Social foraging and the associated benefits of group-living in Cliff Swallows decrease over 40 years

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Abstract

Animals that feed socially can sometimes better locate prey, often by transferring information about food that is patchy, dense, and temporally and spatially unpredictable. Information transfer is a potential benefit of living in breeding colonies where unsuccessful foragers can more readily locate successful ones and thereby improve feeding efficiency. Most studies on social foraging have been short-term, and how long-term environmental change affects both foraging strategies and the associated benefits of coloniality is generally unknown. In the colonial Cliff Swallow (*Petrochelidon pyrrhonota*), we examined how social foraging, information transfer, and feeding ecology changed over a 40-year period in western Nebraska. Relative to the 1980's, Cliff Swallows in 2016-2022 were more likely to forage solitarily or in smaller groups, spent less time foraging, were more successful as solitaries, fed in more variable locations, and engaged less in information transfer at the colony site. The total mass of insects brought back to nestlings per parental visit declined over the study. The diversity of insect families captured increased over time, and some insect taxa dropped out of the diet, although the three most common insect families remained the same among the decades. Nestling Cliff Swallow body mass at 10 days of age and the number of nestlings surviving per nest declined more sharply with colony size in 2015-2022 than in 1984-1991 at sites where the confounding effects of ectoparasites were removed. Adult body mass during provisioning of nestlings was lower in more recent years, but the change did not vary with colony size. The reason(s) for the reduction in social foraging and information transfer over time are unclear, but the consequence is that colonial nesting may no longer offer the same fitness advantages for Cliff Swallows as in the 1980's. The results illustrate flexibility of foraging behavior and dynamic shifts in the potential selective pressures for group-living.

KEYWORDS

coloniality; diet composition; group-living; information transfer; Petrochelidon pyrrhonota*; social behavior; social foraging*

INTRODUCTION

One of the major potential benefits of living in groups is enhanced foraging efficiency (Alexander 1974, Pulliam and Millikan 1982, Brown and Brown 2001, Evans et al. 2016). Individuals in groups can improve their foraging success in different ways, and one of the best studied is social foraging and information transfer on the whereabouts of patchily distributed but locally abundant food (Ward and Zahavi 1973, Waltz 1982, Giraldeau and Caraco 2000, Barta and Giraldeau 2001, Kohles et al. 2022). That social animals, especially those living in breeding colonies, use information exchange during foraging has been documented in various species (Brown 1986, Waltz 1987, Marzluff et al. 1996, Buckley 1997, Burger 1998, Thiebault et al. 2014, Jones et al. 2018), and the benefits of social foraging—as measured mostly by prey intake rates—under certain ecological conditions have been well established (Giraldeau and Caraco 2000, Brown 2016, Kohles et al. 2022). When information transfer occurs at a fixed site, such as a breeding colony, it may favor or at least maintain colonial nesting (Waltz 1982, Wittenberger and Hunt 1985, Barta and Szep 1992, 1995, Brown and Brown 2001).

The relatively few studies that have examined social foraging and information transfer in relation to the fitness benefits of particular group sizes (Horn 1968, Hoogland and Sherman 1976, Brown 1988a, Brown and Brown 1996, Mariette and Griffith 2013) have been largely short-term, focusing on only one or a few seasons. Almost all research has sought to determine food intake rates, typical foraging group size, or extent of information transfer on a scale of minutes, hours, or days (reviewed in Giraldeau and Caraco 2000), and foraging studies spanning multiple years are rare (Miles 1990, Scheuerell et al. 2005, Szigati et al. 2018). Yet with environmental change that may disrupt trophic structure (Wagner 2020), and the fact that other benefits and costs of group-living can fluctuate among seasons (Brown et al. 2016, Riehl and Fox 2002), long-term studies are critical for evaluating whether the advantages of foraging in groups potentially change over time and how those changes may alter the adaptive significance of group-living.

Temporal shifts in foraging behavior are especially relevant for species that feed on insects, given the reported declines in insect taxa in some areas (Wagner 2020). As insect biodiversity is reduced by habitat loss through landscape change (Evans et al. 2007, Attwood et al. 2008, Bellavance et al. 2018, Musters et al. 2021), increasing pesticide use (Nocera et al. 2012, Hallman et al. 2014, Sharma et al. 2020, Brühl et al. 2021, Sánchez-Bayo 2021), and climate change (Grüebler et al. 2008, Ewald et al. 2015, Imlay et al. 2018, Funghi et al. 2019, Berzins et al. 2021, Halsch et al. 2021), the effects on organisms in upper trophic levels could be profound (Harvey et al. 2023).

Socially foraging birds and bats that rely on aerial insects and that actively or passively share information on the whereabouts of food (Brown 1986, Brown et al. 1991, Chantler 2000, Johnson et al. 2016, Kohles et al. 2022) might be particularly good candidates to exhibit behavioral changes in response to altered insect distributions. For example, a fundamental assumption underlying much of social foraging theory is that food is locally abundant enough to support multiple individuals that feed together, at least after food discovery. That animals eschew social foraging when food is scarce is generally assumed but not often empirically reported (Davies 1976). The variation in food availability is the basis for the well-known ideal-free distribution that leads to higher densities of foragers in some areas than others (Sutherland 1983, Kennedy and Gray 1993, Giraldeau and Caraco 2000). In addition, effective information sharing often requires a patchy distribution of food resources with certain characteristics (Waltz

1982, Giraldeau and Caraco 2000, Kohles et al. 2022). Quantitative and/or qualitative changes in flying insect distribution and abundance could thus lead to either increases or decreases in social foraging and temporal shifts in the fitness payoffs associated with group-living.

In this study, we use a 40-year dataset to examine temporal changes in social foraging and information transfer and the associated fitness advantages of coloniality in Cliff Swallows (*Petrochelidon pyrrhonota*). Our goals are to document (1) how social foraging behavior has changed over time, (2) whether taxa in the diet have exhibited quantitative or qualitative shifts that could explain any temporal changes in social foraging and information transfer, and (3) to what extent foraging-associated fitness measures for birds in different colony sizes have changed over the 40 years of the study. We rely on direct observations of foraging birds and the behavior of birds following others at the colony site to examine temporal change in social foraging and information transfer; the number of parental foraging trips, the amount of food delivered to nestlings, and diet samples to address quantitative and qualitative changes in food resources; and clutch size, reproductive success, and body mass of nestling and adult bids to measure fitness changes for birds in different sized colonies.

Our general prediction is that increases in social foraging over time should lead to greater benefits of coloniality, whereas decreases in social foraging should diminish the advantages associated with colonial nesting. Our study thus provides a rare test of the relative importance of social foraging in colonial animals; we are aware of no other work that has measured foraging behavior and its consequences over such a long-term scale. The results allow insight into potential temporal change in the selective pressures favoring coloniality and indirectly address how changing insect populations (Wagner 2020) may affect the costs and benefits of group-living in a socially foraging insectivore.

The Cliff Swallow is a highly colonial passerine bird that often forages in groups on aerial insects (Emlen 1952, Brown 1988b, Brown et al. 1991). Extensive research on our study population in western Nebraska in the 1980's showed that social foraging conferred benefits to Cliff Swallows through greater food intake and more rapid location of food sources, and these advantages increased in larger breeding colonies (Brown and Brown 1996), in part because colonies acted as information centers that promoted efficient foraging (Brown 1986). Fluctuation in foraging-associated benefits of different colony sizes are probably one reason that individual survival varies both among and within years (Brown and Brown 1996, 2004b), leading to selection on colony size that oscillates between years (Brown et al. 2016, Brown and Brown 2018).

Here we focus on Cliff Swallows after the birds have settled in breeding colonies and primarily during the period of feeding nestlings, a time when social foraging and information transfer was most common in the 1980's (Brown 1986, Brown et al. 1992, Brown and Brown 1996). As in other work on temporal ecological change (Brown et al. 2021), we rely on retrospective analyses of data collected in the 1980's originally for other purposes. We used the same protocols for collecting more recent data that we used in the earlier years—even when modification might have been desirable—to allow direct temporal comparisons. In some cases, we re-analyzed the older data with newer statistical methods. Because blood-feeding ectoparasites represent the single greatest cost of coloniality in Cliff Swallows (Brown and Brown 1986, 1996, 2002a) and the dynamics of these parasites and their swallow hosts have also shown long-term temporal change (Brown et al. 2021), for fitness analyses we used only fumigated (parasite-free) colonies in this study to better infer potential consequences of foraging shifts on Cliff Swallow fitness in the absence of the confounding effects of ectoparasites.

METHODS

Study animal and study site

The Cliff Swallow is a migratory, sparrow-sized passerine bird found commonly throughout the Great Plains and westward to the Pacific coast of North America (Brown et al. 2020). Historically, these birds built their gourd-shaped mud nests underneath horizontal overhangs on the sides of steep cliffs, but now many Cliff Swallows nest under the sides of bridges and buildings or inside concrete culverts underneath roads (Brown et al. 2013). The birds arrive in our study area beginning in late April, with most colony sites being first occupied in May and early June, but colonies can begin as late as mid-July. Most birds have completed nesting by early August. The species winters in southern South America (Brown et al. 2020). Cliff Swallows feed exclusively on flying insects caught on the wing from 1-50 m above the ground (Brown and Brown 1996, Brown et al. 2020).

We studied Cliff Swallows near the Cedar Point Biological Station (41°12'34.91"N, 101°38'51.50"W) in western Nebraska, USA, along the North and South Platte rivers. The study area includes portions of Keith, Garden, Deuel, Lincoln, and Morrill counties. Our work was done primarily at Cliff Swallow colonies on highway bridges and box-shaped culverts underneath roads or railroad tracks (Brown et al. 2013). Colonies were defined as birds from groups of nests that interacted at least occasionally in defense against predators or by feeding in the same general area (Brown and Brown 1996). Typically, all the nests on a given bridge or culvert constituted a single colony. Colony size varied widely, ranging from 1 (solitary nests) to

6000 nests (mean ± SD: 398 ± 618, $n = 4051$ colonies). Colony size in all cases refers to the maximum number of active nests at a site in a season, with an active nest defined as one containing one or more eggs. See Brown and Brown (1996) and Brown et al. (2013) for details on determining colony sizes. We use the term “colony” to refer to the collection of birds occupying a structure in a given year, whereas “colony site” refers to the physical substrate.

Fumigation procedures

We removed parasites, principally swallow bugs (Hemiptera: Cimicidae: *Cimex vicarius*), from Cliff Swallow nests by fumigation with an organophosphate insecticide, naled (Dibrom 8). Some colony sites were fumigated in their entirety, while others had a split design, with some nests fumigated and others left untouched. For analyses involving specific nests, only those from the fumigated sections of split colonies were used in this study. Fumigation methodology is given in Brown and Brown (1986, 1996) and Brown et al. (2021). Naled works primarily as a contact insecticide, although for semantic convenience we use the term “fumigation.” There was no experimental evidence that swallow bugs at the fumigated sites had developed resistance to naled over the course of the study (Runjaic et al. 2017).

Years included

The years included in this study were generally the periods of 1983-1991 and 2015-2022 when comparable data were collected in the same ways; in most cases no observations were available in the intervening years (see Brown et al. 2021). A continuous-year data set (1984-2009) was used only in the analysis of transient birds because we had no transient estimates for the years beyond 2009 but wished to determine if any temporal trend in these observations was consistent with the other analyses. Differences in the years included within the 1983-1991 and 2015-2022 periods in different analyses simply reflected what years relevant data were collected.

Climate comparisons

For climatic comparisons among different time periods of the study, we used the Palmer Drought Severity Index (PDSI), an integrative measure of temperature and rainfall that predicts Cliff Swallow breeding time and annual survival (Brown and Brown 2014, Brown et al. 2016): colonies start earlier in drier years, while annual survival is affected by an interaction between drought conditions and colony size. PDSI metrics were retrieved from the National Climate Data Center of the National Oceanic and Atmospheric Administration (NOAA; available online: https://www.ncdc.noaa.gov/cag). We used PDSI calculated for Nebraska's Climate Division 7 (southwest Nebraska), corresponding to the location of our study area (Brown and Brown 2014). NOAA currently provides PDSI for 1-month intervals, and here we used the PDSI for June because that is the month when most Cliff Swallows in the study area were feeding nestlings and parental foraging was at a maximum.

