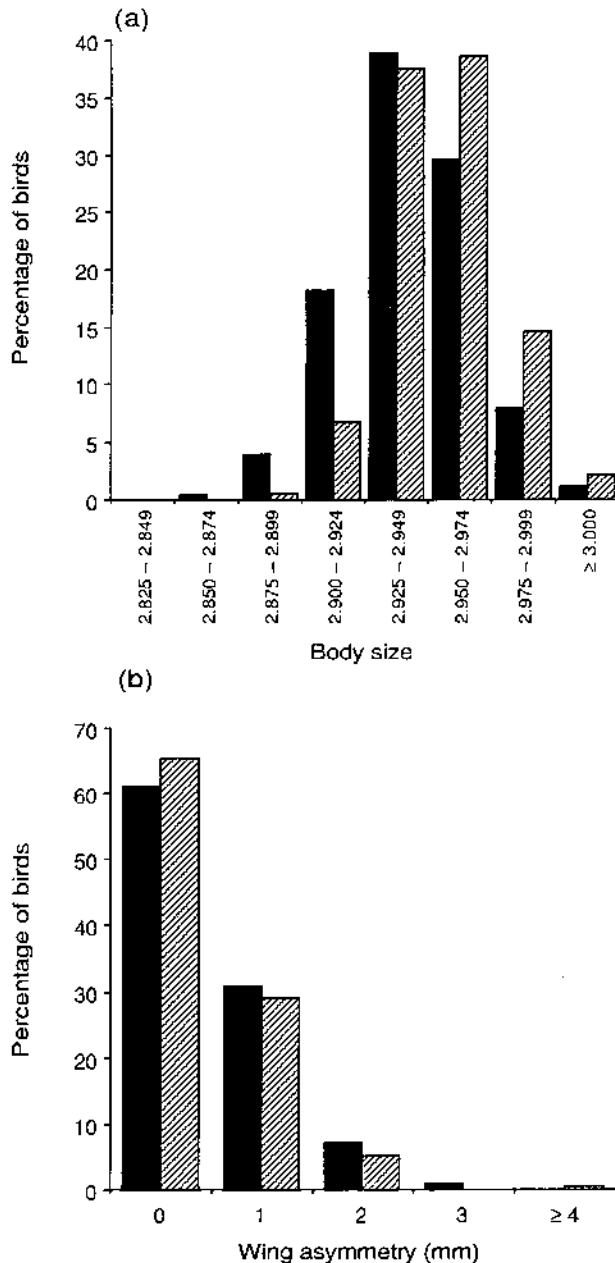** Mature offspring of survivors.
*** Unsigned R − L.

FIG. 5. Percentage distributions of mean body size (a) and extent of unsigned R − L asymmetry in wing (b) for cliff swallows that survived a period of cold weather in 1996 (solid bars) and their mature offspring in 1997 (hatched bars). Sample sizes in (a) were 1027 birds in 1996 and 192 in 1997; in (b), 891 birds in 1996 and 193 in 1997. The distributions in (a) differed significantly (χ^2_6 = 32.2, $P < 0.0001$) but not those in (b) (χ^2_4 = 4.9, P = 0.30).

intense selection events, relative to swallow generation time (see below). Johnston and Selander (1971) reported essentially the same result for male house sparrows undergoing directional shifts toward larger size, brought about through overwintering mortality caused by climate.

