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Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*)

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Abstract An unusually long period of cold weather in May 1996 caused extensive mortality among insectivorous cliff swallows (*Petrochelidon pyrrhonota*) in the northern and central Great Plains. We analyzed how viability selection affected spring arrival time in a migratory Nebraska population by comparing capture histories of survivors with those of birds known to have died and by documenting how arrival time changed in the year following the selection event. Surviving birds had significantly later first-capture dates (an index of arrival time) in the years prior to selection than those that died; a significant selection differential suggested directional selection for birds that arrived later. Colony sites were occupied significantly later following the selection event, and the distribution of first-capture dates in the season after selection was significantly shifted toward later arrivals. Offspring of the survivors tended to arrive later than birds of the same age prior to the selection event. While major weather-caused mortality events of this magnitude are rare in the study area, spells of cold weather severe enough to cause limited mortality are frequent in April and early May. At least 25 probable mortality events of varying severity were identified in the last 50 years based on climatological data. Periodic weather-mediated selection against early arrival constrains the cliff swallow's breeding season and may partly prevent directional selection for earlier nesting.

Key words Climate · Life history · Mortality · Nebraska · Seasonality · Survival

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Introduction

In seasonally breeding organisms of north temperate areas, breeding time is a critical determinant of reproductive success. Migratory species in particular face opposing environmental constraints that work against arriving too early and breeding before weather conditions allow it and those that select against arrival too late when odds of success also diminish. In north temperate birds, the pervasive pattern among species is for reproductive success to decline with date within the typical seasonal breeding period (Perrins 1970; Price et al. 1988; Brown and Brown 1999a). Several hypotheses to explain this pattern have been proposed, mostly concerning female condition and environmental constraints (declining resources) in the latter part of the breeding season (Brinkhof et al. 1993, 1997; Nilsson 1994; Rowe et al. 1994; Verhulst et al. 1995; Winkler and Allen 1996; Svensson 1997; Aparicio 1998; Price 1998; Visser et al. 1998).

Almost all of the extensive empirical work on avian breeding times has focused on egg-laying times, probably because those are relatively easy to measure in the field. Most migratory species, however, arrive on the breeding grounds up to several weeks before actual egg-laying begins, and during this period, individuals may be subject to late spring storms and generally the most severe weather of the breeding season. Time of arrival on the breeding grounds may thus determine whether a bird survives to ever make a choice of egg-laying time. It has been implicitly assumed that inhospitable conditions early in the breeding season set an early limit on when birds can arrive, but little field data from natural populations exist to show either this constraint or whether environmental conditions early in the nesting season can at times directly select for later arrival. Periodic viability selection for later arrival on the breeding grounds could partly counterbalance directional selection for earlier nesting based on environmental conditions during brood rearing in the latter part of the breeding season.

Insectivorous birds of higher latitudes are especially prone to catastrophic climatic events that potentially select for later arrival. Relying exclusively on insects for food, which may be reduced or temporarily eliminated during late spring cold snaps, these species can experience mortality when cold weather is unusually long in duration (Ligon 1968; Whitmore et al. 1977; Brown and Brown 1998). Depending on the timing of these selection events, a large fraction of the breeding population may be killed and consequently average breeding date shifted forward in time. Yet despite a large literature on migration, we know little about how often survival selection occurs among early arriving migratory birds, how it potentially affects breeding seasonality, or the nature of the costs and benefits associated with early arrival (Møller 1994). This is partly because arrival time itself is difficult to determine for most species, requiring continual monitoring of large geographic areas in order to directly observe an individual's arrival, and because the smaller numbers and more scattered spatial distribution of the first arrivals make it difficult to impossible to know how they are affected by extreme weather events.