The mean (± SE) Palmer Drought Severity Index (PDSI) for June was 0.79 (± 0.99, $n = 8$ years) for the 1982-1989 decade, compared to -0.532 (± 0.87, $n = 8$ years) for the 2015-2022 decade; although the trend was for the later years to be drier, the difference was not significant (Wilcoxon test, $Z = 0.5776$, $P = 0.56$). Across the entire 41-year period of the study, the June

PDSI showed no significant directional change (Spearman rank correlation, $r_s = -0.11$, $P = 0.49$, $n = 41$ years).

Observing foraging birds

For foraging observations, we selected Cliff Swallow colonies that were situated in open terrain with unobstructed, level views for distances of at least a 1-km radius from the site (Appendix S1: Fig. S1; Brown 1986, 1988b, Brown et al. 1992). The visibility allowed us to see with binoculars any Cliff Swallows feeding around these sites and their relative positions. We used the same sets of sites for observations in the 1980's and in 2016-2022: one set of observations came from a single colony site in a road culvert (Whitetail) active in all years of the study (Appendix S1: Fig. S1) and the other set from four colony sites (Canal) all situated on similar concrete bridges along an irrigation canal in roughly linear fashion within a distance of ≤ 3.35 km from each other. These four sites were used as a set because, although they varied from year to year in whether Cliff Swallows occupied them, they were all in similar habitat and of the same sort of nesting substrate. Land use at Whitetail changed during the study as cultivated crops replaced nearby pasture (Appendix S1: Fig. S1). At the Canal colonies, adjacent land was mostly pasture, cedar (*Juniperus virginiana*)-clad bluffs, or a riparian corridor of deciduous trees along the North Platte River. These habitats were unchanged over time (other than the trees becoming larger). Details of the sites used each year and observation effort at each are given in Appendix S1: Table S1.

Because Cliff Swallow foraging behavior can be affected by colony size (Brown and Brown 1996), for observations we selected colonies from 2016-2022 that matched as closely as possible the size of those at the same sites in the 1980's (Appendix S1: Table S1). The Whitetail site was fumigated to remove parasites in each year of this study, while none of the Canal colonies was fumigated. Analyses of foraging behavior used a 2-factor categorical variable denoted as site (Whitetail, Canal) to investigate potential behavioral differences between birds using the two locations.

Surveys (scans) of foraging birds' positions were made at successive 10-min intervals for continuous periods of 1.5-4 h/day, in both mornings and afternoons (Brown et al. 1992). A single scan was typically accomplished within 3-4 min, so each scan was considered an instantaneous record of where all foraging was occurring at that time. A disturbance to the colony (predators, people) occasionally would require skipping 1-2 intervals before resuming once the birds returned to normal activity. The observer was positioned at the colony site sitting above the nests or on a road surface. The surrounding landscape was scanned 360° around the colony site. Foraging Cliff Swallows could be identified by their characteristic twisting and turning movements as they pursued prey (Brown 1985, 1988b; Video S1). Typically, birds could be easily designated as foraging solitarily or within a group based on proximity to other birds (< 10-15 m) and on birds staying together in the same place (Video S1). Birds commuting between the colony site and foraging areas were not included, as commuters generally flew in straight lines without stopping or turning and were recognizable as non-foragers (Brown et al. 1992). The size of a foraging group was recorded or estimated for large groups, with group size ranging from 1 to 1500 birds. Data were collected only on days with $\leq 50\%$ cloud cover, as Cliff Swallow foraging and activity at a colony site were reduced on cloudy days (Brown 1998, Brown et al. 2021). Each colony was observed on 2-14 days per year, and we observed a total of 16,383 foraging groups (counting solitaries as group size 1) among 1820 10-min scans during this study (Appendix S1: Table S1).

When a foraging group or solitary bird was first spotted, the compass direction (relative to the colony site) at that moment and proximity to a nearby landmark (e.g., stop signs, utility poles, road intersections, clumps of trees, irregularities of a creek bank) were noted. We plotted the one-way distance from each foraging group/solitary to the colony site on Google Earth Pro and considered this the travel distance while foraging. Distances from the colony site estimated strictly using landmarks in the 1980's (Brown et al. 1992) were re-calculated on Google Earth Pro to make them comparable to the more recent data. If a foraging group was large and relatively spread out, we used the compass heading of the group's center and calculated the distance based on the proximity of the center to the nearest landmark. In calculating average one-way distance from the colony site to a foraging group per scan, we weighted each distance by the number of birds in each group (or 1 for solitaries).

We could see Cliff Swallows up to a radius of about 1 km from each site. From doing surveys around colony sites by vehicle at 1-2 km away, we rarely saw birds foraging more than 1 km away and thus are confident we were not routinely overlooking more distant birds (Brown et al. 1992). Total forager counts within a scan were always lower than the number of birds that lived in the colony. For one analysis we divided the total number of foragers per scan by the colony size (number of nests × 2) to determine the percentage of the colony foraging in any 10-min interval. Any colonies at sites that might have shared their foraging range with birds at a nearby site (Brown and Brown 2002b) were not used for these observations. All scans were made by two observers only (CRB, MBB). The observers closely calibrated their estimates of foraging group size and proximity to landmarks by repeatedly scoring the same foraging groups on the same day at the same site with little difference between the observers (Brown et al. 1992).

Prey capture attempts for individuals within groups and for solitary foragers were observed at Whitetail in 2017-2018 using the methods of Brown (1988b) and by the same observer (CRB) in both decades. Prey capture attempts were designated from the birds' behavior as described in Brown (1988b). Birds were watched for as long as possible, usually between 45 s and 5 min. An observation was stopped when a bird terminated foraging and began flying back to the colony, disappeared from view, or switched from solitary to group foraging or vice versa. Prey capture rates were expressed in attempts per minute and computed for separate foraging bouts. We defined a foraging bout as a period of time (usually 1-2 h) on a given day during which weather conditions were unchanging for the entire time and during which prey capture rates for different birds were considered comparable (Brown 1988b). With so few birds foraging solitarily at Whitetail in the 1980's (Fig. 1), we had to compare the success of solitary foragers at Whitetail in 2017-2018 to that of solitary foragers at other sites in the 1980's (Brown 1988b). Further details on observational methods are provided in Brown (1988b).

Estimating change in transient birds

Because our observations suggested that parental Cliff Swallows might adjust their foraging behavior in response to the number of transient Cliff Swallows passing through colonies and investigating nests, we used our intensive mark-recapture data (Roche et al. 2013, Brown et al. 2016, Brown and Hannebaum 2022) to estimate the relative proportion of transient birds among those caught each year and how that might have changed over time. Transients are defined as birds not resident at a colony that pass through the site on a temporary basis. Those individuals caught only once at a colony include the transient class, but they also may include some residents who were not re-caught a second time.

The proportion of transients (τ) was determined with the method of Pradel et al. (1997). By fitting an age-dependent survival model to the capture data, the ‘‘first-year’’ age class was used to approximate the transients, who, by virtue of not reappearing at a site, had much lower apparent survival, ϕ, than the residents who tended to be caught multiple times. The proportion of transients (τ) in each time interval ($_t$) was calculated as $1 - (\phi_{1t}/ \phi_{2t})$, where ϕ_{1t} was the apparent annual survival probability of the ‘‘first-year’’ age class, and ϕ_{2t} was the apparent annual survival probability of the ‘‘beyond first-year’’ age class (Pradel et al. 1997, Brown and Brown 2004a). The calculation of τ for each year thus accounted for the fraction of one-time captures attributed to residents who were never caught again that season. The survival model used year-specific recapture probabilities, given that recapture effort varied with year (Roche et al. 2013).

Survival parameters were produced with program MARK (White and Burnham 1999). Here we combined birds from all colonies within a season and estimated one overall value of τ for each year. All Cliff Swallows caught at least once in a season as an adult were included in this data set, which consisted of 159,095 individuals across all years and varied from a low of 1207 (in 1985) to a high of 8900 (in 2004). Because continuous mark-recapture ended in 2013, the last year-cohort for which we had estimable age-specific annual survival parameters (and thus estimates of τ) was 2009. The years 1982 and 1983 were not included because of sparse data for generating survival estimates.

Scoring information sharing at the colony site

In 2019 we repeated observations from 1984 (Brown 1986) to determine if Cliff Swallows unsuccessful at foraging returned to their nests and then followed neighboring birds to food sources, and if so, were they likely to follow previously successful birds. The same methodology was used, in which we observed groups of about 40 nests at a time and scored (1) whether a focal bird that returned to its nest either had food and fed its nestlings or did not have food, and subsequently (2) whether the focal bird followed another bird upon its departure from its nest and (3) whether a focal bird was followed by another bird upon departure. We defined following as departure within 5 s of the other individual in the same direction (Brown 1986). Observations were conducted when colonies were in later stages of nestling feeding, when nestlings sat in (blocked) the entrances of the gourd-shaped nests and parents clung to the outside upon their return; thus, whether a returning bird had food was easily determined by whether it fed a nestling. We used only periods when all birds in the colony were foraging, and we suspended observations if colony residents began to gather mud for nest maintenance or if transient birds (see Estimating change in transient birds) appeared around the focal nests. No birds were color-marked, and, as in the original study (Brown 1986), some individuals were likely represented multiple times, although we tried to watch as many different nests in a colony as possible. In 1984, we conducted these observations at two colonies of 450 and 800 nests, and in 2019 we used four colonies of 203, 218, 525, and 1700 nests. For these observations, we used only non-fumigated colonies on highway bridges over rivers in which nests were on the outer beams with good visibility, and all consisted of a single long row of nests underneath the beam overhang.

Determining amount of food delivered and diet composition

Parental food deliveries by Cliff Swallows were recorded as the number of times either parent visited a nest and fed nestlings. Visits in which no food was brought were not counted. We observed only nests (usually 5-20/h) for which we knew the brood size and age of nestlings, because both of these variables affect feeding rates (Brown and Brown 1996). Cliff Swallow foraging is strongly dependent on local weather conditions, and thus we included hourly weather covariates (temperature, wind speed, and extent of sunshine, measured as solar radiation in watts/m^2) in our analyses of food deliveries (see Brown et al. 2021 for details). Because the extent of ectoparasitism affects parental provisioning rates (Brown et al. 2021), in this study we used only parental food delivery rates at nests in fumigated colonies (see Fumigation procedures) to better measure consequences of foraging strategies over time in the absence of potentially confounding effects of ectoparasitism. Food-delivery data were recorded in 1985-1989 from four fumigated colonies ranging in size from 22 to 2200 nests and in 2016-2018 from seven fumigated colonies ranging in size from 44 to 1920 nests (see Brown et al. 2021 for details on these colonies).

Cliff Swallows typically deliver a tightly compressed mass (bolus) of insects to one nestling per visit. We used pipe cleaners loosely fitted around a nestling's neck to prevent it from swallowing the bolus (Orians and Horn 1969). Ring-collaring does not harm nestlings if collars are adjusted correctly, and it does not normally affect their growth (Henry 1982). Nestlings were ring-collared for up to 40 min, after which we removed any boluses from the nestlings with forceps and placed the boluses in 70% alcohol. The wet weight of each bolus provided a relative index of the amount of food delivered per trip (Brown and Brown 1996, Brown et al. 2021). We typically ring-collared nestlings that were 10-12 days old, as ring-collaring was ineffective on younger or older nestlings. Ring-collaring was never done at a site during the same time that food deliveries were being counted. We had bolus data from nine colonies ranging in size from 2 to 345 nests in 1984-1988 and 17 colonies ranging in size from 7 to 1920 nests in 2016-2018.

After each bolus was weighed, its contents were processed for identification using field guides, taxon-specific keys, or a web resource (http://bugguide.net). We identified each individual in a bolus (where possible) to family, except for spiders that were all designated as Araneae. Samples from the 1980's had been retained in alcohol, and although these had been identified earlier (Brown and Brown 1996), all were re-identified in this study using current information and taxonomy, primarily by one person (GSW). We recorded the total number of individuals of each family in a bolus sample, but we did not distinguish size or biomass of different taxa. Family-level diversity was calculated for each bolus using the Shannon Index (H) and the number of individuals of each family in the bolus.