Advantages of Low Asymmetry

Cliff swallows with low levels of asymmetry in wing and tail were strongly favored during both selection events, and

wing asymmetry and outer tail asymmetry were targets of selection (Table 5). The asymmetry we report seems inconsistent with either fluctuating asymmetry or antisymmetry, but regardless of its statistical form, more symmetric individuals clearly had survival advantages during these events. Both fluctuating asymmetry and antisymmetry may reflect developmental stability and overall genetic quality (e.g., Parsons 1990; Møller and Pomiankowski 1993; Watson and Thornhill 1994; Rowe et al. 1997; but see Markow 1995; Palmer 1996). That our measures of asymmetry reflected differential growth (not feather breakage) strongly suggests that asymmetry reflects developmental precision in cliff swallows. One interpretation for cliff swallows with low asymmetry being favored is that survivors are the "high quality" birds who for this reason are inherently more capable of enduring stressful conditions. This would be consistent with the assumption that asymmetry is a reliable enough indicator of quality to be useful in mate choice. The selection events for cliff swallows support this assumption: A female choosing a male with low asymmetry is apt to produce offspring who are better able to survive cold spells. The response to selection between generations (Table 7) and the similarity between offspring and parents (Fig. 5b) are consistent with wing asymmetry in cliff swallows being a case of (statistically undetected) antisymmetry, which is thought to have a greater genetic basis than ideal fluctuating asymmetry (Van Valen 1962; Palmer and Strobeck 1992; Rowe et al. 1997; but see Møller and Thornhill 1997).

Does low asymmetry indicate only general superiority or can it directly affect survival? If the former is true, selection likely acts on overall condition, and we see low asymmetry only as a correlated response (Price and Langen 1992). In aerial insectivores such as cliff swallows, there are direct aerodynamical advantages of having symmetric wings and tails (Balmford and Thomas 1992; Thomas 1993; Norberg 1994). These advantages improve flight efficiency (Møller 1991) and might allow symmetric birds to forage at less cost during cold weather than more asymmetric individuals. Lower-cost foraging during bad weather could translate into greater prospects for survival and be directly selected for, as we observed. That birds such as cliff swallows experience such large apparent benefits of low asymmetry during harsh weather suggests that low asymmetry may also confer direct benefits associated with foraging (or perhaps maneuverability during intraspecific fighting; Norberg 1994) in more benign times.

Our results suggest that low asymmetry has been subject to strong natural selection in cliff swallows and lend support to the argument that natural selection has been responsible in part for the evolution of symmetry in the closely related barn swallow (Hirundo rustica; Balmford and Thomas 1992; Borgia and Wilkinson 1992; Norberg 1994). That body mass before the cold weather did not differ significantly between survivors and nonsurvivors in cliff swallows is also consistent with advantages to low asymmetry in cold weather. If low asymmetry is instead a general correlate of overall quality or superiority, the more symmetric birds who survived should have exhibited better condition (greater body mass) before the selection event. We observed the opposite pattern, with the more asymmetric nonsurvivors being in perhaps

better condition (higher log[mass]/log[tarsus length]) than survivors. This reinforces our interpretation that symmetry directly affects survival and can be selected for during extreme conditions.

The central assumption behind the notion of asymmetry being a reliable indicator of quality is that fitness decreases with increasing levels of asymmetry. However, few data exist from natural populations to test this assumption, and those that are available are mostly correlative or come from laboratory populations (Møller 1997 and references therein). While most of these studies are consistent with the assumption that asymmetry varies inversely with fitness, our results are the first demonstration of natural selection for low asymmetry in the wild, independent of selection on other traits, using a method (short-term environmental perturbation) widely regarded to provide strong evidence for selection.

Our results also show selection for low asymmetry in characters under directional selection, in contrast to those of Thoday (1958) and Leamy and Atchley (1985), who found higher levels of asymmetry in experimental lines of *Drosophila* and rats experiencing directional selection on morphology. Lower asymmetry in wing and tail among cliff swallows in the face of intense directional selection on those traits further suggests strong naturally selected advantages of symmetry.

Effects of Age

We found greater mortality among older cliff swallows than among younger birds. This likely shifted the age structure of the population, in the short term, to a higher fraction of younger individuals. This shift may have social consequences. For example, older birds tend to be more likely than younger ones to settle in small colonies (Brown and Brown 1996). We predict, therefore, that fewer small colonies will form in the years immediately after the 1996 event (mortality was too limited in 1992 to expect any subsequent effect on average colony size). With relatively more yearlings and two year olds present, the colony size distribution should skew toward larger colonies, which are favored by younger birds (Brown and Brown 1996).