In 1996, an unusually long period of cold and wet weather in the northern and central Great Plains resulted in widespread mortality and led to intense viability selection on morphology among cliff swallows (*Petrochelidon pyrrhonota*; Brown and Brown 1998) and to a lesser extent barn swallows (*Hirundo rustica*; Brown and Brown 1999b). These species are aerial insectivores, and they starve when flying insect activity is curtailed by periods of cold weather lasting 4 or more days. Swallows are migratory and in the northern Great Plains breed during a relatively short period from May to July (and August for barn swallows). At our study site in southwestern Nebraska, weather conditions during late April and May as the birds arrive are unpredictable on both a daily and yearly basis (Brown and Brown 1996), with periods of cold and wet weather common. During the 18 years of our study, we documented three occasions in which cliff swallows succumbed to cold weather in May, and based on weather patterns there have been other mortality events in April affecting fewer birds that we did not observe. Here we focus primarily on the 1996 event, which reduced the cliff swallow population in the study area by at least half, and thus potentially had a major impact on arrival time and other behavioral parameters. We examine relative arrival time among survivors and nonsurvivors and assess whether viability selection favored later arrivals. We also examine how subsequent arrival time in this population changed as a measure of directional selection on breeding date. Our results provide empirical evidence showing that arrival time in a migratory bird can be adjusted by natural selection.

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 our study area, cliff swallows arrive beginning in late April (earliest 13 April; Brown 1998), with birds continuing to appear throughout May. Breeding is largely completed by the end of July. Nesting success declines as the season advances, largely because of ectoparasite infestations that increase later in the summer (Brown and Brown 1999a).

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, Neb. 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 event and field methods

This paper analyzes mostly a severely cold and wet period 24–29 May 1996 that caused the deaths of thousands of cliff swallows in the study area (see Brown and Brown 1998 for details). Initial estimates were that the population was reduced by at least 53% (Brown and Brown 1998), but later estimates based on mark-recapture data suggest that up to 73% of birds present at the time of the event may have perished (C. and M. Brown, unpublished data). We use the same designation as in Brown and Brown (1998) for survivors and nonsurvivors. Nonsurviving birds were those found dead at colony sites immediately after the bad weather ended. Survivors were birds captured in mist nets at colony sites during the 9 days immediately following the cold weather. Confining our sample to this time period minimized the probability of including as survivors any immigrants that had not experienced the same selection event (see Brown and Brown 1998). Although normally many cliff swallows have laid eggs by the time that the 1996 event occurred, the month prior to the bad weather had been cooler than average and egg-laying had been delayed (see Brown and Brown 1999a for temperature-related effects on egg-laying times). Consequently, many birds in the population were still in the nest-building and colony selection phases of the nesting cycle at the time of the weather event.

First-capture dates (see below) were extracted from an extensive mark-recapture dataset containing capture times for 80,444 banded individuals in 1982–1997. These data were collected by systematically rotating among 30–35 cliff swallow colony sites in the study area, usually mist-netting colony residents by putting nets across culvert entrances or along the sides of bridges where nests were situated. The intent of the mark-recapture sampling was to estimate annual survival probabilities in relation to colony size and chart colony-use histories of individuals. Each time a bird was caught, the date of capture (and numerous other variables) were recorded.

The start time of a colony was defined as when the first birds arrived and settled at the colony site; settlement was inferred by the birds' sleeping in old nests at a site. Start times were determined by monitoring all colony sites situated between Lewellen and Paxton within the study area at intervals of 1–4 days. This region was chosen because of its proximity to our base at the Cedar Point Biological Station. These periodic checks allowed us to specify the approximate date each site became active. We checked colony sites for evidence of occupancy during mornings in good weather when bird activity centered around nest sites and in the evenings when settlers returned to nests to sleep. Typically, cliff swallows first arrived at a site in a group of variable size, so isolated early arrivals were unlikely to have been overlooked.