Determining foraging-related fitness measures

Nests were numbered and their contents monitored by periodic checks using a dental mirror and flashlight inserted through the nest's entrance hole. This technique allowed us to determine laying date, clutch size, hatching date, and nestling survival for all nests. The actual number of nestlings reaching 10 days of age in each nest was a relative index of nestling survival to fledging (Brown and Brown 1986, 1996). Survival was measured only for nests followed from the time of egg-laying, and nests failing before hatching or reaching 10 days were treated as having 0 nestlings surviving. We had reproductive success data from 29 colonies in 1984-1991 (colony size 1 to 2200 nests) and 28 colonies in 2015-2022 (colony size 12 to 1920 nests). Cliff Swallows are generally single-brooded in southwestern Nebraska (Brown et al. 2021), and our measure of reproductive success was for presumed first broods only.

For nests with at least one nestling surviving to day 10, we weighed each nestling with a Pesola scale (to the nearest 0.5 g) to determine body mass (Brown and Brown 1996). Nestlings were banded with U. S. Geological Survey bands. Nestlings were weighed in the same way throughout the study, with the same person (CRB) doing or supervising data collection in all years. We had nestling body mass data from 23 colonies (colony size 5 to 2200 nests) in 1984-1989 and 21 colonies (colony size 32 to 1920 nests) in 2015-2018. Only nests at fully fumigated sites or within the fumigated portions of other sites (Brown et al. 2021) were used in the analyses of reproductive success and nestling body mass.

Body mass of adult Cliff Swallows was recorded in the course of mark-recapture for other purposes (Brown 1998, Roche et al. 2013, Brown et al. 2016, Brown and Hannebaum 2022). For this study we used data from birds caught in 1984-1989 and 2013-2021. Each time an adult was captured in a mist net, we recorded its sex (by presence/absence of a brood patch or cloacal protuberance) and its body mass to the nearest 0.5 g using a Pesola scale. The colony's nesting stage has a greater effect on adult mass than absolute date (C. R. Brown, *unpublished data*), so for each capture the stage was designated as early, middle, or late, depending on the colony's activity on that date. Early was the period when most birds were nest-building or egg-laying, middle the period of incubation, and late the period when parents were feeding nestlings. Because nesting is highly synchronous within each Cliff Swallow colony (Brown and Brown

1987, 1996), using a single designation for all birds caught on a date at a site reflected the probable status of each bird relatively well.

Only adults caught on their day of initial banding were used in this data set; if the same bird was caught multiple times within the same nesting stage that year, a mean body mass was used for that stage. For individuals caught in multiple years, we used only their first year of capture, and thus each bird was represented in only one year for each nesting stage. Only Cliff Swallows captured at colonies that were fully or partially fumigated were used in these analyses. Birds were caught at 20 colonies ranging in size from 30 to 2200 nests in 1984-1989 and at 8 colonies ranging in size from 44 to 1975 nests in 2013-2021. We had body-mass data for adults in the intervening years but did not use those data in order to make the analyses more consistent with others that had a temporal gap. This study was not intended as a comprehensive investigation of all factors potentially influencing adult body mass in Cliff Swallows (*sensu* Paquette et al. 2014), which will be explored elsewhere, but rather to look for general trends over time that might be related to changes in foraging behavior.

Statistical analyses

Analysis of all non-circular data used primarily mixed-model regression implemented with Proc MIXED in SAS (SAS Institute 2004). Independent covariates (fixed effects) were identified a priori based on past work and presented for each analysis (Appendix S1). In some cases, we also included one or more relevant interaction terms related to decade, but interactions that were not significant were dropped and only models with main effects and significant interactions are presented and used for inference. Models with significant interactions contained the same variables as main effects, but in those cases the main effects were not interpreted. Because colony size can sometimes affect fitness in curvilinear ways (Brown et al. 2016, Brown and Brown 2018), analyses included a colony-size*colony-size interaction term. We designated a 2-level categorical variable of decade, with data from 1982-1991 considered as one and those from 2015-2022 the other. Year itself was treated as a random effect (see below). Because we had a biological rationale for all of the independent predictor variables used (Grueber et al. 2011), we did no model selection for these analyses (other than excluding non-significant interactions). Date within the season was treated as a continuous variable, with 1 May = 1, 1 June = 32, etc. Proc PLM in SAS was used to generate predicted regression lines (which held other fixed effects in the mixed model at their average values); whenever model-predicted lines are shown, we also present the actual data as represented by means.

To account for non-independence of observations (and potential pseudoreplication), we used the following random intercept variables: **colony site**, coded as the same site designation for all years, to account for potential spatial dependence of a colony site's physical location across years; **colony-by-year**, coded the same for all observations at a colony site in the same year but different between years, to account for dependence of observations at a single colony within a year; **nest identity**, coded the same for all observations within the same nest in a given year at a given colony but different among years at that colony, to account for potential dependence among nestlings or behavioral observations from the same nest; and **year**, coded the same for all observations in a given year, to account for year-specific variation in cases where a categorical fixed-effect of decade was used. Analyses of foraging behavior also used an **observation-session** random effect, to account for non-independence of bird foraging activity within a given observation session (set of 10-min scans) at a colony on a single day; each 2-3 h session at a given colony was coded uniquely. Most analyses could not include all of these potential random effects, either because of model structure, sample size, data distribution, or missing data. The random effects were coded to implicitly describe a nested data structure (e.g., year and colony-by-year, colony-by-year and nest identity), as described by Schielzeth and Nakagawa (2013).

The compass bearings of foraging groups (relative to the colony site) were initially analyzed with circular statistics implemented in Oriana (Kovach 2011). We used the circular standard deviation of compass heading for all foraging groups (or solitaries) as a measure of group clustering in space around the colony site. Typically, most birds along a given compass bearing on a scan were in the same foraging group, although rarely two groups had the same bearing. The circular standard deviation of compass bearings for each scan was averaged across the observation session to yield the within-scan standard deviation. The mean compass heading for each scan was used to calculate the within-day circular standard deviation. For scan-level calculations, each compass bearing was weighted by the number of birds in foraging groups with that bearing, and for within-day calculations each scan's mean compass bearing was weighted by the total number of birds in all foraging groups seen on that scan. Finally, we took the average of the daily compass bearings to determine the between-day circular standard deviation for each colony that year. Once calculated with circular methods, the standard deviations for scan, day, and colony permitted analysis with linear models as described above (e.g., Brown and Brown 1996). Circular graphs (Appendix S1: Figs. S2, S3) were constructed with Oriana (Kovach 2011).

RESULTS

Changes in social foraging and information transfer

Extent of social foraging

In the 1980's, Cliff Swallows foraged at Whitetail and the Canal colonies in well-defined groups over relatively open habitat that surrounded each site (e.g., Appendix S1: Fig. S1). While feeding nestlings, birds commuted from the colony site to foraging areas in direct, rapid flights, and those that departed in close proximity (≤ 5 s) tended to travel together until reaching a foraging site, where they began feeding together and often as part of a group that was already present. Birds rarely made any attempts at prey capture while commuting either to or from the colony site. Foraging groups at any given time could be easily located by the streams of birds going out from the colony site directly to the feeding sites.

In contrast, in 2016-2022 groups were more diffuse and shorter-lasting at any one location; birds leaving the colony site together often veered in different directions at short distances from the colony site and rarely traveled together in streams. Cliff Swallows often made abortive prey capture attempts while traveling to foraging sites in 2016-2022, and thus commuting flights were less direct in those years. Foraging groups in both decades often fed at heights of 50 m or more, although solitaries and small groups (especially in 2016-2022) were more likely to feed relatively low, often < 3 m above the ground.

The size of foraging groups and the extent of solitary foraging changed over time (Fig. 1). Cliff Swallows in the 1980's rarely fed as solitaries at the focal colonies, and groups of 100-200 birds were most common, whereas by 2016-2022 solitary foraging or as groups of 2-5 birds was predominant, and this pattern held at both Whitetail and the Canal sites (Fig. 1). These distributions yielded large differences in mean foraging group size (Fig. 2A). The largest foraging group observed in the 1980's was 1500 birds, compared to 500 birds in 2016-2022. With the mean foraging group size per 10-min scan as the dependent variable, we found that the categorical fixed effect of decade was significant, but date within the season and site (Whitetail, Canal) were not (Appendix S1: Table S2). There was a curvilinear effect of colony size on foraging group size (Fig. 2B; Appendix S1: Table S2), with the largest foraging groups occurring at colonies of about 1100-1300 nests. The curvilinear effect did not vary significantly with decade (Appendix S1: Table S2). This analysis controlled for the significant effect of the total number of birds seen on a scan (Appendix S1: Table S2), because, with a limited foraging area, group size might be expected to increase when more birds were foraging during a 10-min period. The random effects of colony-by-year and observation-session were significant or almost significant (Appendix S1: Table S2).

In 1982-1986, prey capture attempts per min were 3.6 (± 0.3, *n* = 504 birds, *n* = 29 bouts) for solitary foragers, versus 5.9 (± 1.4, *n* = 1615 birds, *n* = 29 bouts) for group foragers (Brown 1988b). At Whitetail in 2017-2018, mean (± SE) prey capture attempts per min per foraging bout was 4.8 (± 0.20, *n* = 196 birds, *n* = 10 bouts) for solitary foragers, versus 3.8 (± 0.3, *n* = 75 birds, *n* = 10 bouts) for group foragers. Based on overlap of 95% confidence intervals, solitary foragers were more successful (i. e., captured more insects) in 2017-2018 than they were in 1982-1986, but there was no difference between the decades for group foragers. Solitary foragers were significantly less successful than group foragers, on average, in 1982-1986 (Brown 1988b), but solitary foragers were significantly more successful than group foragers in 2017-2018 (based on overlap of confidence intervals).

We found no detectable change over time in the one-way foraging distance from the colony site (Fig. 2C). Foraging distance increased significantly as the season wore on and at larger colonies, and was greater at Whitetail than at the Canal colonies, but decade was not significant nor were interactions involving decade or colony size (Appendix S1: Table S3). The random effects of colony-by-year and observation-session were significant (Appendix S1: Table S3).

Time spent foraging

The percentage of the residents of a Cliff Swallow colony that were foraging during any 10-min scan showed a steep decline between the decades (Fig. 2D). Decade and date within the season were significant predictors of the percentage of the colony foraging, but there was no effect of colony size or site, nor were any of the interactions among the fixed effects significant (Appendix S1: Table S4). The random effects of colony-by-year and observation-session were significant (Appendix S1: Table S4).

Transient Cliff Swallows often passed through colonies, stopping to investigate existing nests by clinging to the entrances or perching on the tops. Such activity seemed to peak later in the season when most colonies were engaged in nestling feeding. Parental Cliff Swallows vigorously defended their nests whenever transients were present and often ceased making foraging trips to and from the nest as long as transients remained nearby.

The proportion of transients (τ) in our mark-recapture study generally increased over the period of 1984-2009 (Fig. 3). Over all years, the increase was not statistically significant, but when 1984 (the first year) was excluded, the increase was significant (Fig. 3). Although we did not have mark-recapture data suitable for estimating transients in the 2015-2022 time period considered here in other analyses, the proportion of transients per year in the 1980's (except 1984) was lower than in the other years of the study.

Spatial clustering during foraging

The within-scan circular standard deviation in compass bearings of foraging groups/solitaries around the colony per 10-min scan did not vary significantly with decade, colony size, or site (Whitetail, Canal), nor were there any significant interactions among these variables (Appendix S1: Table S5, Fig S2). The random effect of observation-session was significant but that of colony-by-year was not (Appendix S1: Table S5). However, the within-day circular standard deviation of mean compass bearings per scan varied with decade in a colony-size interaction (Fig. 4; Appendix S1: Table S6, Fig. S3). The within-day standard deviation declined with colony size in 2016-2022 but hardly changed with colony size in 1984-1988 (Fig. 4). The standard deviation tended to be smaller (or the same) in the 1980's than during 2016-2022 at most colony sizes. Neither the fixed effect of site (Whitetail, Canal) nor the random effect of year had a significant effect on within-day circular standard deviation, and there were no other significant interactions among the fixed effects (Appendix S1: Table S6). For the between-day circular standard deviation per colony within a season, the Whitetail colonies had a significantly higher mean value (mean = 76.0, SE = 10.7, n = 10 colonies) than the Canal colonies (mean = 41.0, SE = 6.2, n = 8 colonies; $F_{1,15}$ = 6.65, P = 0.021), but decade had no significant effect ($F_{1,15}$ = 0.05, P = 0.83) on between-day variability in foraging location.

