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Natural selection on tail and bill morphology in Barn Swallows *Hirundo rustica* during severe weather

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An unusual six-day period of cold, rainy weather caused mortality among Barn Swallows *Hirundo rustica* in southwestern Nebraska, USA, in May 1996. We compared birds that died during the cold to those still alive when the severe weather ended. Among males, survivors had significantly longer culmens and significantly less variance in outer-tail asymmetry than non-survivors. Among females, survivors had significantly longer outer tails and significantly less variance in outer-tail length, overall body size and outer-tail asymmetry than non-survivors. Larger birds in general and those with less asymmetry in wing and outer tail tended to be favoured during this weather event. Long tails may reflect condition in females and, along with high levels of symmetry in wing and outer tail, improve foraging efficiency during extreme conditions. Males with long tails did not appear to suffer survival costs. Larger size probably allows more fat to be stored and may confer thermal benefits to swallows during late spring cold snaps. Similar mortality events have apparently occurred in the study area on only one other occasion since 1875.

Unusual climatic events can cause measurable change in avian morphology (e.g. body size, bill size) over very short periods of time (Bumpus 1899, Boag & Grant 1981, Price *et al.* 1984, Grant & Grant 1993, 1995). These environmental perturbations thus provide excellent opportunities for witnessing natural selection in contemporary populations (Endler 1986, Hairston & Walton 1986) and can reveal whether certain morphological traits confer naturally selected advantages or disadvantages during extreme conditions. The elaboration of traits important in mate choice is often assumed to be constrained by survival costs (Selander 1965, Searcy 1979, Searcy & Yasukawa 1981) or to reflect accurately an individual's overall genetic quality (reviewed in Andersson 1994). Periods of intense survival selection allow us to test these assumptions.

In Barn Swallows *Hirundo rustica*, males have longer outer-tail streamers than females, and tail length and degree of outer-tail asymmetry are subject to sexual selection (Møller 1994a). Tail length in males correlates with many components of fitness (e.g. time to acquire a mate, extra-pair copulation success, quality of mate, ectoparasite load) and, even among females, those with longer tails appear to be higher quality birds that are better parents (Møller 1994a). Males with high asymmetry in length of the outer-tail streamers tend to be less likely to attract mates, and females with more symmetrical tails tend to lay eggs earlier (Møller 1994b). However, the advantages associated with longer and more symmetrical tails have usually been inferred from correlations between morphology and components of reproductive success or the probability of resighting. An exception was Møller's finding (Møller 1994c) that males surviving an unusually cold period in early spring had longer tails than those found dead due to the cold. This result supported the assumption that tail length is a reliable indicator of male quality and suggested no naturally selected disadvantage of an exaggerated tail, at least during adverse weather.

We examined natural selection in Barn Swallows during a rare climatic event in the central Great Plains, USA in 1996. Events of this severity apparently have occurred only twice in the last 123 years, and this period of severe weather killed thousands of Cliff Swallows *Petrochelidon pyrrhonota* (Brown & Brown 1998). This episode represented conditions far beyond normal environmental extremes and provided an opportunity for natural selection. We investigated morphological shifts associated with viability selection and how patterns of wing and tail asymmetry were affected by survival selection (Brown & Brown 1998). Since degree of asymmetry is considered by some to be

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an indicator of individual quality useful in mate choice (Møller & Pomiankowski 1993, Gangestad *et al.* 1994, Watson & Thornhill 1994, Møller & Thornhill 1998; cf. Markow 1995, Palmer 1996), we predicted that more symmetrical individuals – and those with longer tails – should have been more likely to survive the adverse weather. Our data also allow us to test whether tail length might be constrained by opposing natural selection during unusual events and whether other components of body size in Barn Swallows undergo directional selection during severe weather (*sensu* Bumpus 1899, Boag & Grant 1981, Brown & Brown 1998).

METHODS

Study animal and study site

Barn Swallows are widely distributed throughout the world. In the Western Hemisphere, the subspecies *H. r. erythrogaster* breeds throughout most of North America and winters throughout most of South America (Turner & Rose 1989). These 16–23 g birds feed on flying insects. In North America, Barn Swallows tend to breed in small colonies, often ten nests or fewer in number (Snapp 1976, Brown & Brown 1996, unpubl. data), and in our study area frequently nest solitarily. Barn Swallows typically raise two broods, and most birds arrive in our study area in early May.