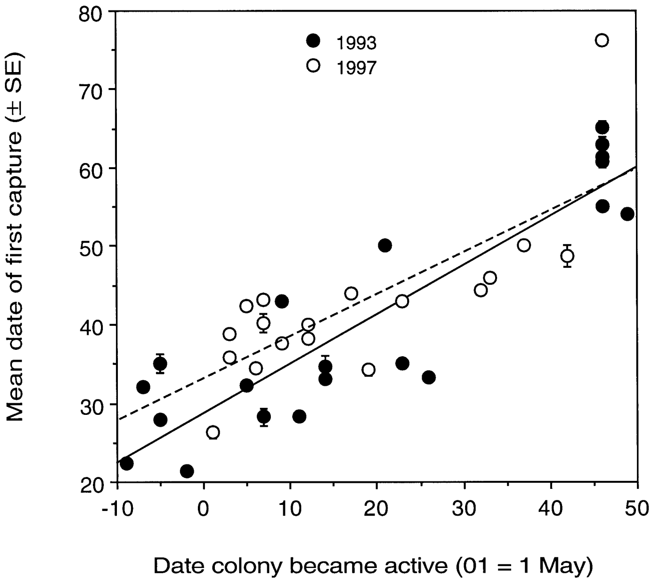

Fig. 1 Mean (±SE) date of first capture of cliff swallows at a colony in relation to the date the colony became active (site was first occupied) before a natural selection event (1993, *solid line*) and after the event (1997, *dashed line*). Mean date of first-capture increased significantly with date colony became active in 1993 (r_s=0.82, n=21 colonies, P<0.001) and in 1997 (r_s=0.76, n=18 colonies, P<0.001). Lines indicate best-fit least-squares regression

First-capture date as an index of arrival

Our measure of arrival time for each individual was the date it was first captured in a net each year (1=1 May). This is a relative index that provides a useful comparison between groups of birds (see Brown and Brown 1996). That first-capture date reflects arrival time is shown by comparing actual start dates of colonies (above) with the average first-capture date of birds caught at those sites (Fig. 1). There was a strong correlation between when birds first arrived at a colony and first-capture dates at that colony (Fig. 1). Birds that arrive early in the season are more likely to be caught early in the season, and late-arriving birds can only be caught late.

Although our colony sampling schemes have been largely the same each year since 1991, first-capture dates are sensitive to capture effort and weather conditions. Cool weather, even that not directly threatening the birds' survival, can curtail our netting activities by forcing the birds to spend considerable time away from the colonies foraging. Thus, a season with frequent cool weather results in fewer opportunities for us to catch birds, especially early in the year, and potentially results in later dates of first capture on average. We accounted for this yearly variation where possible in two ways. In analyzing repeatability of first-capture dates for individuals across years, we normalized each individual's first-capture date by converting it to a *z* score (using the BLOM option of the RANK procedure in SAS 1990). This gave a relative first-capture date, comparable among years with different mean first-capture dates. We present the repeatability of normalized first-capture dates and that calculated from actual first-capture dates (see Results). Second, for other analyses we compared first-capture dates or colony-start times only between years in which early season weather conditions (measured as mean daily high temperature for the period 18 April to 31 May) did not differ significantly. This time period was when most colonies were initiated in the study area and when cool weather most often curtailed netting activities. We found that daily high temperatures in 1993 did not differ significantly from those of 1997, the year immediately after the event (t=–1.387, P=0.17, n=44); 1993 was the only year prior to the weather event which matched 1997 climatologically. By restricting comparisons to these years, our analyses were unlikely to have been confounded by seasonal differences in weather conditions. Thus, we consider data from 1993 as that taken "before" the selection event, and that from 1997 as "after" the event. For other analyses, years were combined to analyze actual first-capture dates only when both groups were being compared across the same years. For analyzing the response to selection, we compared yearlings in 1997 that were offspring of the survivors of the 1996 selection event with birds of the same age in 1993 (before the event).

Weather data

Climatological data for 1949–1999 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, amount of precipitation, and other variables. We had no climatological data for April in the years prior to 1949, so we confined our weather analyses to the last 51 years (cf. Brown and Brown 1998). Based on conditions known to cause cliff swallow mortality, we designated periods of ≥4 days in length with daily high temperatures of 11°C. or less as probable mortality events (Brown and Brown 1998). We searched the climatological dataset for the frequency of these occurrences from 1949 to 1998. We confined our search to the period 13 April (representing the earliest date cliff swallows have been recorded in the study area) to 31 May each year; mortality events seldom if ever occur in June or July (Brown and Brown 1998).

Statistical analysis of selection

Standardized directional (i) and variance (j) selection differentials 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. In calculating differentials, we weighted the mean before selection by the relative proportions of survivors (27%) and nonsurvivors (73%) in the population as estimated from mark-recapture sampling in 1996 (C. and M. Brown, unpublished data). Repeatability in first-capture dates was calculated using intraclass correlation (Zar 1974).