Information sharing at the colony site

One characteristic of Cliff Swallow foraging behavior in the 1980's was information transfer at the colony site, often among birds that occupied nests in close physical proximity within a colony. Birds returning to their nest without food (presumably unsuccessful) were significantly more likely to follow other birds on the next foraging trip than were birds that returned with food (Table 1A), and previously successful birds were significantly more likely to be followed on the next trip than previously unsuccessful birds (Table 1C). However, this pattern had disappeared in 2019, with prior success having no significant effect on whether a bird followed another on the next trip (Table 1B) or whether it was followed (Table 1D). In 1984, 74.9% of previously unsuccessful birds ($n = 1809$) followed others, whereas in 2019 only 21.1% did so ($n = 601$); this difference was highly significant ($\chi^2_1 = 550.9$, $P < 0.0001$). Overall success did not differ significantly over time: in 1984, 63.4% of returning birds ($n = 4943$) had been successful, compared to 63.7% ($n = 1687$) in 2019 ($\chi^2_1 = 0.04$, $P = 0.85$). In comparing each of the four categories of birds (followed, did not follow, was followed, was not followed) separately with respect to prior success (Table 1), in all cases the distributions differed significantly between 1984 and 2019 (chi-square contingency tests, $P < 0.0001$ for all).

Because some of the colonies included in the 2019 observations were smaller or larger in size than those in 1984, we also examined these results separately for the two colonies of the closest size in these years (one of 450 nests in 1984 and one of 525 nests in 2019). We found the same pattern at these two sites, with following or being followed dependent on success in 1984 but not in 2019 (Appendix S1: Table S7). Similar to the overall data set, at these two sites alone, 78.6% of unsuccessful birds (*n* = 740) followed others in 1984, whereas only 20.1% (*n* = 388) did so in 2019 ($\chi^2_1 = 359.4$, $P < 0.0001$).

Quantitative and qualitative changes in diet

Amount of food collected

Based on 1-h watches at nests combined across all fumigated colonies, the mean (± SE) number of parental food deliveries/h/nest was 12.25 (± 0.19, *n* =1185 watches) in 1985-1989 and 12.02 (± 0.16, *n* = 1661 watches) in 2017-2018. Food deliveries varied significantly with brood size, nestling age, and weather variables such as wind speed and extent of sunshine, but decade had no significant effect (Appendix S1: Table S8).

Using the food boluses collected from nestlings at fumigated nests, we found a reduction across the decades in the amount of food per delivery: mean (± SE) bolus mass was 0.56 g (± 0.051, *n* = 106) in 1984-1988, compared to 0.31 g (± 0.013, *n* = 246) in 2017-2018. Decade was a highly significant predictor of bolus mass (B = 0.2384, SE = 0.04321, $F_{1,349} = 30.43$, $P < 0.0001$, relative to 2016-2018 decade as baseline), but neither colony size ($F_{1,349} = 0.09$, $P = 0.77$) nor colony-size*colony-size ($F_{1,348} = 0.66$, $P = 0.42$) were significant.

The change in bolus mass accompanied an apparent reduction in the total number of insects per bolus. Using data from all colonies, the mean (± SE) number of insects per bolus was 66.1 (± 12.4, *n* = 322) in 1983-1988, compared to 51.2 (± 6.0, *n* = 396) in 2016-2018. There was a significant interaction between decade and colony size (Appendix S1: Table S9), with the number of insects delivered per trip increasing with colony size in the 1980’s but no apparent relationship with colony size in 2016-2018 (Fig. 5). Colony-by-year was a significant random effect (Appendix S1: Table S9). However, the statistical interaction between decade and colony size (Appendix S1: Table S9) was driven largely by the colony of 1400 nests in 1988 and the colony of 32 nests in 2016 (Fig. 5), because excluding the 29 samples from these two sites resulted in a non-significant interaction term ($P = 0.95$) and no effect of decade ($P = 0.48$). These two colonies were not anomalous in any obvious biological way.

Diet composition

Family-level insect diversity per food bolus as measured by the Shannon Index (*H*) averaged (± SE) 1.14 (± 0.0697, $n = 232$) in 1983-1988, compared to 1.83 (± 0.0560, $n = 397$) in 2016-2018. Decade was a significant predictor of diversity, but colony size was not, and there was no decade*colony-size or colony-size*colony-size interactions (Appendix S1: Table S10). Colony-by-year was a significant random effect (Appendix S1: Table S10).

Qualitative change in the Cliff Swallow's diet over time was assessed with the five most common families per decade, based on total insects in all boluses. For all colonies combined, three families were represented in the top five in both decades (Fig. 6), although their rank order varied slightly. The other two families in the top five for each decade were represented by relatively few individuals of those families in the other decade (Fig. 6). For two sites that were sampled in both decades, one site (Whitetail, Fig. S4A) shared only two of its five most common families between decades, and the other site (Clary, Fig. S4B) had only one of its five most common shared between decades. The single most common family at each site in each decade was different, and in some cases the more common families were barely represented by those families in the other decade (Fig. S4). Overall, across all sites and years, the two most common families in the Cliff Swallow's diet were the hemipteran families Cicadellidae (leafhoppers) and Aphididae (aphids). There were 56 total families represented in 1983-1988 and 64 in 2016-2018.

Changes in foraging-related fitness measures

Fitness components that could be influenced by changes in foraging efficiency include clutch size, reproductive success as measured by the number of nestlings surviving to 10 days of age, and body mass of nestlings and adults. Clutch size in Cliff Swallows was significantly predicted by colony size and laying date but not by decade (Appendix S1: Table S11). The random effect of colony-by-year was also significant (Appendix S1: Table S11). The effect of colony size was negative, indicating birds laid fewer eggs in larger colonies, but this was irrespective of decade, as there was no significant interaction between decade and colony size (Appendix S1: Table S11). Across all nests and sites, the mean (± SE) clutch size per nest in the 1980's was 3.49 eggs (± 0.012, *n* = 5972 nests), compared to 3.56 eggs (± 0.018, *n* = 2725 nests) in 2015-2022.

Reproductive success varied significantly with decade, colony size, laying date, and clutch size (Appendix S1: Table S12). Both laying date and colony size interacted with decade (Fig. 7, Appendix S1: Table S12). Reproductive success declined more steeply with laying date in 2015-2022 than in 1984-1991 (Fig. 7A). Colony size had no obvious effect on reproductive success in 1984-1991, but in 2015-2022 success declined with colony size (Fig. 7B). The random effect of colony site was significant, although colony-by-year was almost significant (Appendix S1: Table S12). Across all nests and sites, the mean (± SE) survival to 10 days per nest in 1984-1991 was 2.44 nestlings (± 0.019, *n* = 5461 nests), compared to 2.53 nestlings (± 0.027, *n* = 2622) in 2015-2022.

Nestling Cliff Swallow body mass at 10 days of age was significantly predicted by brood size, hatching date, and an interaction between decade and colony size (Fig. 8; Appendix S1: Table S13). The effect of colony size was curvilinear, and nest identity, colony-by-year, and year were significant random effects (Appendix S1: Table S13). The interaction between colony size and decade showed that nestling body mass at 10 days declined more with colony size in 2015-2018 than in 1984-1989 (Fig. 8). Across all nests and sites, the mean (± SE) 10-day body mass for nestlings was 22.89 g (± 0.027, *n* = 10688 nestlings) in the 1980's, compared to 21.65 g (± 0.081, *n* = 1665 nestlings) in 2015-2018.

Adult Cliff Swallow body mass during the late stage (feeding of nestlings) was significantly predicted by decade and sex (Appendix S1: Table S14), with both sexes weighing less on average in 2013-2021 than in 1984-1989 during this nesting stage (Fig. 9). Colony size had no significant effect on body mass during the late stage (Appendix S1: Table S14). Adult body mass during the middle stage (incubation) was significantly predicted by sex but did not vary significantly between the decades (Fig. 9; Appendix S1: Table S15). There was a significant effect of colony size on middle-stage body mass, with mass decreasing with colony size, but the colony-size effect was independent of decade (Appendix S1: Table S15). For the early period (nest-building and egg-laying), body mass (Fig. 9) showed a significant three-way interaction between decade, sex, and colony size (Appendix S1: Table S16). Both sexes in 1984-1989 were more likely to exhibit a negative effect of colony size on body mass, and females in 2013-2021 a positive effect of colony size, relative to the baseline of males in 2013-2021 (Appendix S1: Table S16). However, in an analysis without interactions, decade alone had no significant effect on adult body mass during the early period ($P = 0.49$). The random effect of colony-by-year was significant for all three nesting stages (Appendix S1: Tables S14-S16).

DISCUSSION

This study revealed 40-year changes in the foraging behavior of Cliff Swallows: relative to the 1980's, birds now fed less socially and solitary foragers were more successful; foraging locations were more predictable and birds less clustered in space; and less use was made of breeding colonies as information centers. Although qualitative change in the diet was not pronounced across the study area as a whole, less total food was collected for nestlings, and foraging-related fitness benefits of larger colonies declined. The temporal shifts in behavior are generally consistent with changes in the distribution and abundance of the flying insects that Cliff Swallows eat, although we had no direct measures of insect availability and other interpretations are possible. The reduced reliance on social foraging and information transfer at present suggest less benefit to occupying the larger colonies than in the 1980's.

Changes in social foraging

Social foraging in Cliff Swallows in the 1980's was thought to result from birds' concentrating at localized dense swarms of insects and, based on prey capture attempts of individuals in the center versus on the edges of a foraging group, did not seem to reflect grouping to avoid predators (Brown 1988b, Brown and Brown 1996). Still, could the shift to more asocial foraging over time be related to changes in predation pressure? The American Kestrel (*Falco sparverius*) is the Cliff Swallow's primary aerial predator that sometimes attacks foraging groups. Kestrels have neither increased nor decreased in the study area (Brown et al. 2012, Silcock and Jorgensen 2022) or Nebraska more generally (Sauer et al. 2020) over time. The Cooper's Hawk (*Accipiter cooperii*) has increased since the 1980's as its breeding range has expanded southward to include western Nebraska (Brown et al. 2012, Silcock and Jorgensen 2022), but Cooper's Hawks typically hunt Cliff Swallows only at or very close to a colony site. Unless the increased presence of Cooper's Hawks has made social foraging away from colonies riskier now than in the 1980's, which seems unlikely, there is no evidence that shifts in predation have driven the changes in foraging behavior documented here.

In the 1980's, Cliff Swallows fed on patches of insects that aggregated in mating swarms or around livestock and on swarms that formed by local convection currents and thermals (Brown and Brown 1996). These insect swarms were presumably dense enough and insects abundant enough within them to support large numbers of foraging Cliff Swallows, often for an hour or more. Some foraging groups reached > 1000 birds in the 1980's, and prey capture attempt rate was significantly higher for birds in groups than for solitary foragers (Brown 1988b). In contrast, by 2016-2022, groups ≥ 200 birds had almost disappeared (Fig. 1). This change could not be accounted for by differences in colony size or colony site, as we used colonies of similar sizes and at the same sites for the behavioral observations of foraging in each decade (Appendix S1: Table S1). Consistent with the much greater incidence of solitary foraging in 2016-2022, solitary foragers were more successful than were birds in groups in the later years. These observations suggest that insect swarms by 2016-2022 were likely not sufficient enough to support group foraging, or if they were, they did not last long enough at any one location to allow foraging Cliff Swallows to accumulate in large groups. We should note that although solitary foraging did occur in the 1980's (Brown 1988b), it was at colonies smaller than any observed in 2016-2022, likely reflecting the relatively few birds in the smaller colonies and consequent dearth of opportunities for foraging socially (Brown and Brown 1996).

