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Breeding time in a migratory songbird is predicted by drought severity and group size

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Breeding time in a migratory songbird is predicted by drought severity and group size

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Abstract. Global climate change is altering the breeding phenology of many organisms, and one reported consequence of warmer average temperatures is earlier breeding times in migratory songbirds of north temperate latitudes. Less studied are the potential interactions between earlier breeding and social behavior in colonial species. We investigated how breeding time, as measured by colony initiation dates across the entire summer, in Cliff Swallows (*Petrochelidon pyrrhonota*) of southwestern Nebraska, USA, changed over a 30-year period and could be predicted by climatic variables, year, and colony size. Mean colony initiation date became earlier over the study, with variation best predicted by the extent of drought severity on the breeding grounds: colonies initiated earlier in warmer and drier years. Colony initiation dates were more asynchronous across the population in cooler and wetter years. There was no effect of climatic conditions during the nonbreeding season. Larger colonies started earlier in the year than smaller ones, probably because of the cost of ectoparasitism and the benefit of social foraging, both of which varied with colony size, date, and climatic conditions. The inverse relationship between breeding time and colony size was more pronounced in years with more severe drought. This study is one of the few to show that breeding phenology of a long-distance migrant bird is sensitive primarily to drought severity on the breeding grounds and that climate change can influence social behavior. If climate change exacerbates drought in the future, Cliff Swallow breeding time will likely become more strongly linked to group size.

Key words: breeding phenology; Cedar Point Biological Station, Nebraska, USA; Cliff Swallow; climate change; colonial nesting; colony size; drought; ectoparasitism; group living; Petrochelidon pyrrhonota; *social behavior; western Great Plains, USA.*

Introduction

The phenology of plant and animal breeding seasons is attracting increasing attention, largely because of the recognition that global climate change has altered the timing of reproduction in many organisms (Sparks and Menzel 2002, Walther et al. 2002, Parmesan 2006). One of the more widely reported results is the advancement of spring arrival times in migratory birds, with some studies indicating that first arrival dates have become ~7–10 days earlier in recent decades (Murphy-Klassen et al. 2005, Lehikoinen et al. 2006, Van Buskirk et al. 2009, Knudsen et al. 2011). One consequence of widespread phenological change is that individuals are no longer synchronizing their reproductive timing with the period of maximum resource abundance (Visser et al. 1998, 2006, Both et al. 2006), and population declines of some species may have resulted (Møller et al. 2008, Both et al. 2010, Jones and Cresswell 2010, Saino et al. 2011).

Directional changes in breeding time may alter other aspects of life history (Jonzén et al. 2007, Votier et al. 2009). In highly social species such as those breeding in colonies, advancing arrival and earlier breeding can lead to changes in the temporal distribution of group sizes or compositions and to changes in parasite load. For example, if warmer springs reduce the costs of early arrival (Kokko 1999, Spottiswoode et al. 2006), individuals previously constrained to later arrival may arrive earlier, potentially changing the composition of colonies active at different times of the year. Changes in colony composition could affect the benefits of group-living, such as better vigilance against predators or enhanced food-finding via social foraging that can depend on the individuals in the group (Brown and Brown 1996), alter the opportunities to pursue mixed mating strategies (Morton et al. 1990), or lead to changes in the risk of mortality caused by spells of bad weather in late spring (Brown and Brown 1998). The nest ectoparasites commonly associated with colonial birds (Moss and Camin 1970, Duffy 1983, Brown and Brown 1986, Cote and Poulin 1995) may also change their phenology to become active earlier or increase more rapidly (Cumming and Van Vuuren 2006, Brooks and Hoberg 2007), which may fundamentally alter one

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of the universal costs of group-living (Brown and Brown 2001) and lead to further evolution of breeding time in response to the parasites (Brown and Brown 1996). To date, almost no studies have investigated the potential links between climate-mediated changes in breeding time and group size or nesting density (Reed et al. 2006, Votier et al. 2009).