Our research was conducted along the North and South Platte rivers, centred near Ogallala, in primarily Keith County, southwestern Nebraska. Barn Swallows are common throughout the study area, nesting exclusively on artificial structures such as bridges, buildings and highway culverts. Our research site was described in detail by Brown & Brown (1996).

Field collection

Barn 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 & Moore 1985, Elkins 1988, Møller 1994a, 1994c). The period of bad weather in this study extended from 24 to 29 May 1996. During this time, daily maximum temperatures ranged from 5.5–15.5°C and daily minimum temperatures ranged from 2.8–10.0°C (compared with normal daily averages of 24.0 and 9.0°C, respectively, for those dates) with rain on four of the six days (Brown & Brown 1998). When the cold weather ended, we surveyed 11 colony sites where one or more Barn Swallows were known to have settled and found at least one dead bird at each site. Specimens were placed in plastic bags and frozen immediately. Only dead birds found in the 1–3 days immediately after the cold weather were used in morphometric analyses. We had never before observed mortality of this magnitude in Barn Swallows at our study site. Birds designated as survivors were those captured in mist-nets at four of the 11 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 the possibility that recent immigrants might have joined our 'survivors', the geographical scope of the weather event was extensive enough that immigrants had probably experienced the same conditions elsewhere (Brown & Brown 1998).

Measurements

We measured the length of each unflattened, closed wing (from the most anterior part of the carpal joint to the tip of the longest primary) to the nearest 1 mm with a stopped wing rule, and the length of the middle and two outer-tail feathers (from their emergence from the skin to the tip) to the nearest 1 mm with a ruler. We also measured the 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 the length and width of the exposed culmen (length from the proximate end of the exposed culmen to the bill tip and width of the exposed mandibles at the nostrils) to the nearest 0.1 mm with calipers.

Survivors were measured while living, and non-survivors at 3–4 months after death. Non-survivors were completely thawed before measurement, and measurements were taken before the specimens were prepared as museum 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). We assume no such measurement bias here. Due to the relatively small number of Barn Swallows available, we could not directly test this assumption for this species; however, the assumption was met for a sample of Cliff Swallows measured while living and later when dead (Brown & Brown 1998). Measurements of these Cliff Swallows showed no systematic bias. Since Barn and Cliff swallows are similar in size and shape, and specimens of the two species were collected simultaneously, treated identically and measured by the same person (M.B.B.), it is unlikely that the accuracy of our Barn Swallow measurements of survivors versus non-survivors was any different from that for Cliff Swallows. As all measurements of both living and dead birds were made by the same person, no correction factors (Price & Grant 1984, Bryant & Jones 1995, Grant & Grant 1995) for multiple measurers were necessary. Repeatibilities for Cliff Swallow measurements (including asymmetry) were 0.615–0.921 for living birds and 0.851–0.988 for dead birds (Brown & Brown 1998). Given the similarities in species and method of measurement, we assumed repeatibilities for Barn Swallows to be within these ranges, which are comparable with other studies of morphological variation in birds (Balmford *et al.* 1993, Møller 1994b). Wing-length and outer-tail length in our analyses represent the average of the right and left values per bird. Following Via & Shaw (1996), we use a multivariate measure of overall body size, the mean of the log-transformed p original variables, $[\sum \ln (X_i)]/p$, where X_i is the value of the ith variable for a given observation (Brown & Brown 1998).

Our measure of asymmetry in most analyses was the absolute difference between right and left sides. Observed asymmetry in Barn Swallows seemed to be consistent with that expected from ideal fluctuating asymmetry: signed right minus left values for both wing and outer tail in each sex were not significantly different from 0 and did not differ significantly from a normal distribution ($P \geq 0.09$ for each, SAS univariate normal procedure; SAS Institute 1990). We saw no evidence of antisymmetry in either trait for either sex: 5th percentiles in each case were 0 (Rowe *et al.* 1997).

Statistical analysis of selection

Standardized directional (i) and variance (j) selection differentials (Endler 1986) were calculated using the combined set of survivors and non-survivors as the before-selection group, and the survivors as the after-selection group. Significance tests for i and j followed Endler (1986, pp. 172–173) where non-survivors represented the unselected group and survivors the selected group, yielding two independent samples. We applied sequential Bonferroni corrections (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 indicated.