Changes in time spent foraging

Another major change in Cliff Swallow foraging strategy over the study period was a reduction in the percentage of a colony's residents feeding in any given 10-min interval. This indicates birds spent more time at their nests and less time foraging away from the colony by 2016. Smaller brood sizes could explain this if parents had less food demand from their nestlings. Although brood sizes did decline between the decades, as indicated by the number of nestlings surviving to 10 days (Fig. 7B), this effect was small and probably could not account for such large changes in parental time budgets.

Foraging decisions could be partly based on a parent's perceived threat of nest usurpation by other Cliff Swallows. As the Cliff Swallow population in the study area has increased since 1982 (Brown et al. 2013), the number of non-breeding transient Cliff Swallows has also increased (Fig. 3; Brown 1998). By the mid-1990's, we estimated hundreds to over a thousand transients passing through a colony in a single day, based on mark-recapture (Rannala 1995, Brown 1998, Brown and Brown 2004a). The increase in transients over time may indicate a growing population that is exceeding the capacity of the available nesting sites to accommodate them, or, because most arrive later in the summer, increasing difficulty for birds on the wintering grounds to achieve molt completion and/or good enough body condition to migrate early enough in the season to breed. The transients, who are likely prospecting for future nesting sites, appear mostly while colonies are feeding nestlings (Brown 1998, Brown et al. 2000, 2007, Roche et al. 2013), and parents seem obsessed at defending their nests from them, even while nestlings beg for food. The deleterious consequences of leaving nests unattended and having conspecifics intrude earlier in the season (Brown and Brown 1988, 1989) may have led to intense selection for nest guarding that is manifested even when nestlings are older and do not need continual defense against other Cliff Swallows.

While controlling for brood size, nestling mass at 10 days decreased between the decades, suggesting that nestlings might pay some of the cost of a reduction in parental effort because of transients. In addition, the reduction over time in adult body mass during feeding of nestlings could also indicate that breeding adults experience a foraging-related cost of transients. We cannot at present determine if the increasing transient presence is leading to changes in parental foraging behavior independent of any changes in food resources. However, if the Cliff Swallow population continues to increase in the study area, transient presence (and its effect on foraging) may also increase. The number of transients seems to directly track population size, a conclusion supported by the dip in the number of transients in 1996 and for several years thereafter (Fig. 3) following an unusual weather-related mortality event that eliminated about 50% of the breeding population (Brown and Brown 1998). A cost of large colonies in general could be that, because they attract more transients (Brown and Brown 2004a), residents spend less time foraging for their young. However, we found no significant effect of colony size on percent of residents foraging (Appendix S1: Table S4), suggesting either that transients *per se* are not directly responsible for changes in foraging or that the number of transients did not vary enough among the colonies where we conducted these observations (which were mostly large colonies, Appendix S1: Table S1) to result in a colony-size effect.

Changes in spatial clustering of foraging

Social foraging in the 1980's was thought to be beneficial because groups were better able to locate insect patches, or track the patches' movements, due to the increased number of foraging individuals (Brown 1988b, Brown et al. 1991). This implies that insect swarms were closely enough spaced that when one swarm was depleted or vanished because convection stopped, a Cliff Swallow foraging group could locate and shift to another nearby insect swarm without disbanding. That no longer appeared to be the case by 2016; even when relatively large groups formed, they usually did not persist for long in any one location and rarely collectively moved nearby. As a consequence, observed variability in foraging locations (Figs. S2, S3) was higher in 2016-2022 than in the 1980's, indicating that at present birds move through the foraging habitat and visit more parts of it. Although inferring insect distributions solely from the activity of foraging birds can be difficult (Brown 1988b, Brown and Brown 1996), these results taken together suggest that the aerial insects on which Cliff Swallows feed are now distributed in smaller and more widely spaced patches than in the 1980's.

Changes in use of colony-based information centers

Resource patches that are small, short-lasting in time, and widely dispersed do not promote information sharing, either at or near the colony site via an information center or through local enhancement on the foraging grounds (Waltz 1982, Clark and Mangel 1984, 1986, Beauchamp and LeFebrve 1988, Barta and Szep 1992, Giraldeau and Caraco 2000, Kohles et al. 2022). In these cases, animals cannot easily gain by recruiting to a patch because it cannot support many foragers or will not last long enough for some individuals to find it and for others then to learn of it, and because fewer nearby alternative patches are available if one follows another forager to a patch that is in decline. A food resource distribution with these characteristics is consistent with the changes we documented in information sharing among Cliff Swallows at colony sites. We found that unsuccessful Cliff Swallow foragers at present relatively rarely followed successful birds from the colony site—and when they did, they were unlikely to go to the same foraging location—despite this sort of information transfer at the colony site being a predominant part of the birds' foraging strategy in the 1980's (Brown 1985, 1986, Brown and Brown 1996). Lack of information-center foraging is also consistent with the now-reduced benefits of group foraging and the increased benefits of solitary foraging, both as measured by prey capture attempts.

In the 1980's, Cliff Swallows shared information on the foraging grounds when birds gave specific food calls that recruited other foragers to the location. Brown et al. (1991) hypothesized that calling was a benefit to the caller by increasing the likelihood that an insect swarm could be tracked in space when more foraging birds were present. We heard these calls relatively often among foraging Cliff Swallows in the 1980's (Brown et al. 1991). However, by 2016-2022 food calls were rarely if ever given in any circumstance (C. Brown, *pers. obs*.). Quantitative data on call frequency were not collected, but the birds' apparent abandonment of the use of food calls over time was consistent with the food resource becoming less patchy, less abundant, and shorter-lived at any given location.

Changes in distribution, abundance, or types of flying insects?

The marked changes in Cliff Swallow foraging behavior are largely consistent with insect distributions not being the same as they were 35-40 years ago in western Nebraska. Possible reasons for these foraging shifts include a quantitative reduction in flying insect abundance, as reported elsewhere (Hallman et al. 2017, Møller 2019, Sánchez-Bayo and Wyckhuys 2019, Wagner 2020), and/or a qualitative change in the insect taxa being fed on, with insects present today being less likely to occur in patchy swarms. We acknowledge that no comparative insect sampling has been done across time in our study area, in part because aerial insects—particularly the many families represented in the Cliff Swallow's diet—are difficult logistically to sample in a meaningful way (Johnston 1967, Brown and Brown 1996). Without such sampling, we cannot know with certainty whether insect populations have changed quantitatively or qualitatively over time, and making such statistical inferences even with relevant data can be difficult (Didham et al. 2020).

Although Cliff Swallows in our study area have been increasing since the 1980's (Brown et al. 2013), which would not be expected if insect abundance was declining drastically, evidence of fewer insects at present was the reduction in bolus weights from 1983-1988 to 2016-2018 among the fumigated nests in this study. With no change in the rate of parental food deliveries across the decades, nestlings presumably are receiving less food now than in the 1980's. This inference, however, is somewhat complicated by our also finding that Cliff Swallows in colonies that were not fumigated (i.e., exposed to natural infestations of swallow bugs) have increased their rate of food delivery over time to the extent that the total amount of food provided is not different now than in the 1980's (Brown et al. 2021). While it is not clear why such a modulation in parental effort depends on parasite load, it may indicate that food now is harder enough to find that a correspondingly greater effort is required to maintain nestlings at some threshold level of condition (perhaps mediated in part by adults' reactions to ectoparasites in the nest).

Across all colonies sampled for food boluses delivered to nestlings, the evidence for qualitative changes in the insects in the diet was mixed: three of the top five most common families remained the same in both decades, with the remaining two in each decade being relatively uncommon in the other decade (Fig. 6). At specific sites sampled in both decades, family-level turnover was more obvious (Appendix S1: Fig. S4). For example, mosquitoes (Culicidae) disappeared in the bird's diet at Whitetail over time, while phorid flies (Phoridae) greatly increased. Aphids (Aphididae) in general were well represented in both decades study-area-wide, but at Clary they almost disappeared in the later decade after being the most common family in the 1980's (Appendix S1: Fig. S4). The most common families in both decades included taxa that can be gregarious in various contexts, and some are pest species subject to outbreaks (Freeman 1945, Downes 1969, Southwood and Jepson 1962, Kuroli and Németh 1987, Evans 1988, Disney 1994, Brown and Brown 1996, Pires et al. 2000, Biedermann 2003). Thus, Cliff Swallows even in 2016-2018 were still foraging on insects that potentially may swarm or occur in localized concentrations.

On the other hand, the fact that within-bolus family-level diversity increased over time could suggest that Cliff Swallows more recently rely less on large patches of the same taxa and forage on more kinds of insects in less concentrated patches, consistent with our finding fewer insects per bolus and with their shift in foraging behavior. However, despite the difference in diversity and the qualitative differences in insects detected between the decades, and in the absence of generic- or species-level identification, we do not have sufficient evidence to conclude that the diet has shifted to non-swarming taxa to the extent that such a change *per se* could account for the differences in Cliff Swallow foraging behavior.

In Tree Swallows at a site in Canada, weather conditions deemed “good” for foraging decreased over a 43-year period, resulting in fewer nestlings fledged over time (Cox et al. 2020), a possible consequence of the effects of global climate change. However, we found no evidence of strong climate change over the years of our study in Nebraska: the decades did not differ significantly in average Palmer Drought Severity Index, a metric that predicts Cliff Swallow breeding time (Brown and Brown 2014). Furthermore, we detected no directional shift in the PDSI for the month of June (when Cliff Swallows are foraging to the greatest extent) over the 41 years of the study. While climate change may be affecting insects in other areas (Halsch et al. 2021, Harvey et al. 2022), it does not appear to be a compelling correlate of the changes in Cliff Swallow foraging ecology we observed.

Changes in land use are hypothesized to affect insect distribution and abundance, largely through conversion of native habitat to agriculture-intensive uses (Ghilain and Bélisle 2008, Paquette et al. 2013, 2014). Some recent conversion to agriculture has occurred in western Nebraska, with cultivation of corn increasing over time at the expense of areas formerly used for livestock grazing. The area surrounding Whitetail (Appendix S1: Fig. S1), all pasture with horses and cattle in 1982-1988, now contains agricultural land (alternating between corn, cereal crops, or alfalfa) on two sides of the colony site, with almost no livestock grazing within the colony’s foraging range anymore. However, whether land use changes have altered insect abundance in the study area is unclear, because crop monocultures do not always have lower (and sometimes have higher) insect abundance than more diverse areas such as pasture (Andow 1991).

Changes in land use could also affect insect patchiness by reducing the formation of thermals that concentrate insects and that the birds often cue on in foraging (Brown and Brown 1996). Convection is more likely on surfaces that warm easily (Wallington 1961, Drake and Farrow 1988), and the conversion of pasture to relatively tall row crops at sites like Whitetail may have decreased the formation of thermals that move insects upward. However, these potential consequences of land use change would not apply to the Canal colonies, where the surrounding land use has not changed over time yet the birds' behavior has changed.

Pesticide use is another possible driver of insect change (Sharma et al. 2020) that could potentially affect populations of insectivorous birds such as Cliff Swallows. Insecticides and herbicides can directly reduce insect abundance or alter communities by selectively removing certain taxa, and application of fungicides may also negatively affect insects (Tamburini et al. 2021). The application of pesticides to agricultural landscapes over which the birds forage could expose Cliff Swallows to chemically contaminated food and lead to the lower fitness we observed for birds in the most recent decade (Fig. 7B). In our study area, corn is the principal crop that is routinely sprayed, with aerial application usually occurring at least once per field during the Cliff Swallow's breeding season. That our results could be explained in general by increasing pesticide use seems unlikely, though, given that insecticide and herbicide application to corn in the United States has declined over time as use of genetically engineered corn varieties has increased (Fernandez-Cornejo et al. 2014). In addition, a study on Tree Swallows found no effect of local pesticide use (that did lead to bolus contamination) on the birds' reproductive performance (Poisson et al. 2021).