In this study, we examine factors potentially affecting breeding time in one of the world's longest-distance and most social migratory birds, the colonially nesting Cliff Swallow (*Petrochelidon pyrrhonota*). Breeding throughout North America, the Cliff Swallow winters exclusively in southern South America (Brown and Brown 1995), with an average distance of ~9500 km between the wintering and breeding ranges. Phenological responses to climate change are particularly relevant in this species, in that arrival time and spring weather often interact to affect adult survival (Brown and Brown 1998, 2000*b*), and time of breeding and climatic conditions influence the birds' exposure to hematophagous nest parasites that represent the single largest source of reproductive failure (Brown and Brown 1996).

We used a 30-year study to examine annual changes in Cliff Swallow breeding time and the extent to which any changes could be predicted by climatic conditions, either on the breeding grounds or during the nonbreeding season. Our measure of breeding time was a colony's initiation date (defined as when the first birds settled at a colony site) for all colonies throughout the summer. Because initiation date was an accurate index of a colony's egg-laying dates, this measure reflected directional trends in breeding phenology for the population as a whole. Our focus is not on arrival time itself, but on how colony initiation date reflects onset of nesting. In contrast to many studies that have correlated spring arrival primarily with changes in temperature per se (Dunn 2006), we examined the possible effect of moisture and how changing extent of drought on the breeding grounds may affect nesting phenology. In addition, we investigated the extent to which group size was associated with breeding time and potential interactions between group size and climate in affecting colony initiation date. Our study is among the few to explore how changing climate potentially alters social behavior through advances in breeding time of a colonial species.

Methods

Study site

We have studied Cliff Swallows since 1982 in the western Great Plains, USA, centered near the Cedar Point Biological Station (41°13′ N, 101°39′ W) in Keith County, southwestern Nebraska, along the North and South Platte rivers and including portions of Deuel, Garden, Lincoln, and Morrill counties (Brown and Brown 1996, Brown et al. 2013). Cliff Swallows construct gourd-shaped mud nests, often in dense, synchronously breeding colonies. In our study area the birds nest mostly on the sides of bridges, in box-shaped road culverts, or underneath overhangs on the sides of cliffs. A colony is defined as a group of birds, typically all those nesting on a given bridge or culvert, that interact during foraging or during predator alarm responses (Brown and Brown 1996). Colony size varies widely; in our study area it ranges from 2 to 6000 nests (404 ± 13 nests, mean ± SE; $n = 2318$ colonies), with some birds nesting solitarily (Brown et al. 2013).

Field methods

Cliff Swallows begin arriving in our study area in mid-to-late April in most years. Colony initiation date was when birds were first seen at a colony site in a given year and remained there daily thereafter. We monitored 727 colonies during 1983–2013 in which initiation date could be determined exactly or estimated to the nearest three days by virtue of our visit schedule. Because Cliff Swallows in western Nebraska now use predominately road-associated nesting sites such as highway bridges or drainage culverts and we knew the locations of all potential colony sites (Brown et al. 2013), sites were easily and frequently checked for bird presence by driving among them, and birds even in small colonies were unlikely to be missed if present. In a few cases we relied on observations by others prior to our arrival in the study area to pinpoint initiation dates. We had complete information on colony initiation dates for 24 total years; this did not include seven other years in which we did not arrive in the study area early enough to observe or estimate dates for colonies starting in April or early May. Initiation dates for all colonies throughout the season were recorded, including for a few colonies that began as late as early July. The late colonies consisted primarily of yearlings that had not nested elsewhere that season and contained few birds having attempted to nest elsewhere earlier (Brown 1998; C. Brown and M. Brown, *personal observation*). Colonies that were fumigated to remove ectoparasites were not included in these analyses, as fumigation affects Cliff Swallow settlement patterns (Brown and Brown 1996).

For each colony, we recorded the colony size, defined as the number of active nests (with ≥1 egg) and determined by checking the contents of nests with a dental mirror and flashlight inserted into each nest's mud neck or from the estimated number of birds present during alarm responses (Brown and Brown 1996). For graphical purposes, we relied on colony size categories, which, based on our extensive experience with the species, were ones that were biologically distinct from each other and used in other studies of colony size in Cliff Swallows (Brown et al. 2013). Colonies occurring at a given colony site in different years were considered independent units for analysis, because colony size at a site and the birds resident there often varied widely from year to year. However, to control for any nonindependence brought about by site effects, we incorporated colony site as a random effect in statistical analyses involving colony size.