RESULTS

Among males, Barn Swallows that survived the severe weather had significantly longer culmens than non-survivors (Table 1). Among females, survivors had significantly longer tails than non-survivors (Table 1). None of the other morphological measures differed significantly between survivors and non-survivors after Bonferroni corrections. There was a trend, however, in both sexes for generally larger birds to be more likely to survive the weather event (Fig. 1). This result

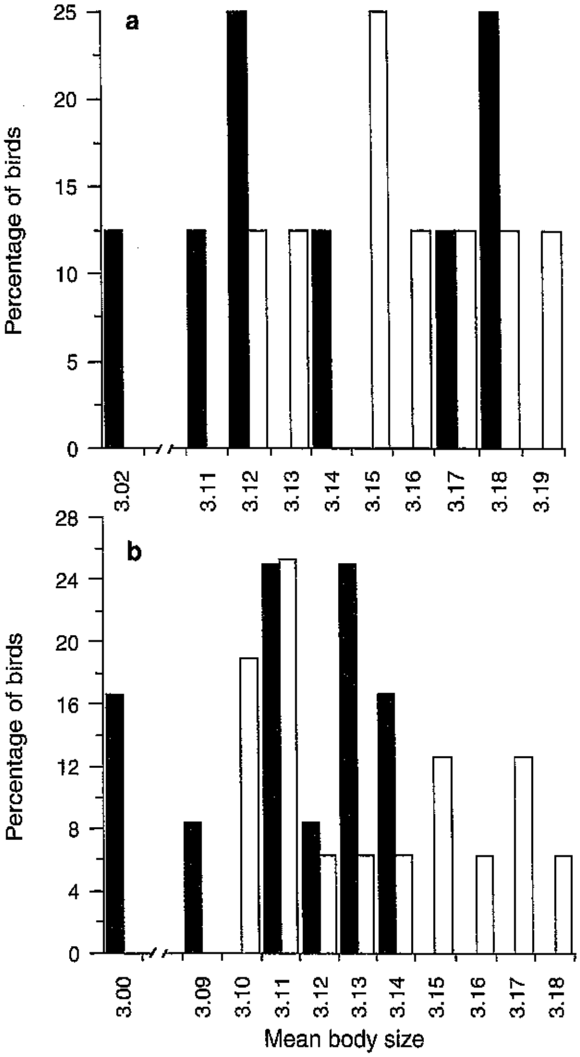

Figure 1. Percentage distributions of mean body size (expressed as the mean of the log-transformed morphological measurements) for (a) male and (b) female Barn Swallows that survived (□) and did not survive (■) a period of cold weather. Sample sizes are shown in Table 1. The body size distributions of survivors versus non-survivors did not differ significantly for either males ($\chi^2_9 = 8.7$, $P = 0.46$) or females ($\chi^2_{10} = 13.2$, $P = 0.21$).

Table 1. Morphological characteristics of Barn Swallows that survived and did not survive a period of severe weather in southwestern Nebraska and tests of significance of differences (those significant after sequential Bonferroni corrections in boldface, Wilcoxon rank sum test).

	Survivors			Non-survivors			
	Mean	se	*n*	Mean	se	*n*	*P*
Males							
Wing-length (mm)	115.06	0.91	8	117.38	1.31	8	0.16
Middle-tail length (mm)	42.38	0.56	8	43.38	1.07	8	0.63
Outer-tail length (mm)	86.38	2.77	8	82.88	5.40	8	0.96
Tarsus-length (mm)	9.90	0.14	8	9.80	0.21	8	0.43
Culmen-length (mm)	7.19	0.04	8	6.63	0.07	8	0.0006
Culmen-width (mm)	5.69	0.17	8	5.38	0.13	8	0.34
Mean body size	3.16	0.01	8	3.13	0.02	8	0.27
Wing asymmetry (mm)	0.63	0.32	8	1.00	0.19	8	0.26
Outer-tail asymmetry (mm)	5.25	3.73	8	14.75	11.53	8	0.30
Females							
Wing-length (mm)	114.12	0.70	16	113.73	0.73	13	0.47
Middle-tail length (mm)	42.56	0.51	16	41.92	0.43	13	0.46
Outer-tail length (mm)	78.50	1.63	16	67.11	3.96	13	0.0056
Tarsus-length (mm)	9.71	0.13	16	9.69	0.11	13	0.82
Culmen-length (mm)	7.13	0.08	16	7.03	0.10	12	0.41
Culmen-width (mm)	5.58	0.09	16	5.64	0.09	12	0.71
Mean body size	3.13	0.01	16	3.10	0.01	12	0.13
Wing asymmetry (mm)	0.50	0.16	16	1.00	0.25	13	0.12
Outer-tail asymmetry (mm)	2.88	1.01	16	14.69	7.43	13	0.046