Changes in foraging-related fitness benefits of coloniality

Given the changes in foraging behavior over time, are Cliff Swallows in western Nebraska more food-stressed now than in the 1980's? Three fitness components—the number of nestlings surviving to 10 days of age, the body mass of nestlings at 10 days, and late-season adult body mass—declined over the decades, especially in the larger colonies, suggesting that the birds now might be finding less total food. Earlier work showed declines in annual survival of adult birds over the period 1984-2013 at the same fumigated colonies used in this study (Brown et al. 2021), possibly reflecting the reduction in adult body mass.

In addition, later nesting appears costlier now than in the 1980's with fewer nestlings surviving to 10 days of age as the season progresses. Late nesting was originally thought to be disadvantageous to Cliff Swallows primarily because increased ectoparasite infestations later in the summer reduced nestling survival before fledging (Brown and Brown 1986, 1996), but late nesting also lowers annual survival of both nestlings and adults at sites where swallow bugs are removed (Brown et al. 2015). Our results here, from fumigated colonies, are consistent with reductions in food resources that constrain nestling survival prior to fledging at later dates, and this effect has clearly increased over time (Fig. 7A). Whether aerial insects are less abundant later in the summer at our study site is unknown in the absence of direct sampling on a wide scale, but studies elsewhere on other swallows have shown that insects are more abundant later in the breeding season (Johnston 1967, Bryant 1975). For whatever reason(s), the widespread avian pattern of nesting success decreasing during the summer (Perrins 1970, Rowe et al. 1994, Verhulst and Nilsson 2008) has apparently intensified for Cliff Swallows in recent years even in the absence of ectoparasites. One possible explanation could be phenological mismatch

(Parmesan 2006, Saino et al. 2011), if warmer springs have recently accelerated flying insects' phenology more than the birds can compensate for by earlier arrival or egg-laying.

However, despite these greater fitness costs that are consistent with reduced food availability, four other lines of evidence argue against Cliff Swallows being highly food-stressed. (1) We detected no effect of decade on average distance traveled to foraging locations at Whitetail and the Canal colonies. Distance traveled while foraging is one of the more direct indices of resource depletion around a site for central-place foragers (Andersson 1978, 1981), and longer travel distances presumably mean food is insufficient closer to the colony (Hamilton and Watt 1970, Orians 1971, Furness and Birkhead 1984, Patterson et al. 2022). We found no significant lengthening of travel distance (Fig. 2C) that might be expected from greater food stress. (2) Clutch size did not differ between the decades. To the extent that the number of eggs laid reflects the resources available to a female Cliff Swallow prior to laying (Bryant 1975, Hussell and Quinney 1987, Brown and Brown 1999, Ward and Bryant 2006), it does not appear that adults now have less food available to them early in the season. (3) Despite the observed decline in adult survival over time at fumigated colonies, the opposite pattern was observed at non-fumigated sites (Brown et al. 2021). The reason for the difference is unclear but may include relaxation of parasite-driven selection on birds at colony sites that are perennially fumigated (Brown et al. 2021). Regardless of cause, when averaged across non-fumigated and fumigated sites, adult survival in general does not seem to be declining in the study area as a whole.

(4) The most important argument against food stress is the reduction in time spent foraging by adult Cliff Swallows in the 2016-2022 time period, relative to the 1980's, as measured by the percent of a colony's residents foraging at any one time (Fig. 2D). Food stress

should lead to more time investment in foraging, and the fact that Cliff Swallows apparently invest less now may suggest food might be more available than in the 1980's. Even if the increased presence of transients causes parents to reduce foraging in order to guard nests more, the cost of this heightened level of parental neglect still seems relatively minor, judging by the lack of change in the number of food deliveries to nestlings over the decades. Nevertheless, the reduction in the amount of food brought back per trip with no change in travel distance or frequency of trips implies that Cliff Swallows are now probably decreasing the total time in each food patch, possibly to allow more time at the nest to ward off transients. They conceivably could also be spending more time searching for a patch. Time-budget studies of marked birds are needed to discriminate among these possibilities.

The most closely similar studies to ours, on Tree Swallows (*Tachycineta bicolor*; Paquette et al. 2014, Berzins et al. 2021), found declines in adult body mass over time at a magnitude comparable to those we observed. However, those studies found that mass declines in adults were unrelated to breeding-habitat quality, and neither nesting success nor nestling body mass declined over time. Paquette et al. (2014) suggested that changes in adult mass in Tree Swallows were perhaps more likely related to carry-over effects from the non-breeding season caused by habitat degradation and reduction in insects on the wintering range. While we have no information on potential changes in habitat or food availability for Cliff Swallows on their wintering range, the fact that early-season body mass did not change between the decades suggests that Cliff Swallows are not arriving on the breeding grounds in worse shape now than in the 1980's, despite a long-term trend for earlier nesting (Brown and Brown 2014).

Is social foraging still an advantage of coloniality?

Based on studies in the 1980's that showed frequent information transfer at colony sites and more food brought back by parents in larger colonies, enhanced foraging efficiency seemed to be a major benefit of coloniality for Cliff Swallows (Brown et al. 1991, Brown and Brown 1996, 2018). Foraging advantages are at least partly expressed in both daily (Brown and Brown 2004b) and yearly survival, which varies with colony size depending on annual climatic conditions (Brown et al. 2016). Previous work indicated that other potential benefits of coloniality in Cliff Swallows (predator avoidance, limited nesting sites) were minor in magnitude compared to foraging advantages, and that ectoparasitism is the greatest cost that co-varies with colony size (Brown and Brown 1996). Thus, fitness differences among colony sizes and/or time periods at fumigated colonies (i.e., without ectoparasites), as in this study, should reflect mostly benefits associated with foraging. Given the changes in social foraging and information transfer documented here, and the potentially greater food-related fitness costs of larger colonies at present, do Cliff Swallows no longer receive the same advantages of colonial nesting as in the 1980's?

A full exploration of the different costs and benefits of coloniality in Cliff Swallows (Brown and Brown 1996, 2001) and how each may have changed over time (Brown et al. 2016, 2021) is beyond the scope of this paper. Yet, the cessation of widespread information sharing at the colony site, the shift to more frequent solitary foraging, the smaller amounts of food brought back, and the decline in nestling mass and survival with colony size, all suggest that foraging-related advantages of group living might be less now than 40 years ago. If these patterns continue, selection on fecundity could favor birds nesting in smaller colonies and those earlier in the season, and might result in directional shifts toward smaller colonies, on average, and earlier laying dates (or at least against later laying dates). There was evidence for a cost of larger colonies (reduced food availability) even in the 1980's despite the birds' use of information transfer: for example, we detected an increase in brood reduction (loss of some but not all nestlings in a nest) with colony size among fumigated nests and (in a different data set) longer travel distances in larger colonies (Brown and Brown 1996). Average laying dates have become earlier since the study began in 1982 (Brown and Brown 2014), but the distribution of colony sizes has remained stable (Brown et al. 2013, C. Brown, *unpublished data*). Cliff Swallows are better tolerating their ectoparasites now than in the 1980's (Brown et al. 2021), and the amelioration of the parasite-driven costs of larger colonies (that were formerly severe) could reduce selection for smaller colonies despite the greater foraging-related costs of larger colonies.

We were unable to investigate potential annual variation in the costs and benefits of social foraging, with sample sizes of fumigated colonies and the laborious nature of collecting the foraging observations forcing us to group years together into discrete decades for most analyses. Annual survival of both adult and first-year Cliff Swallows varies among years and often fluctuates in direction for different colony sizes in different years (Brown et al. 2016). To the extent that these survival differences reflect foraging success (Brown et al. 2016), we could be obscuring important annual variation in the costs and benefits of social foraging with the decadal analyses. However, even with the inevitable variability among years, the differences between decades documented here seem too large to be explicable by yearly variation alone.

The changes in social foraging documented here could also reflect in part the sudden shift to the use of artificial nesting sites that began in the 1980's just as the Cliff Swallow study commenced (Brown et al. 2021). The abandonment of ancestral cliff nesting sites in the study area was almost complete by 1990, with relatively few birds occupying cliffs since then (Brown et al. 2013). Information sharing and social foraging as documented in the 1980s may have been more important on cliff nesting sites. This is because cliff nesting sites (at least in our study area) are usually on cliff faces adjacent to water bodies, and Cliff Swallows tend to avoid foraging over water except in bad weather (Brown and Brown 1996). Foraging space near a cliff colony site is more spatially restricted because of the water and thus affects travel distance (Wittenberger and Dollinger 1984, Brown et al. 1992). Spatial restrictions could have favored social foraging and information transfer in the more “ancestral” cliff-nesting conditions when birds had to routinely travel farther. Social foraging clearly continued to be manifested in the early years of the transition to artificial sites (Brown and Brown 1996, this study). However, with the almost complete shift to colony sites that are mostly surrounded by terrestrial foraging habitat, selection may no longer be as strong for social foraging and information transfer, especially in the larger colonies.

Conclusions

Cliff Swallows exhibited flexibility in their foraging strategy over the course of this 40-year study, shifting from a high degree of social foraging promoted by information transfer at the colony site to more asocial feeding that did not seem to rely on sharing of information. To our knowledge, no other study has shown such a long-term change in the extent of social foraging. These behavioral shifts may reflect a change in the distribution and/or abundance of the birds’ aerial insect food sources, and support recent inferences of major flying-insect decline. However, insect populations in general exhibit extreme local variability in space and over short time scales (Grüebler et al. 2008, Shortall et al. 2009, Ewald et al. 2015, Haan et al. 2020, Musters et al. 2021), and this has often complicated attempts both to document insect declines in statistically rigorous ways (Didham et al. 2020) and to explain population parameters of insectivore predators such as swallows (Ghilain and Bélisle 2008, Paquette et al. 2013, 2014, Imlay et al. 2017, Michelson et al. 2018). Regardless of cause, the long-term changes in foraging behavior and information transfer in Cliff Swallows illustrate that the costs and benefits of group-living can be dynamic and exhibit directional shifts across ecological time.

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Table 1. Number of times a Cliff Swallow departed from the nest and whether its success on the previous foraging trip influenced whether the bird followed or did not follow others on the subsequent trip, and whether its success on the previous foraging trip influenced whether it was followed or was not followed by others on the subsequent trip, in 1984 (**A, C**)[*] and 2019 (**B, D**).

	Previous trip	
Subsequent trip	Successful	Unsuccessful
A. 1984[a]		
Followed	524	1355
Did not follow	2610	454
B. 2019[b]		
Followed	229	127
Did not follow	835	474
C. 1984[c]		
Was followed	1378	172
Was not followed	1756	1637
D. 2019[d]		
Was followed	204	116
Was not followed	870	497

[*] data from 1984 taken from Brown (1986).

[a] $\chi^2_1 = 1648$, $P < 0.0001$

[b] $\chi^2_1 = 0.35$, $P = 0.85$

[c] $\chi^2_1 = 633$, $P < 0.0001$

[d] $\chi^2_1 = 0.001$, $P = 0.97$

Fig. 1. Percentage distribution of Cliff Swallow foraging group sizes (solitary foragers = group size 1) in 1984-1988 versus 2016-2022 at (A) Whitetail (same site used each year) and (B) the Canal colonies, a collection of 4 sites in similar habitat near each other (see text).

Fig. 2. (A) Mean (± SE) Cliff Swallow foraging group size per 10-min scan at Whitetail and the Canal colonies in 1984-1988 versus 2016-2022. Decade significantly affected foraging group size while controlling for other variables (Appendix S1: Table S2). Actual means denoted by solid bars and predicted ones after controlling for other predictors in the model by shaded bars. (B) Curvilinear relationship between foraging group size and Cliff Swallow colony size while controlling for other variables (Appendix S1: Table S2). Solid lines indicate predicted values (± SE) and dots the actual mean (± SE) foraging group size for each colony size. (C) Mean (± SE) one-way distance from the colony site to a Cliff Swallow foraging group (or solitary forager) per 10-min scan at Whitetail and the Canal colonies in 1984-1988 versus 2016-2022. Decade did not affect travel distance while controlling for other variables (Appendix S1: Table S3). Actual means denoted by solid bars and predicted ones after controlling for other predictors in the model by shaded bars. (D) Mean (± SE) percent of a Cliff Swallow colony's residents (based on colony size) foraging per 10-min scan at Whitetail and the Canal colonies in 1984-1988 versus 2016-2022. Decade significantly affected the percent of a colony's residents foraging while controlling for other variables (Appendix S1: Table S4). Actual means denoted by solid bars and predicted ones after controlling for other predictors in the model by shaded bars. Numbers above bars indicate number of scan means for each.