To verify that colony initiation date was an unbiased predictor of breeding time with respect to actual egg-laying date, colony size, and colony synchrony, we compared initiation date to egg-laying dates for a subset of 31 colonies where we monitored laying times through nest checks every two days (Brown and Brown 1996). This subset of sites spanned the years of the study, 1983–2013, and ranged from 1–785 nests in size and from 2 May to 4 July in initiation date. At these colonies, either all nests were checked for egg-laying dates (1983–1990) or a sample of nests was chosen randomly with respect to date and spatial position (all other years). Within-colony egg-laying synchrony was measured by the standard deviation of egg-laying date across all nests in a colony (Brown and Brown 1996), and synchrony of colony initiation date within years was measured by the standard deviation of initiation date across all colonies in a season.

Climate data

Temperature and rainfall are the climatic variables having the largest potential effects on Cliff Swallows, both by influencing availability of the aerial insects that they feed on and the abundance of swallow bugs that feed on them (Brown and Brown 1996). We used mean temperature, cumulative rainfall, and Palmer Drought Severity Index (PDSI) data for Nebraska's Climate Division 7 (southwest Nebraska) from the National Oceanic and Atmospheric Administration, NOAA (*available online*).[4] Division 7 encompasses the center of our study area, and the regional metrics should be broadly representative of climatic conditions that the birds experienced each season. The PDSI is a measure of drought intensity used by NOAA, and it integrates both local temperature and rainfall data into a single index useful in describing soil moisture and extent of runoff (Palmer 1965, Dai et al. 2004). Lower values of the PDSI indicate more severe drought. Because Cliff Swallow colonies are initiated primarily from April through June, and thus are most likely to be affected by the climatic environment at that time, we used three-month averages for April–June as determined by NOAA. However, we also investigated whether a subset of these months might have been a better potential predictor of Cliff Swallow breeding time. The three months individually, as well as the preceding month of March (in case lagged conditions might be important), were all strongly correlated with the three-month average (correlation coefficients ranging from 0.62 to 0.75, $P < 0.001$ for all). Thus, any climatic influence would be the same regardless of which month(s) we used, and we chose to use the three-month average to dampen the within-season effect of any slight monthly fluctuations (brought about by, for example, a single heavy rainstorm).

As a measure of potential climatic influences during the winter season and during the birds' spring migration to Nebraska, we used the annual mean November–April value for the Southern Oscillation Index, SOI (*available online*).[5] A measure of El Niño or La Niña events in the Pacific Ocean, the SOI is associated with annual climatic variation in much of the western hemisphere (Trenberth and Caron 2000) and has been shown to correlate with spring arrival dates in some migratory birds breeding in North America (Miller-Rushing et al. 2008) and with annual survival and fecundity in others (Sillett et al. 2000). Broadscale climatic measures such as the SOI are particularly useful for studying species with wide geographic ranges (Forchhammer and Post 2004), such as the Cliff Swallow. We used the SOI for November–April because that is the time of the annual cycle when most Cliff Swallows are either resident in South America or migrating north through Central America (Brown and Brown 1995).

Statistical analyses

Potential temporal autocorrelation (Brown et al. 2011) in our data set was examined with the Durbin-Watson statistic (SAS Institute 2004). To assess which climatic variables best predicted breeding times, we used the Akaike information criterion corrected for small sample size (AIC_c) to compare the fit of multiple regression models and to identify those models with the greatest support (Burnham and Anderson 2002). Temperature and rainfall were not included in models also containing PDSI, because temperature and rainfall are accounted for in the calculation of the PDSI. Statistical analyses were done with SAS (SAS Institute 2004).

Results

Colony initiation dates for 727 Cliff Swallow colonies in our population ranged from 18 April to 4 July. Colonies were typically initiated by 5–300 initial settlers at a site, with the remaining residents arriving at the site within a few days of the first ones. Colony initiation dates became earlier across the study, but exhibited moderate annual variation (Fig. 1a). The latest mean date, 23 May, occurred in 1984, and the earliest, 8 May, in 2012. Colony initiation date exhibited no significant first-order temporal autocorrelation (Durbin-Watson statistic = 1.82, positive autocorrelation, $P = 0.22$; negative autocorrelation, $P = 0.78$), so further analyses did not consider temporal autocorrelation.