matched that seen for Cliff Swallows in the same weather event (Brown & Brown 1998). Asymmetry in both wing and outer-tail was lower in survivors than non-survivors for both sexes, with most birds of 0 mm asymmetry surviving (Fig. 2). However, the differences were not statistically significant after Bonferroni corrections (Table 1).

These results on asymmetry also parallel those seen for Cliff Swallows, although differences between survivors and non-survivors in Cliff Swallows were statistically significant, possibly because of much larger sample sizes for that species (Brown & Brown 1998).

Directional selection differentials (*i*), showing the net effect of selection on trait means, were significant for culmen-length among males and outer-tail length among females (Table 2). That both were positive illustrates directional viability selection for longer bills in males and longer tails in females during this weather event. Variance selection differentials (*j*), a measure of the net change in variance, were predominantly negative (Table 2), indicating reduced phenotypic variance in most traits after selection. Those for outer-tail asymmetry in males and outer-tail length, mean body size, and outer-tail asymmetry in females were significant after Bonferroni corrections.

DISCUSSION

Female Barn Swallows with longer tails were favoured during this selection event, supporting for the North American subspecies the finding in Europe that long-tailed females are better quality birds (Møller 1994a). Tail exaggeration is probably a reliable indicator of condition in females, although Møller (1991a, 1994a) found no relationship between female tail-length and viability in general. Longer tailed females in our study had a clear survival advantage, suggesting that long tails in females may also reflect better survival skills, at least during adverse weather. Long tails may be particularly advantageous in improving foraging efficiency whenever aerially feeding birds prey on large and highly manoeuverable insects detected at a distance (Norberg 1994). If large insects only were active during the cold weather, this could have favoured long-tailed Barn Swallows, perhaps especially in females at a time in the season when they were energetically stressed through egg production (Ward 1996). Both Barn and Cliff swallows spent variable amounts of time foraging during the cold weather. That they were actively foraging at times and not just fasting supports the conclusion that tail-length and possibly other morphological traits directly affected foraging efficiency during this event.

Table 2. Standardized directional (*i*) and variance (*j*) selection differentials and significance levels of each (those significant after sequential Bonferroni corrections in bold), for an episode of selection on Barn Swallows in southwestern Nebraska.

	i	*P*	*j*	*P*
Males				
Wing-length	−0.34	0.08	−0.40	0.16
Middle-tail length	−0.21	0.21	−0.55	0.045
Outer-tail length	0.15	0.29	−0.56	0.038
Tarsus-length	0.10	0.35	−0.34	0.14
Culmen-length	**0.85**	< 0.0001	−0.88	0.055
Culmen-width	0.35	0.14	0.22	0.19
Mean body size	0.33	0.10	−0.67	0.020
Wing asymmetry	−0.25	0.17	0.49	0.07
Outer-tail asymmetry	−0.20	0.22	**−0.81**	0.002
Females				
Wing-length	0.07	0.35	0.09	0.41
Middle-tail length	0.16	0.18	0.23	0.14
Outer-tail length	**0.43**	0.004	**−0.70**	0.002
Tarsus-length	0.02	0.46	0.26	0.18
Culmen-length	0.13	0.21	−0.01	0.45
Culmen-width	−0.08	0.30	0.22	0.20
Mean body size	0.34	0.014	**−0.60**	0.007
Wing asymmetry	−0.28	0.047	−0.37	0.08
Outer-tail asymmetry	−0.28	0.046	**−0.95**	< 0.0001

In contrast, we found no evidence that long-tailed male Barn Swallows had a survival advantage during severe weather. This is unlike Møller's studies in Europe (Møller 1994a), which demonstrated an effect of tail-length during similarly adverse conditions with comparable sample sizes (Møller 1994c) and generally higher survival for longer-tailed males (Møller 1991a). Perhaps this discrepancy is explainable by generally less intense sexual selection on outer-tail length in the North American subspecies. Male Barn Swallows in North America incubate more than their European counterparts, and the potential for breakage of long outer-tail streamers during incubation may limit tail exaggeration (Smith & Montgomerie 1991). If so, tail-length in males may be less likely to reflect individual quality *per se*. Although there is some evidence that longer-tailed males in Europe suffer long-term survival costs (Møller 1994a), we saw no indication during this climatic event that tail exaggeration imposed any cost or was subject to opposing natural selection.