Results

Colony-start times

One measure of arrival time is when colony sites first become occupied. The percentage distribution of colony start times after the mortality event was significantly different from that prior to the event (Fig. 2). In 1993, over a third of all colony sites were occupied in April, versus only about 3% in 1997. This reflected an obvious lack of cliff swallows in the study area in April following the mortality event of the previous summer. There were more late-starting colonies (in mid June) prior to the mortality event (Fig. 2). These late colonies are composed of many yearlings and immigrants from outside the study area, some of which are in apparently too poor a condition to eventually breed (C. and M. Brown, unpublished data). Fewer of these birds were present after the mortality event, accounting for fewer late colonies in 1997.

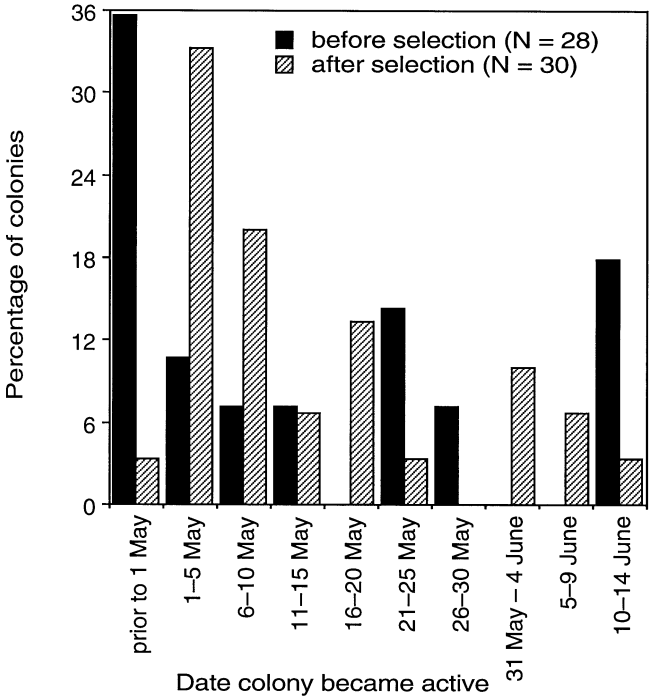

Fig. 2 Percentage distributions of dates that cliff swallow colony sites were first occupied in a year (1993) before a weather-related selection event and in the year (1997) immediately after the event. These years had similar weather conditions in April and May. The distributions differed significantly (χ^2_9=28.6, P<0.001)

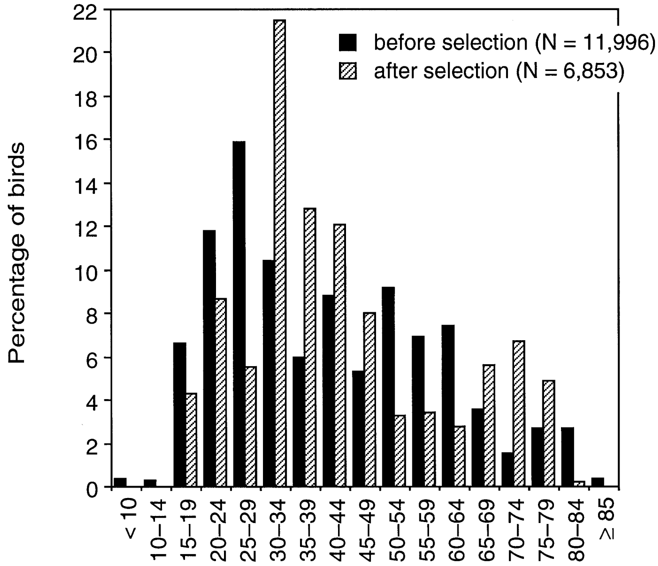

Fig. 3 Percentage distributions of first-capture dates (an index of arrival time) for cliff swallows in a year (1993) before a weather-related selection event and in the year (1997) immediately after the event. These years had similar weather conditions in April and May. The distributions differed significantly (χ^2_{16}=2310.5, P<0.0001)

Selection on arrival time

We compared an individual's average first-capture date in the years prior to selection (1995 and earlier) for survivors (mean=47.9, SE=0.8, n=380) and nonsurvivors (mean=45.5, SE=0.7, n=626); first-capture dates differed significantly between survivors and nonsurvivors (Wilcoxon test, z=2.08, P=0.037). Surviving birds thus tended to have been later arrivals on average in the years before the weather event. This resulted in a significant directional selection differential for arrival time (measured by first-capture date; i=0.106, t_{1004}=1.629, P=0.05). There was no evidence of any reduction in phenotypic variance for arrival time; the variance selection differential was not significant (j=–0.010, $F_{626,380}$=1.010, P=0.46).