Colony initiation date vs. egg-laying date and colony size

Colony initiation date was strongly related to mean date of egg-laying among all nests in a colony ($r = 0.90$,

[4] www.ncdc.noaa.gov/cag/time-series/

[5] www.cpc.ncep.noaa.gov/data/indices/soi

$P < 0.001$, $n = 31$ years) and to the date when the first nest initiated laying ($r = 0.91$, $P < 0.001$). Egg-laying synchrony did not vary significantly with colony initiation date ($r = -0.31$, $P = 0.11$, $n = 28$) or colony size ($r = 0.14$, $P = 0.46$, $n = 28$). Colony size was unrelated to the interval of time (number of days) between colony initiation date and both the mean egg-laying date ($r = -0.11$, $P = 0.54$, $n = 31$) and the first egg-laying date at a site ($r = 0.08$, $P = 0.67$).

Effects of climate

The strongest climatic predictor of mean colony initiation date was the PDSI, with the best-fitting model being one that contained only the PDSI (Table 1). Each of the other climatic variables, alone, had $AIC_c > 3$, relative to the model with only the PDSI. Addition of year and/or the SOI to the PDSI did not improve model fit (Table 1). The effect of the PDSI on colony initiation date was positive (Fig. 1b), meaning that colonies started earlier in years with greater drought severity.

The synchrony of colony initiation dates across colonies in a given year was also related to the PDSI, with colonies initiated less synchronously in the years with less drought severity (Fig. 1c). PDSI was a significant predictor of initiation date synchrony ($\beta = 0.477$, $P = 0.05$, multiple linear regression), whereas year was not ($\beta = -0.059$, $P = 0.49$).

Effects of colony size

Cliff Swallow colony size was strongly associated with colony initiation date (Fig. 2a). Across all years and all 727 colonies, the largest colonies ($\geq$2000 nests) were the earliest ones to start, often in late April, whereas the smallest ones (1–9 nests) were the latest, beginning on average about a month after the largest ones (Fig. 2a). Using colony site as a random effect in a mixed model, we found that colony size ($F_{1,617} = 54.97$, $P < 0.001$) and the annual PDSI ($F_{1,617} = 4.33$, $P = 0.04$) were each predictors of colony initiation date, but year was not ($F_{1,617} = 1.30$, $P = 0.25$). Initiation date varied inversely with colony size (-0.008 ± 0.001, $\beta \pm$ SE), while PDSI had a positive effect (0.669 ± 0.258).

We also found a significant interaction between colony size and the PDSI ($F_{1,617} = 4.42$, $P = 0.03$). Exploring this interaction with a series of within-year analyses of the effect of colony size on colony initiation date revealed negative beta values for each year, in agreement with the combined-years analysis (e.g., Fig. 2a). However, the effect of colony size on initiation date was stronger in the years with greater drought severity (Fig. 2b). The yearly regression coefficients that were statistically significant ($P < 0.05$) occurred in years with