As in Cliff Swallows during the same selection event (Brown & Brown 1998), Barn Swallows with lower levels of wing and outer-tail asymmetry tended to survive the cold weather (Fig. 2). The significant variance selection differentials indicate that the individuals with highly asymmetric tails were selected against (Table 2). This could be because the more symmetric birds were generally superior. For this reason, perhaps they were in better condition prior to the severe weather and thus more likely to survive a period of food deprivation. Another possibility is that there are direct aerodynamic advantages of having symmetric wings and tails (Balmford & Thomas 1992, Thomas 1993, Norberg 1994). These advantages improve flight efficiency (Møller 1991b) and might allow symmetric birds to forage at less cost during cold weather than more asymmetric individuals. Lower cost foraging

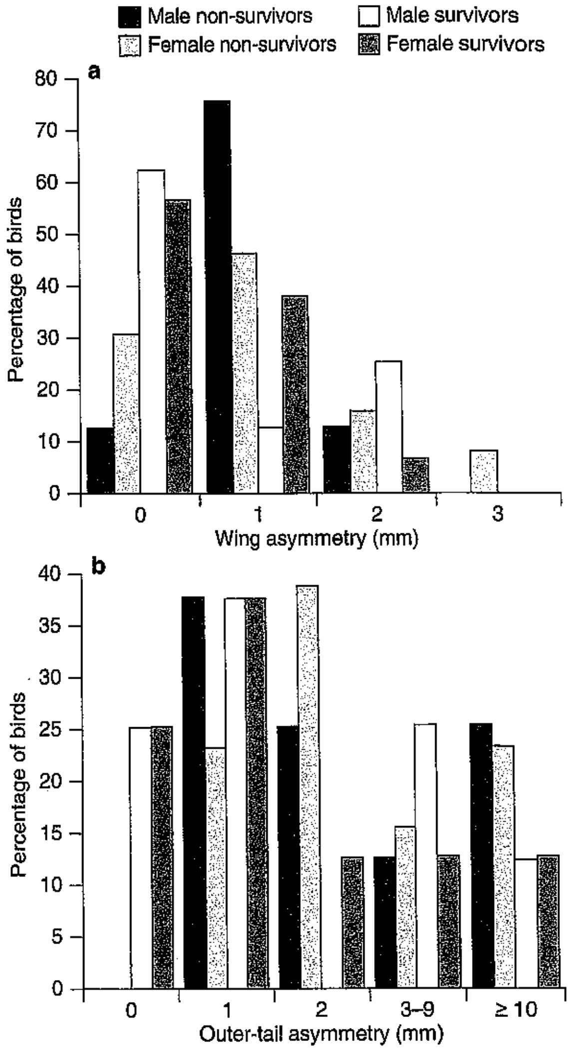

Figure 2. Percentage distributions of extent of unsigned asymmetry in (a) wing and (b) outer-tail for male and female Barn Swallows that survived and did not survive a period of cold weather. Sample sizes for each are shown in Table 1. In (a), the distributions of survivors versus non-survivors differed significantly for males ($\chi^2_2 = 6.6$, $P = 0.037$) but not for females ($\chi^2_3 = 3.0$, $P = 0.39$); in (b), the distributions of survivors versus non-survivors did not differ significantly for either males ($\chi^2_4 = 4.7$, $P = 0.32$) or females ($\chi^2_4 = 6.2$, $P = 0.18$).

during bad weather could translate into better prospects for survival and be selected directly. In either case, the degree of bilateral symmetry would appear to be a reliable cue for picking a fit mate (Møller & Thornhill 1998). We were surprised, however, that the effects of wing and tail symmetry were not stronger in Barn Swallows (there was no statistical significance in Table 1), given the apparent importance of symmetry in mate choice for the European subspecies (Møller 1994b) and the pronounced selection for low wing and outer-tail asymmetry in Cliff Swallows during the same weather event (Brown & Brown 1998).