Fig. 3. The proportion (± SE) of non-breeding transient Cliff Swallows (τ) each year based on mark-recapture from all colonies throughout the study area. τ was derived from the formula in Pradel et al. (1997) based on age-specific survival estimates. τ did not increase significantly over time when using all years ($r = 0.33$. $P = 0.10$, $n = 26$ years) but increased significantly when 1984 was excluded ($r = 0.43$, $P = 0.031$, $n = 25$ years). 1984 was the first year of widespread mark-recapture, and our methods were not fully standardized at that time. Line indicates best-fit, least-squares regression (with 1984 excluded).

Fig. 4. Circular standard deviation of mean compass bearings per 10-min scan of foraging Cliff Swallow groups or solitaries within a day in relation to colony size in 1984-1988 and 2016-2022. Lines indicated predicted values (± SE) based on the model presented in Appendix S1: Table S6 and dots the actual mean (± SE) circular standard deviation for each colony size.

Fig. 5. Number of insects contained per bolus for Cliff Swallows feeding nestlings in relation to colony size in 1983-88 and 2016-2018. Lines indicated predicted values (± SE) based on the model presented in Appendix S1: Table S9 and dots the actual mean (± SE) number of insects for each colony size. The interaction between decade and colony size was driven largely by two colonies (see text).

Fig. 6. Percentage of total insects represented in the 5 most common families per decade from Cliff Swallow food bolus samples in 1983-1988 and 2016-2018 at all colonies combined. Corresponding percentage from the other decade is shown for each.

Fig. 7. Number of nestling Cliff Swallows surviving to 10 days of age in relation to (A) laying date and (B) colony size in 1984-1991 and 2015-2022 at fumigated colonies. Lines indicate predicted values (± SE) based on the model presented in Appendix S1: Table S12 and dots the actual mean (± SE) number of nestlings for each laying date or colony size.

Fig. 8. Nestling Cliff Swallow body mass (g) at 10 days of age in relation to colony size in 1984-1989 and 2015-2018 at fumigated colonies. Lines indicate predicted values (± SE) based on the model presented in Appendix S1: Table S13 and dots the actual mean (± SE) nestling body mass for each colony size.

Fig. 9. Mean (± SE) adult body mass of (A) female and (B) male Cliff Swallows in 1984-1989 and 2013-2021 in relation to colony nesting stage (early, nest-building and egg-laying; middle, incubation; late, nestling-feeding). Mass varied significantly with decade for the late stage (Appendix S1: Table S14) but not for the middle or early stages after controlling for other variables (Appendix S1: Tables S15, S16). Numbers above bars indicate sample size (number of birds).

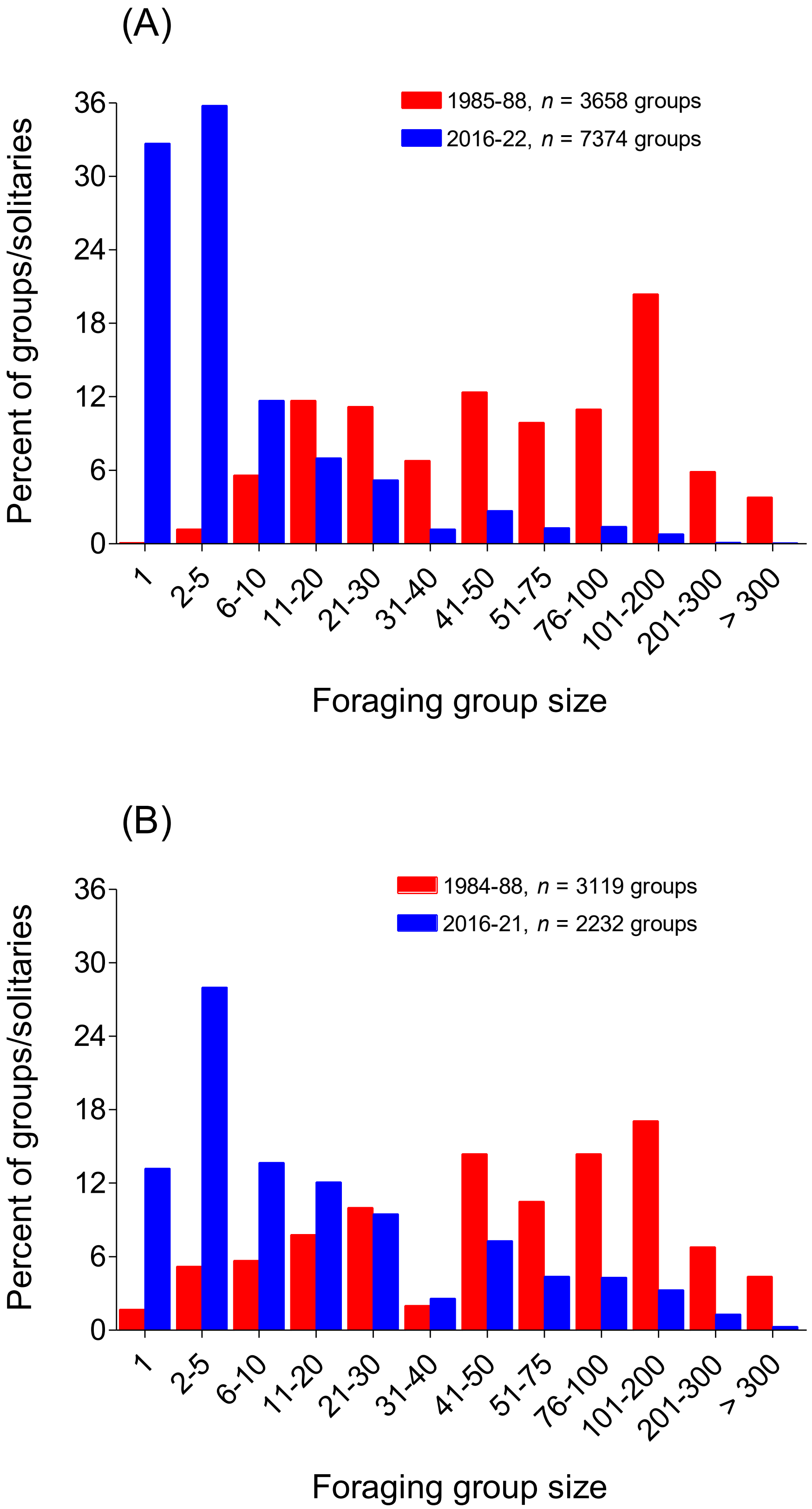

(A)
🟥 1985-88, *n* = 3658 groups
🟦 2016-22, *n* = 7374 groups
Percent of groups/solitaries
0
6
12
18
24
30
36
1
2-5
6-10
11-20
21-30
31-40
41-50
51-75
76-100
101-200
201-300
> 300
Foraging group size
(B)
🟥 1984-88, *n* = 3119 groups
🟦 2016-21, *n* = 2232 groups
Percent of groups/solitaries
0
6
12
18
24
30
36
1
2-5
6-10
11-20
21-30
31-40
41-50
51-75
76-100
101-200
201-300
> 300
Foraging group size

Fig. 1

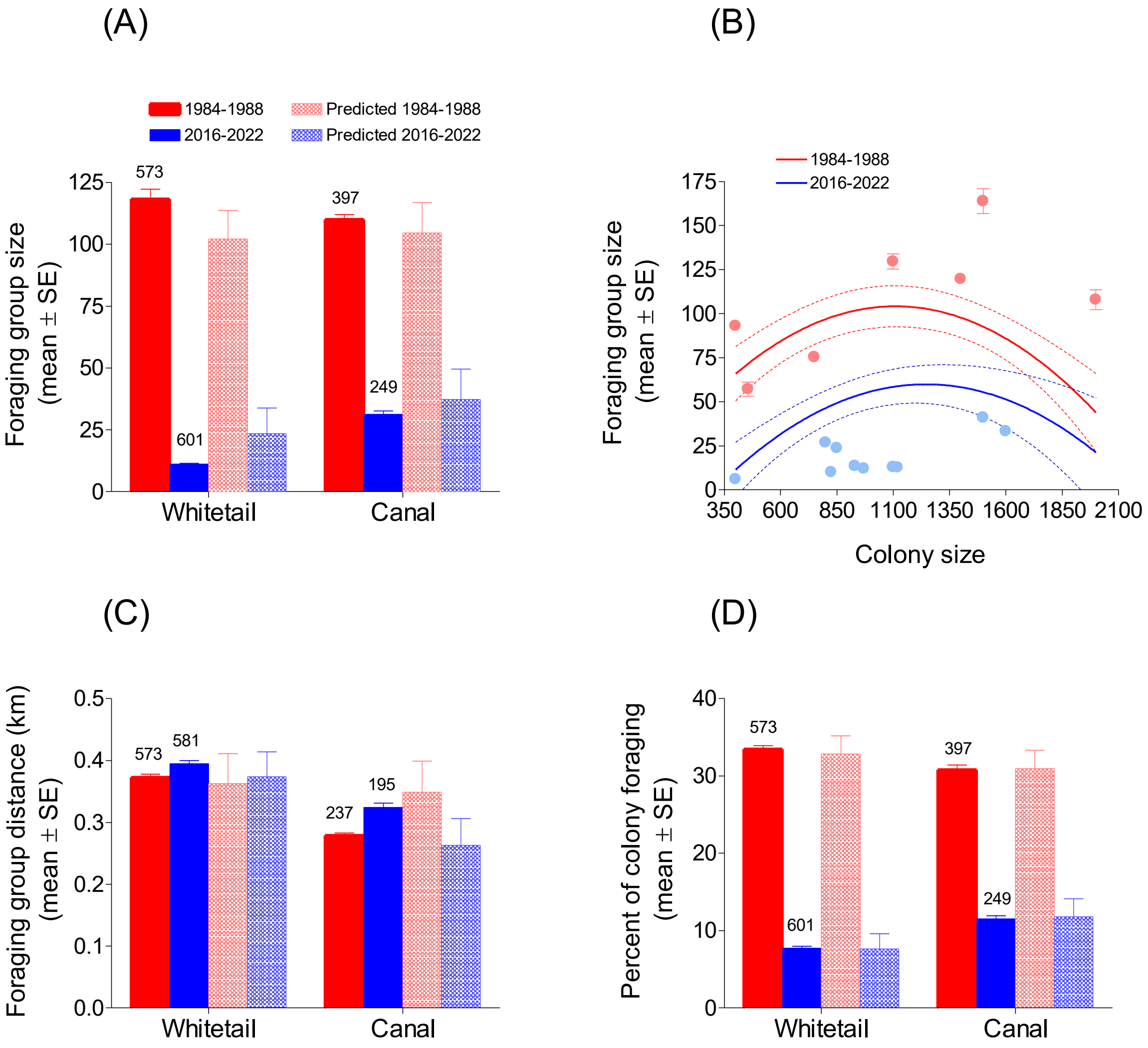

(A)
1984-1988
2016-2022
Predicted 1984-1988
Predicted 2016-2022
Foraging group size (mean ± SE)
0
25
50
75
100
125
573
601
397
249
Whitetail
Canal
(B)
1984-1988
2016-2022
Foraging group size (mean ± SE)
0
25
50
75
100
125
150
175
350
600
850
1100
1350
1600
1850
2100
Colony size
(C)
Foraging group distance (km) (mean ± SE)
0.0
0.1
0.2
0.3
0.4
0.5
573
581
237
195
Whitetail
Canal
(D)
Percent of colony foraging (mean ± SE)
0
10
20
30
40
573
601
397
249
Whitetail
Canal