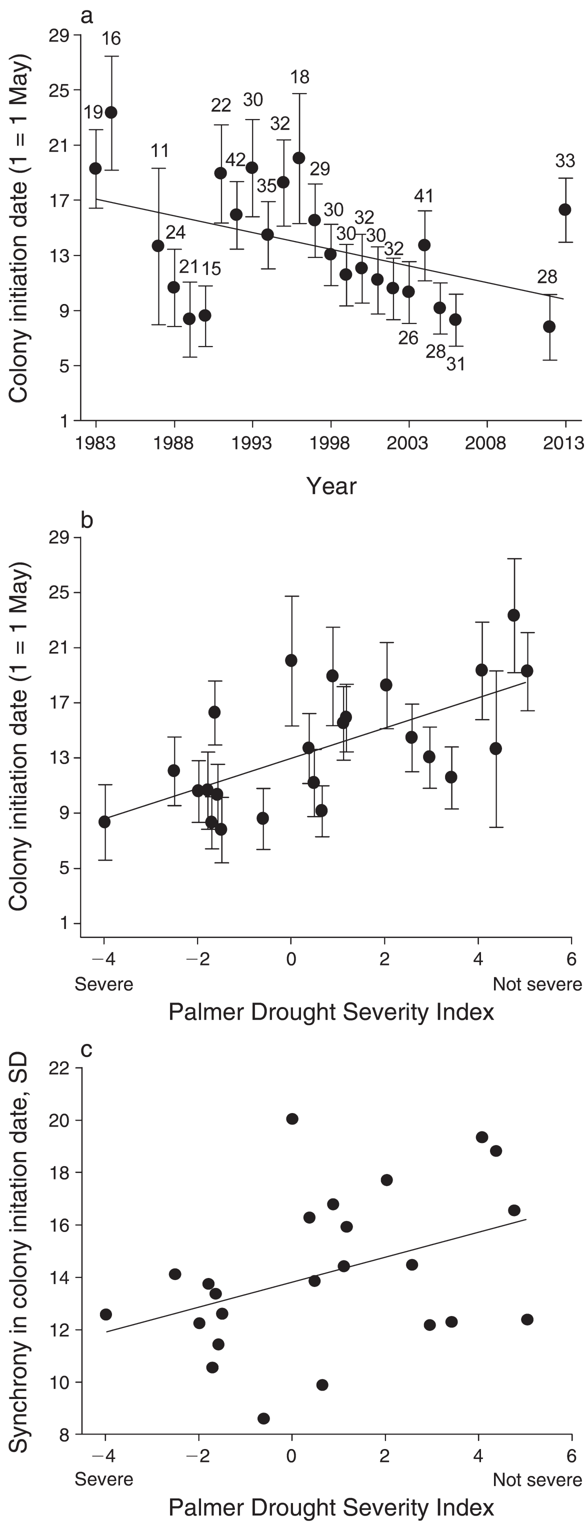

FIG. 1. Cliff Swallow colony initiation date (mean ± SE, where 1 on the *y*-axis is 1 May) in southwestern Nebraska in relation to (a) year and (b) the Palmer Drought Severity Index (PDSI) as calculated for April–June, and (c) extent of synchrony in colony initiation date within a season (as measured by the standard deviation of the mean initiation date ← across all colonies in that year) in relation to the PDSI. The number of colonies each year is shown near the error bars in (a). Lines indicate best-fit, least-squared regression based in panels (a) and (b) on the mean initiation date per year. Extent of drought varies inversely with the PDSI.

TABLE 1. Results of model fitting for the effect of climatic variables on Cliff Swallow colony initiation dates over 24 years.

Model	Variable(s) in model	AIC_c	ΔAIC_c	w_i
1	PDSI	68.21	0.00	0.321
2	PDSI, year	69.63	1.42	0.224
3	PDSI, SOI	70.34	2.13	0.111
4	year, temperature	70.97	2.76	0.081
5	temperature	71.29	3.08	0.069
6	PDSI, year, SOI	71.64	3.43	0.058
7	temperature, rain	73.18	4.97	0.027
8	temperature, SOI	73.38	5.17	0.024
9	year, temperature, rain	73.42	5.21	0.024
10	year, temperature, SOI	73.70	5.49	0.021
11	year	74.70	6.49	0.012
12	year, rain	75.28	7.07	0.009
13	temperature, rain, SOI	75.39	7.18	0.009
14	rain	76.46	8.25	0.005
15	year, rain, SOI	77.60	9.39	0.003
16	SOI	78.30	10.09	0.002

Notes: Model fit was assessed with the Akaike information criterion corrected for small sample size (AIC_c); models are presented top to bottom from best to worst fit, along with w_i, the AIC_c weight. Variable abbreviations are: PDSI, Palmer Drought Severity Index; temperature, mean daily temperature; rain, cumulative rainfall; SOI, Southern Oscillation Index.

lower PDSI values, and the magnitude of the size effect diminished as the year became wetter (Fig. 2b). Relatively drought-free years showed weaker (and nonsignificant) effects of colony size as measured by beta values (Fig. 2b). Colony size itself was not affected by either the PDSI ($\beta = -13.06$, $P = 0.20$) or year ($\beta = 0.624$, $P = 0.88$).