That first-capture date as a relative index of arrival time reflects consistency among individuals from year to year is shown by repeatability measures (r_I) calculated for a sample of 14,031 birds for which first-capture dates were known in at least two successive seasons. Using normalized first-capture dates, repeatability was significant (r_I=0.09, P<0.0001); repeatability was also significant using actual first-capture dates (r_I=0.11, P<0.0001).

Arrival times before and after selection

Directional selection for later arrival times was also suggested by a comparison of first-capture dates in 1997 (the first season after the mortality event) with those in 1993, a season equivalent to 1997 climatologically (see Methods; Fig. 3). The percentage distribution of first-capture dates in the 2 years differed significantly, with early dates more common in 1993 prior to selection and later dates more common after selection. These data, based on capture data for individuals, are consistent with those on colony-start times from the same years (Fig. 2), showing relatively few individuals present in the study area early in the season after the selection event.

Response to selection

We compared first-capture dates for yearlings after selection in 1997 (those banded as nestlings or fledglings in the study area in 1996) to those for birds of the same age before the selection event (birds banded as nestlings or fledglings in 1992 and recaptured as yearlings in 1993; Fig. 4). Average first-capture date for the generation after selection (mean=37.4, SE=0.1, n=274) and birds of the same age before the selection event (mean=39.1, SE=0.8, n=482) did not differ significantly (Wilcoxon test, z=0.30, P=0.76). However, the overall distributions of first-capture dates for the survivors of the selection event and birds before it were significantly different, with later arrivals after selection (Fig. 4; we used fewer classes of capture dates for this comparison because sample sizes of yearlings were much smaller than for analyses based on all birds). Fewer yearlings were caught in May after the selection event (Fig. 4).

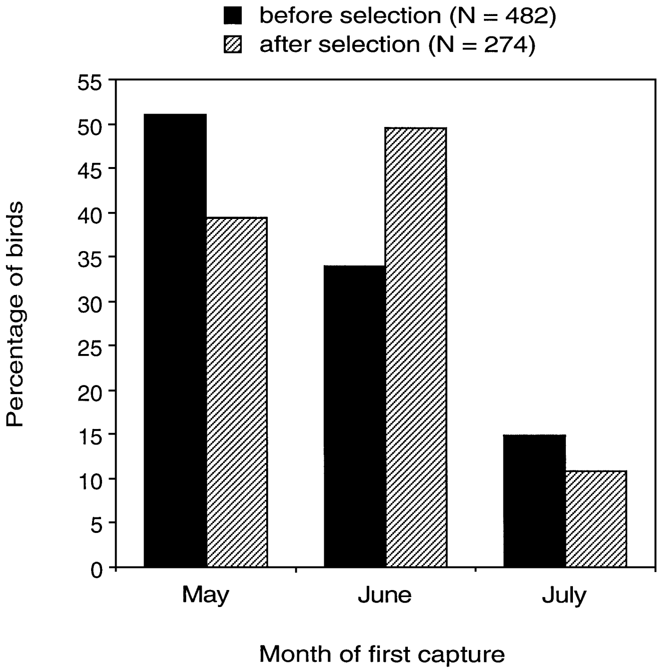

Fig. 4 Percentage distributions of first-capture dates (an index of arrival time) by month for cliff swallows in the generation after a selection event (1997) and birds of similar age before the selection event (1993). The distributions differed significantly (χ^2_2=17.83, P<0.001)

History of weather events

The climatological record suggests that weather conditions leading to cliff swallow mortality have occurred at least 25 times during April and May, 1949–1999. Our designation of conditions likely leading to mortality was conservative, and it is possible other mortality events occurred during that period. Cold weather lasting 4 days leads to detectable but relatively low cliff swallow mortality (Brown and Brown 1998): 4-day events occurred in 1953, 1954, 1972, 1976 (twice), 1982, 1983, 1984, 1988, 1991, 1992, and 1993. Weather conditions leading to major mortality events (≥5 days in duration) occurred in 1953, 1958, 1959, 1961, 1967 (twice), 1970, 1978 (twice), 1994, 1995 (twice), and 1996. This tabulation includes events occurring in April and early May, in contrast to that in Brown and Brown (1998) which included only events in mid to late May that impacted a large number of birds. Among the 25 events identified within the last 51 years, 20 have been in April or during the first 7 days of May. Counting both early season and later mortality events, these have occurred at intervals of 1, 2, 3, 4, and 6 years (average interval, 2.3 years). A minor or major weather-related mortality event occurred either early or later in the season each year from 1991 to 1996.