Barn Swallows of greater skeletal size seemed to be favoured during this period of severe weather (Fig. 1). Natural selection experiments in other birds also suggest that larger individuals are favoured during adverse conditions (Bumpus 1899, Johnson *et al.* 1980, Fleischer & Johnston 1984, Pugesek & Tomer 1996; cf. Bryant & Jones 1995). Why might larger swallows be favoured? 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 (James 1970, Kendeigh 1969, Calder 1974, Ketterson & King 1977, Westerterp & Bryant 1984). Migratory insectivorous birds such as Barn Swallows typically arrive on the breeding grounds with high levels of subcutaneous body fat; these reserves decline as the nesting season progresses (Brown & Brown 1996), often being used 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.

Survivors and non-survivors might have differed in attributes other than morphology which affected their performance in the adverse weather. For example, age, sex, arrival time, nesting stage or colony location could have influenced whether a bird survived the cold spell. The dispersed nature of Barn Swallows in our study area prevented us from collecting enough data to examine these possibilities rigorously, although we are in the process of studying them among Cliff Swallows for which we have a much larger data set. Age differed significantly among survivors and non-survivors in Cliff Swallows, with younger birds being more likely to survive (Brown & Brown 1998). This is most likely because younger birds were more recently arrived at the time of the weather event and thus had greater remaining migratory fat reserves on which to rely. The same pattern may have occurred in Barn Swallows, since in Europe younger (i.e. shorter-tailed) males typically arrive slightly later (Møller 1994a).

The reduced phenotypic variance among survivors (Table 2) is consistent with stabilizing selection. Unfortunately, our sample size was not sufficient to calculate a variance selection gradient, which provides the best evidence for true stabilizing selection independent of directional selection (Lande & Arnold 1983). Thus, we cannot exclude the possibility that the reduced phenotypic variance after the mortality reflects simply directional change toward one end of a trait's distribution, coupled with selection against individuals at the other end (Brown & Brown 1998). We also note that we have no information on heritabilities of these morphological traits for Barn Swallows, but the response to selection in Cliff Swallows (Brown & Brown 1998) and the high heritability of body size in other species (van Noordwijk et al. 1988, Wiggins 1989, Grant & Grant 1995) suggest that change in gene frequencies between generations (i.e. selection) is likely in this case.

A direct comparison of levels of mortality between Barn and Cliff Swallows during this weather event is complicated by the more dispersed nesting distribution of Barn Swallows and their smaller overall population in the study area. Nevertheless, it still seems likely that Barn Swallows were less affected by this weather than Cliff Swallows. This is probably because Barn Swallows feed on relatively large single insects captured near the ground, whereas Cliff Swallows prefer small swarming insects concentrated in thermals of warm air (Brown & Brown 1996). Larger insects near the ground are more likely to be active in cold weather, and thus Barn Swallows probably did not experience as severe food deprivation as Cliff Swallows.

The six-day weather event of 1996 was clearly unusual, however, even for Barn Swallows. Analysis of the climatological record for the study site dating to 1875 revealed that this event was one of only two periods of extreme weather of more than four days in duration occurring after 20 May (a time likely to affect large numbers of swallows) during those 123 years (Brown & Brown 1998). Intense episodic evolutionary events like this may represent a large part of the total natural selection imposed on a species (O'Donald 1973, Wiens 1977). These kinds of extreme environmental perturbations also provide one of the best opportunities to witness natural selection and microevolutionary change (Endler 1986), especially when the events allow direct observation of surviving and non-surviving individuals. In these cases, assignment of relative fitness is unambiguous and does not require making assumptions about survival, death, dispersal and offspring recruitment among individuals not seen again in a study area. The natural experiment that we document here thus provides strong evidence for selection on morphology in Barn Swallows. Character response to strong directional selection is rarely seen in natural populations, although microevolutionary shifts are known (Johnston & Selander 1971, Endler 1986, Hairston & Walton 1986, Seeley 1986, Bryant & Jones 1995). The next step is to follow this Barn Swallow population over time to learn if this rare climatic event caused a permanent change in tail and bill morphology.

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