DISCUSSION

Cliff Swallow breeding time, as measured by colony initiation date, has become earlier over the last 30 years in southwestern Nebraska. It appears that this directional change can be explained largely by increasing drought during that time, and we found no statistical evidence that breeding time in this long-distance migrant bird was related independently to conditions in the nonbreeding season, as measured by El Niño/La Niña events. Cliff Swallows initiated colonies more synchronously and exhibited a stronger negative relationship between breeding time and group size in the drier years, suggesting that colony size may interact with seasonal drought conditions in determining when individuals breed.

Our measure of breeding time was colony initiation date for colonies started throughout the season. Analysis of egg-laying times for a subset of colonies showed that colony initiation date is a strong predictor of both the mean egg-laying date and the first egg-laying date at a given site, and there was no evidence that earlier or larger colonies were less synchronous in egg-laying than later or smaller colonies. Thus, colony initiation date in this species is a robust measure of breeding time for birds in all colony sizes and for those initiating nesting throughout the summer.

Although we did not systematically record Cliff Swallow first arrival dates per se, we do know that even in years with later mean colony initiation dates, Cliff Swallows were present in the study area by mid-to-late April each year, sometimes in large numbers, but simply did not form colonies. The earliest that we observed Cliff Swallows was 18 April, occurring in an early year (1989) and in two relatively late years (1992, 1993), as measured by mean colony initiation date. The earliest that the species has been recorded (by others) is 13 April, in another late year (1995). In this species, first arrival date in the study area is probably not a good measure of seasonal trends in breeding time.

Could individuals in earlier or larger colonies exhibit more asynchrony in their decision to settle at a site and establish nests? If so, earlier colony initiation dates at these colonies could be an artifact of colonization there being more drawn out over time. This is unlikely, however, because (1) egg-laying synchrony was unrelated to both colony initiation date and colony size, and (2) once Cliff Swallows colonize a site, most of the colony residents arrive within a few days (Brown and Brown 1996), and nest-building often commences shortly afterward. Arrival dates of individuals at a given site are not prolonged in time, even in large colonies, probably because the overwintering swallow bugs at a site begin feeding and reproducing as soon as the first Cliff Swallows arrive there (Brown and Brown 1996), and later nests within a colony are thus at a parasite-related disadvantage.

Drought and availability of food

In contrast to most studies on north temperate birds that have associated temperature per se with arrival time or laying date, ours is one of the few to find a systematic effect of drought severity on nesting phenology. Temperature alone was a poorer predictor of breeding time in Cliff Swallows than was drought as measured by the PDSI. Although temperature is used in calculating the PDSI, this metric also accounts for precipitation, soil moisture, runoff, and other variables (Palmer 1965), and in many ways is a more integrative measure of climate. Drought severity can potentially affect Cliff Swallows in multiple ways. Foremost may be that drier years are simply ones in which the birds' aerial foraging activities are less regularly restricted or curtailed by periods of precipitation, allowing them to feed more often, find more total food, and thus reach breeding condition (and settle in colonies) more rapidly.

In addition, extent of drought is likely to directly affect abundance of the birds' flying insect prey, although generalizations are difficult, given the diverse ways that insects respond to drought (Denlinger 1980, Tauber et al. 1998, Rouault et al. 2006) and the many taxa on which Cliff Swallows feed (Brown and Brown 1996). Some insects are more abundant during drier than normal conditions (Hawkins and Holyoak 1998, Morecroft et al. 2002, Chase and Knight 2003), others are more abundant during wetter years (Pollard et al. 1997, Frampton et al. 2000, Hertl et al. 2001, Ellis et al. 2004), and yet others require intermediate levels of, for example, soil moisture, for maximum reproductive success (Parker 1930, Gaylor and Frankie 1979, LaPointe and Shapiro 1999) or are influenced by complex dynamics between air temperature and soil moisture (Mukerji and Gage 1978). We do not know how extent of drought specifically affects the insects on which Cliff Swallows rely for food, but the birds' earlier nesting in drier years suggests that they are generally less food stressed then than in very wet seasons. The greater asynchrony in colony initiation dates in the wetter years also suggests greater variation in individuals' ability to achieve breeding condition and initiate nesting when food is harder to find.