Discussion

Our results show that a 6-day period of unusually cold and wet weather in late May caused directional selection on arrival time in cliff swallows. This occurred through viability selection against birds which tended to arrive earlier, and the response to selection in the first generation after selection showed a shift toward later arrival. To our knowledge, this is the first direct demonstration of selection against early arrival per se, despite the presumption that survival costs of early arrival are widespread among migratory birds. Selective mortality in response to unusual climatic events, such as that we observed, is one of the best ways of demonstrating selection in natural populations (Bumpus 1899; Endler 1986; Grant and Grant 1993; Brown and Brown 1998).

Weather events leading to starvation probably have two major effects on cliff swallow breeding phenology in the Great Plains. Recurring cold snaps in the early part of the nesting season represent an environmental constraint that prevents increasingly earlier arrival within the population. For example, during our study, the longest interval between cold weather events (counting those in April) was 4 years, 1984–1988. During the three intervening seasons, mean first-capture dates increased by 7 days each year (55.4, 48.3, and 41.4 in 1985–1987). By 1988 (a year with a weather event), mean first-capture date had dropped to 42.9 and was 44.3 after the subsequent mortality events of 1991 and 1992. Although differing capture effort in these years (especially prior to 1991) is a potential confounding factor, the pattern is as expected, with arrival times advancing in years without cold snaps and becoming later just after weather events. Selective mortality of the earliest birds (those arriving in April and early May) probably causes these shifts, as we demonstrated for the major mortality event of 1996. Unfortunately, we have been unable to document mortality directly during the April and early May events because the number of birds involved is relatively small and corpses hard to find. The large sample sizes brought about by the extensive mortality of the late May 1996 event allowed us to study selection associated with arrival times in a way not possible before.

The other major effect of weather events is on egg-laying time. Laying by cliff swallows is delayed in colder seasons (Brown and Brown 1999a). Selection against early birds in those years contributes to later egg-laying by favoring individuals not as far into the nesting cycle. In the severe event of 1996, all nests in the study area that had eggs at the time of the cold weather failed, mostly because the owners died. We suspect that more recently arrived birds that were less advanced in breeding were more likely to survive (Brown and Brown 1998). The consequence is that weather-mediated directional selection for later arrival time leads to young being fledged later in the summer. This might not necessarily be the case when individuals arrive well in advance of nesting, such as in secondary cavity-nesting species in which arrival date may not correlate closely with breeding time (Stutchbury and Robertson 1987). In cliff swallows, however, nest-building and egg-laying begin relatively soon after a colony site is occupied, and thus any delay in arrival time will affect colony occupancy (e.g., Fig. 2), which in turn will affect when eggs can be laid.

With a seasonal decline in reproductive success over the summer, cliff swallows appear to be caught between two opposing selective pressures: later arrival resulting from weather-mediated viability selection and earlier breeding resulting from fecundity selection. Ectoparasitism appears to be the chief factor that reduces cliff swallow reproductive success later in the season and selects for earlier nesting (Brown and Brown 1999a). Selection for early arrival based on fecundity advantages must be strong; we observed that average first-capture dates increased in successive years when no weather events occurred.