Why were younger birds more likely to survive the cold weather? Perhaps younger birds were more recently arrived than older ones and consequently still possessed larger migratory fat reserves. In other species, later migrants tend to have larger fat reserves to start with (Johnston 1966). Yearling cliff swallows arrive in the study area slightly later than older birds (Brown and Brown 1996). Older birds that had been there longer were probably farther into their nesting cycle than yearlings (laying eggs and incubating) and for this reason may have had fewer fat reserves on which to rely during these unusually late and long-lasting cold spells. The nonsurvivors' slightly (although not significantly) lower body mass prior to the 1996 cold weather is consistent with this interpretation. If later-arriving birds (of any age) were more likely to survive these events and if arrival date and breeding time are heritable (Price et al. 1988), we would predict a shift toward later breeding in the population as a whole. Catastrophic weather events, especially ones of the 1996 magnitude, may periodically adjust average breeding date to be later than that which seems to be optimal (van Noordwijk et al. 1981; Price et al. 1988).

The lack of a relationship between age and the variables we identified as most influenced by selection (body size, wing and outer tail asymmetry) suggests that age-related correlations with morphology are unlikely to explain the patterns of selection detected. Selection apparently acted on these morphological traits independent of age.

Climate and Long-Term Evolution

Although rare compared to the generation time (one year) of swallows, episodes of selection caused by unusual climatic events are probably regular for populations of insectivorous birds in the northern Great Plains. Our analysis of the 123-year climate record shows that late spells of cold weather leading to varying degrees of viability selection have probably occurred at least 11 times during that time span. However, three of those have happened within the last eight years, and all of those likely to have had a major impact have been within the last 30 years. This cliff swallow population may have undergone relatively recent body size evolution, mediated especially by the major mortality events in 1967 and 1996.

The rarity of the intense selection events—and the difficulty of detecting selection in the absence of major environmental perturbations (Endler 1986)—have not allowed us to determine whether oscillating selection (Hairston and Dillon 1990; Schluter et al. 1991; Grant and Grant 1995) has prevented unidirectional change in body size or levels of asymmetry in cliff swallows. Short-term change in body size of bank swallows in Great Britain was apparently reversed in a relatively few generations by unknown opposing selective pressures (Bryant and Jones 1995). Climate may frequently produce short-term change in one direction and then reverse it, owing to the seasonality and unpredictability of global climate patterns (Grant and Grant 1993, 1995).

Selection was less intense in 1992 because conditions were less severe. Minor selection events, such as those of 1976, 1988, and 1992, might be expected to result in stabilizing selection because poorly adapted outliers are the first individuals to be removed. Surprisingly, we found little evidence for strong stabilizing selection in either 1992 or 1996. Only the γ regression coefficient for middle tail length in 1996 was significant, although the nature of univariate nonlinear selection cannot always be accurately judged from γ values (Brodie et al. 1995). Instead of stabilizing selection per se, the reduced phenotypic variance in this cliff swallow population after the mortality events must reflect simply a strong directional change toward one end of each trait's observed distribution, coupled with intense selection against individuals at the other end (Lande and Arnold 1983). However, comparison of the variance selection gradients show eight of nine regression coefficients (γ) in 1992 to be negative versus three of six in 1996 (Table 5). To the degree that these indicate tendencies for stabilizing selection, 1992 would appear to have shown greater removal of outliers (see also Fig. 1b).

In contrast, there was intense directional selection in 1996. Permanent microevolutionary shifts have been observed in contemporary populations (e.g., Johnston and Selander 1971;

Endler 1986; Hairston and Walton 1986; Seeley 1986). Our preliminary data show a strong evolutionary response to morphological selection between generations. The next step will be to follow the population over time to learn if this is a permanent change.

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