Formal analyses of how drought severity affects Cliff Swallow fecundity and survival have not been conducted. However, we do know that wetter and cooler years (with weather-related reductions in food availability) are more likely to lead to mortality among adults during nesting (Brown and Brown 1998). In those same years, however, nestling survival is greater, probably because of fewer parasitic swallow bugs (Brown and Brown 1996). Thus, at present there is no suggestion that Cliff Swallows in our study area show any net change in fitness across years with different levels of drought severity.

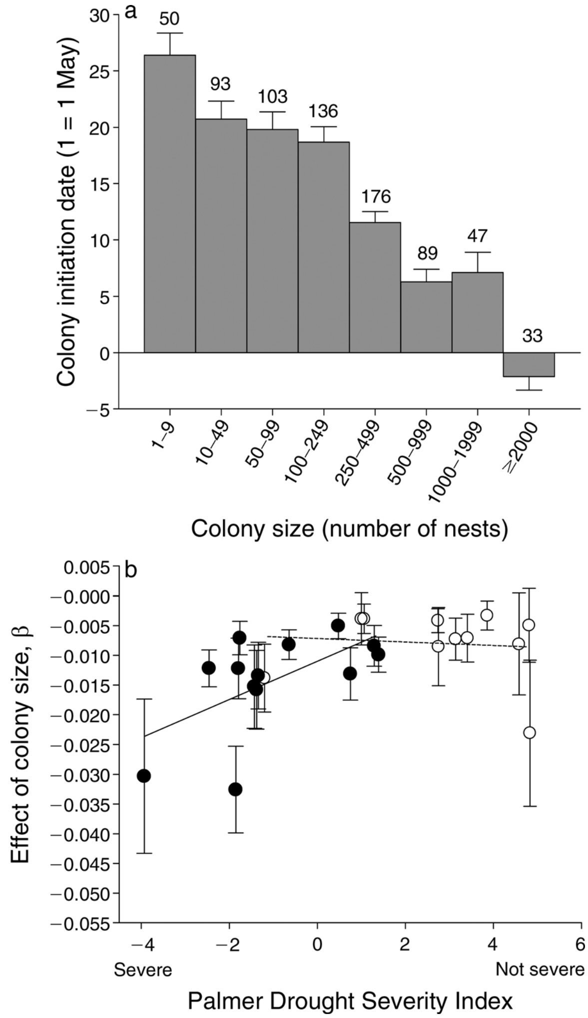

FIG. 2. (a) Cliff Swallow colony initiation date (mean + SE, where 1 = 1 May) in southwestern Nebraska in relation to colony size class across all years. The number of colonies in each size class is shown above the error bars. (b) Effect of colony size on colony initiation date each year, as measured by β values (±SE) from within-year linear regression, in relation to the Palmer Drought Severity Index (PDSI) for April–June. Years in which β was significant ($P < 0.05$) are shown by solid circles and a solid best-fit, least-squared regression line; years in which β was nonsignificant ($P > 0.05$) are shown by open circles and a dashed regression line. For years with significant within-season β values, the effect of colony size was significantly greater in drier years ($r = 0.60$, $P = 0.03$, $n = 13$ years); there was no effect of PDSI on the magnitude of the colony size effect in years with nonsignificant within-season β values ($r = -0.09$, $P = 0.78$, $n = 11$ years).

Colony size and breeding time

Group size was a stronger predictor of breeding time than was drought severity. The earlier a Cliff Swallow colony formed, the larger it tended to be. Potential explanations include the following. (1) Some sites may be preferred because of local food resources or lack of predators and parasites there, with these sites being chosen first and by more birds. (2) Birds with heritable or age-related tendencies to nest in smaller colonies (Brown and Brown 2000*a*, Roche et al. 2011) might arrive later or take longer to choose a site. (3) Birds might have an adaptive response to the increased ectoparasitism by swallow bugs in larger colonies (Brown and Brown 1986, 1996, 2004) by avoiding formation of large colonies in the later part of the season when bugs are most numerous. (4) Birds in the earliest forming colonies might increase aggregation to improve foraging success via information transfer (Brown 1986, Brown and Brown 1996) at a time in the year when insects are hardest to find.