Some north temperate birds have shown a trend for earlier average egg-laying date over the last 25–50 years, apparently in response to warmer climate (Crick et al. 1997; McCleery and Perrins 1998; cf. Visser et al. 1998). We have not detected any long-term change in cliff swallow breeding times over the last 18 years (C. and M. Brown, unpublished data). Regular early season viability selection may work to prevent a long-term change toward earlier nesting in cliff swallows. Periodic bouts of unseasonable weather upon arrival may be particularly important for aerial insectivores such as swallows whose food sources are extremely sensitive to bad weather. In cliff swallows, individuals differ in their ability to withstand weather events, due in large part to their morphology (Brown and Brown 1998), and arrival time could coevolve with morphological traits. Later arrival may be favored in smaller and more asymmetrical cliff swallows that are less likely to survive cold weather (Brown and Brown 1998). This would also maintain the observed distribution of breeding times in the population and help explain why later-nesting persists despite its apparent fecundity disadvantages. As our study continues, we are accumulating data to test whether correlations between morphology and arrival time exist. Arrival date in cliff swallows and other species may also be constrained by condition of birds on the wintering grounds, with birds in poor condition migrating later (Marra et al. 1998), or by perceptual or physiological constraints on selection for earlier egg-laying even when early season conditions are favorable (Visser et al. 1998).

Our assumption that arrival time is subject to selection requires that arrival time be heritable. We have no direct information on heritability of arrival time in cliff swallows, and this has not been reported for any species, probably given the difficulty of measuring actual arrival in natural populations (cf. Stutchbury and Robertson 1987). A few studies have reported that heritability of laying date (which may or may not reflect arrival time) is moderately high in wild birds (van Noordwijk et al. 1981; Findlay and Cooke 1982; Wiggins 1991). That arrival time in cliff swallows has some degree of heritability is suggested by the significant yearly repeatability in an individual's first-capture date. Repeatability can be used as a maximum estimate of heritability (Falconer 1981; Boake 1989). Our repeatability measures indicate that birds tend to be caught consistently at particular times of the year both in terms of absolute date and in relation to whether the year was on average an "early" or "late" year. This conclusion is about all that is warranted, however. Given the variability inherent in first-capture dates, dictated by netting schedules, weather, site accessibility, and other factors, we caution against putting too much stock in the actual repeatability values or trying to use them to quantitatively estimate heritability. Our results are also unlikely to be an artifact of age-related differences in birds before versus after the selection event. We had relatively few surviving and nonsurviving birds of known age with first-capture dates prior to the selection event, but a comparison of first-capture dates of 1997 yearlings with those of their parental generation showed that yearlings did not arrive consistently later than older birds (C. and M. Brown, unpublished data). In general, there are few age-related effects on arrival time in cliff swallows (Brown and Brown 1996).

The climatic record for the last 50 years shows a high frequency of weather events severe enough to cause cliff swallow mortality. While there have only been five mortality events in mid to late May during that period, and only two of those (in 1967, 1996) resulted in massive mortality (Brown and Brown 1998), cold snaps during April and early May are regular and frequent. Cold weather in April and early May is unlikely to affect a large fraction of the population and thus may have a negligible effect on morphological evolution (Brown and Brown 1998), but these events potentially remove many of the earliest individuals. We do not know the average survivorship of birds during the April and early May events. Some individuals probably survive them, as we observed during the later events of 1992 and 1996 (Brown and Brown 1998). But assuming some selective mortality, elimination or reduction of an entire phenotypic category (the earliest arrivals) may still have an impact on intergenerational genetic change (Boake 1994). More drastic directional selection for later breeding occurs during the rarer catastrophic events, such as that of 1996 that we studied. The lack of any evidence for stabilizing selection on arrival time (no significant variance selection differential detected in this study) suggests that the distribution of arrival times was shifted later but that the same degree of population variance was maintained. If so, this will contribute further to the apparent lack of long-term directional change in breeding date.

The breeding period of most organisms is usually thought to reflect the costs and benefits associated with particular times of the season and to reflect the optimal balance between them (Iwasa et al. 1983; Parker and Courtney 1983; Møller 1994). Work by others (Crick et al. 1997; McCleery and Perrins 1998) and our analysis of a major weather-related mortality event reveal that abiotic factors such as climate may play an important role in regulating the timing of avian breeding seasons. While this may not seem surprising, and while there are considerable data on how egg-laying times vary seasonally in nonmigratory birds such as tits, there are few data from natural populations to demonstrate an effect of weather on arrival time per se in migratory species. In cliff swallows, viability selection resulting from bad weather early in the season helps to regulate breeding time (along with other factors; Brown and Brown 1999a). We suggest that this may be a common pattern in other migratory birds.

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