The first potential explanation is unlikely because other analyses have ruled out strong site-related influences on colony size (Brown et al. 2013). For the second possibility, we have no direct information on potential links between colony size preference and time taken to assess and choose sites. However, the smaller colonies contain fewer yearling and emigrant Cliff Swallows than the other colonies (Brown and Brown 1996), and this observation is inconsistent with the conjecture that relatively inexperienced birds take longer to select nesting sites and thus are forced into smaller colonies for that reason.

The ectoparasitic swallow bugs begin reproducing in the spring as soon as the first birds arrive at a site and the bugs take a blood meal (Brown and Brown 1996). However, bug eggs take longer to hatch when ambient temperatures are colder (Loye 1985). Nesting in large groups is less constrained by ectoparasites earlier in the season when cooler temperatures, on average, slow the pace of the swallow bugs' reproductive cycle. In contrast, birds that form large colonies later in the season (when bug reproduction is faster) have fewer options to escape the large numbers of parasites that emerge in the large colonies, and perhaps for this reason we saw no colony of 2000 or more nests initiate later than 21 May in any year. Small colonies, because they have fewer total bugs (Brown and Brown 1996), pay less parasite-related cost of nesting later in the season when bug reproduction is enhanced. The interaction that we documented between colony size and the PDSI is consistent with this hypothesis: in warmer and drier years with accelerated bug reproduction, larger colonies started earlier, relative to smaller ones, than in cooler and wetter years. When climatic conditions lead to slower bug reproduction, there is less penalty for being in a larger colony later in the season, and this may account for the weaker colony size effect in years with higher PDSI values.

In addition, because insects are harder to find early in the season when, even in a season with favorable climatic conditions, periodic spells of cold weather occur with regularity (Brown and Brown 1998, 2000*b*), there are greater early-season benefits to residing in large colonies where these birds more efficiently share information on the whereabouts of ephemeral insect swarms (Brown and Brown 1996). The combination of foraging-related advantages early in the season in large colonies and parasite-related disadvantages later in the year in those same colonies may constrain large colonies collectively to earlier breeding times. The reduced foraging information available to birds in small colonies probably selects for later breeding times, when periods of food scarcity are less common and the lack of foraging information in a small colony is less of a handicap.

Cliff Swallows are periodically affected by periods of inclement weather during the first half of the nesting season (Brown and Brown 2000*b*). The more severe of these weather events (those lasting $\geq$4 days) can cause widespread swallow mortality by curtailing insect availability and leading to the birds' starvation (Brown and Brown 1998). Bad weather in 1996 caused heavy mortality among the earliest-arriving birds, and we interpreted later colony initiation dates during the subsequent nesting season as reflecting natural selection on breeding time (Brown and Brown 2000*b*). However, interpretation is clouded by the fact that we now recognize (from this study) the importance of drought severity in affecting colony initiation, and formal analysis of selection on arrival must take seasonal climatic factors into account. Nevertheless, because the Cliff Swallow is so highly sensitive to brief episodic periods of weather-mediated food restriction early in the season, breeding time in this species might be periodically adjusted by viability selection against arriving too early, especially if the frequency of unusual weather events increases in the future with global climate change (Greenough et al. 2001, Rosenzweig et al. 2001).

From 1895 to 2013, the PDSI for southwestern Nebraska showed an average change of -1.07/century (data *available online*; see footnote 4). If drought severity continues to increase in the Great Plains, we may witness not only earlier nesting by Cliff Swallows, on average, but also breeding date increasingly varying inversely with colony size. One potential consequence of such a change is that a greater fraction of the population (i.e., the birds in the large colonies; Brown et al. 2013) may breed early in the season at a time when the animals are most vulnerable to short-term spells of cold weather that threaten survival (Brown and Brown 1998, 2000*b*). Unusually cold weather lasting a few days can happen even in relatively warm and dry seasons: a mortality event in mid May 1988 (Brown and Brown 1996) was in one of the earlier seasons as measured by colony initiation date. This is a previously unrecognized mechanism that could potentially result in long-term population decline in Cliff Swallows and other insectivorous species that respond to climate change in similar ways.

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