Fig. 2

Fig. 3

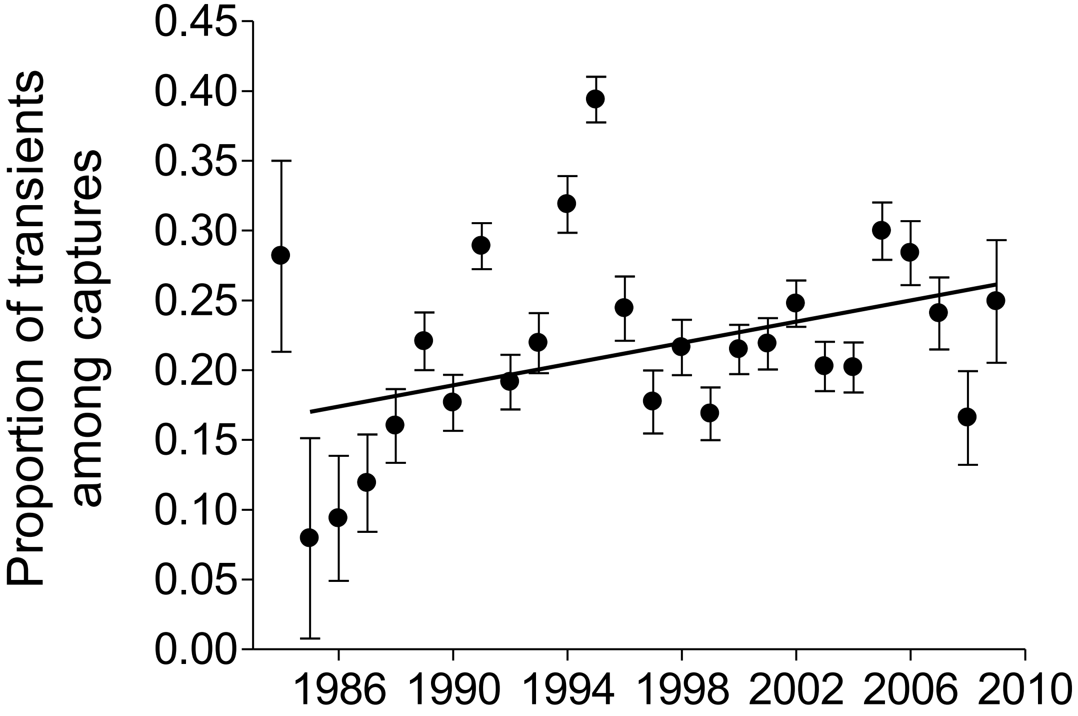

Proportion of transients among captures
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
1986
1990
1994
1998
2002
2006
2010

Fig. 4

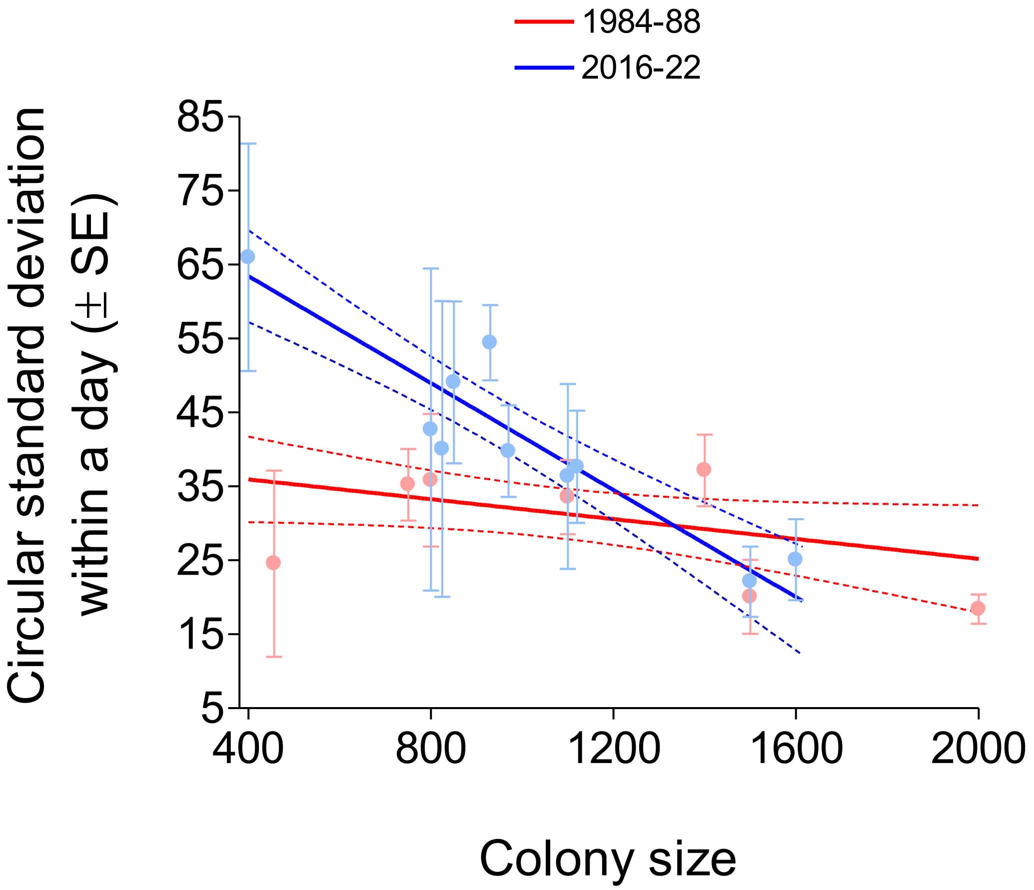

1984-88
2016-22
Circular standard deviation within a day (± SE)
85
75
65
55
45
35
25
15
5
400
800
1200
1600
2000
Colony size

Fig. 5

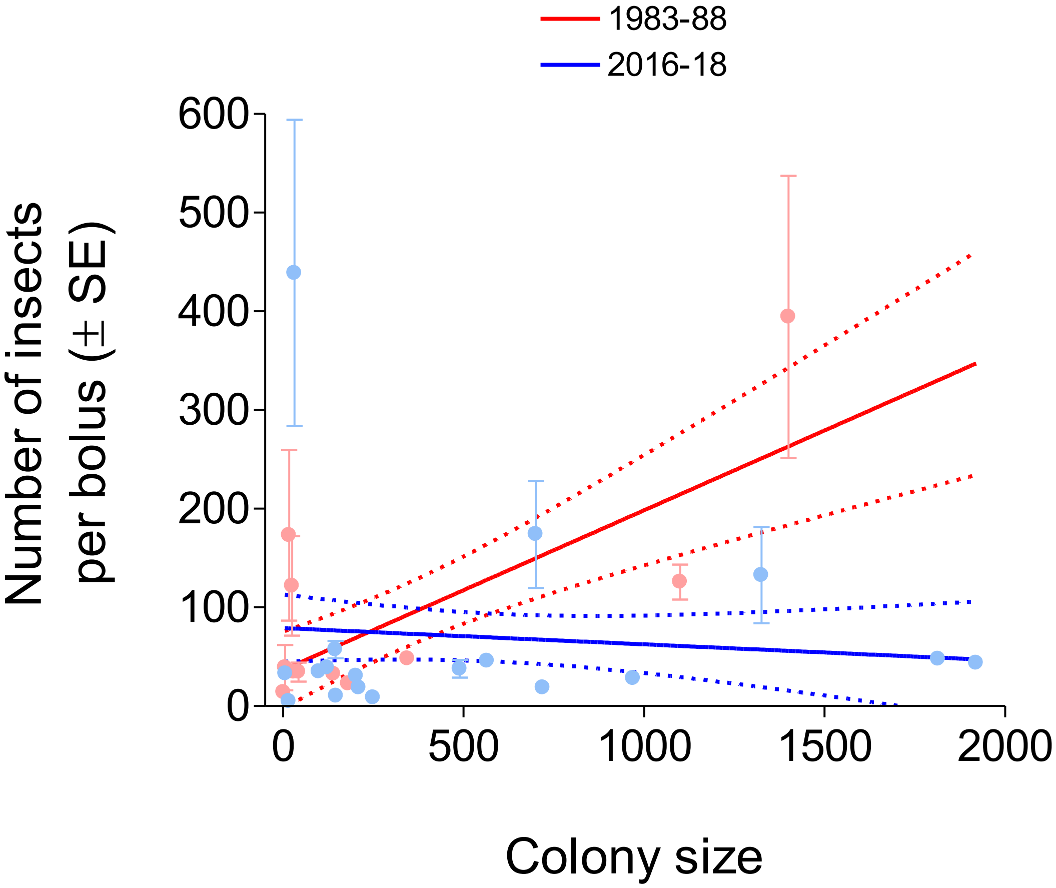

1983-88
2016-18
Number of insects per bolus (± SE)
600
500
400
300
200
100
0
0
500
1000
1500
2000
Colony size

Fig. 6

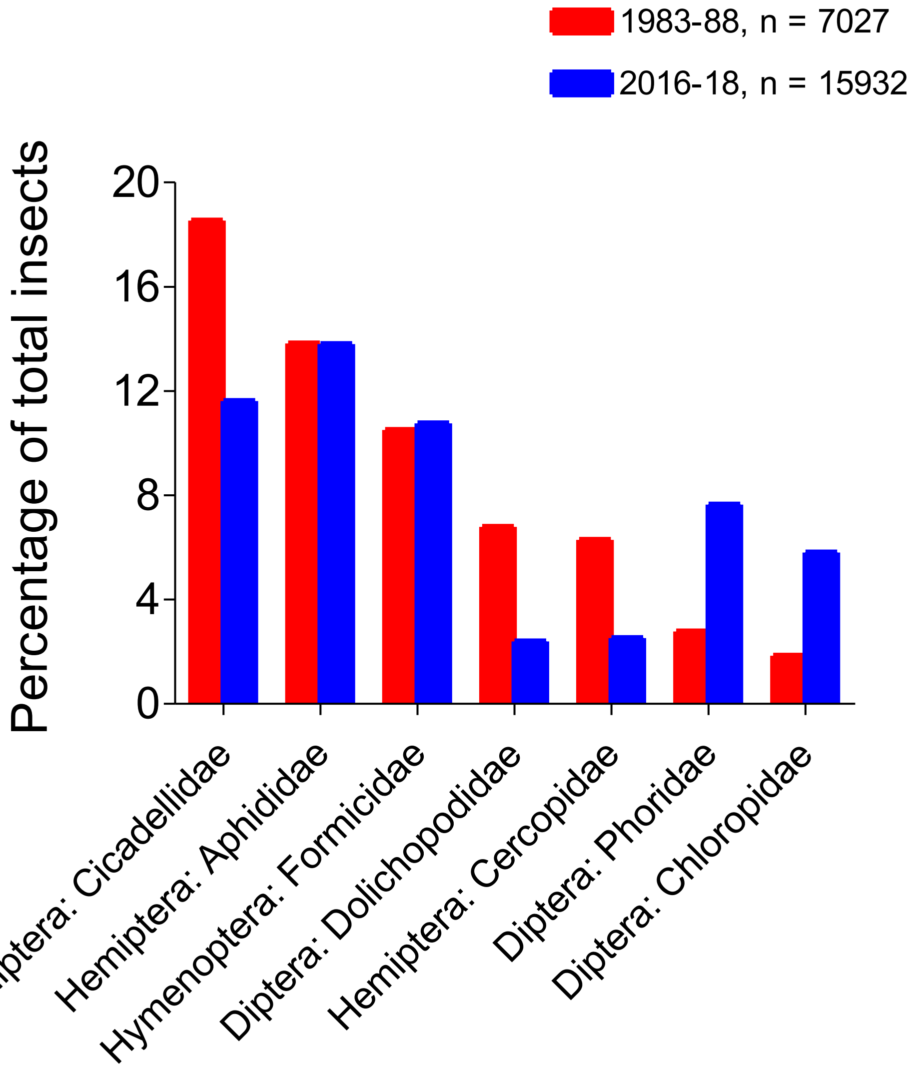

🟥 1983-88, n = 7027
🟦 2016-18, n = 15932
Percentage of total insects
20
16
12
8
4
0
Hemiptera: Cicadellidae
Hemiptera: Aphididae
Hymenoptera: Formicidae
Diptera: Dolichopodidae
Hemiptera: Cercopidae
Diptera: Phoridae
Diptera: Chloropidae

Fig. 7

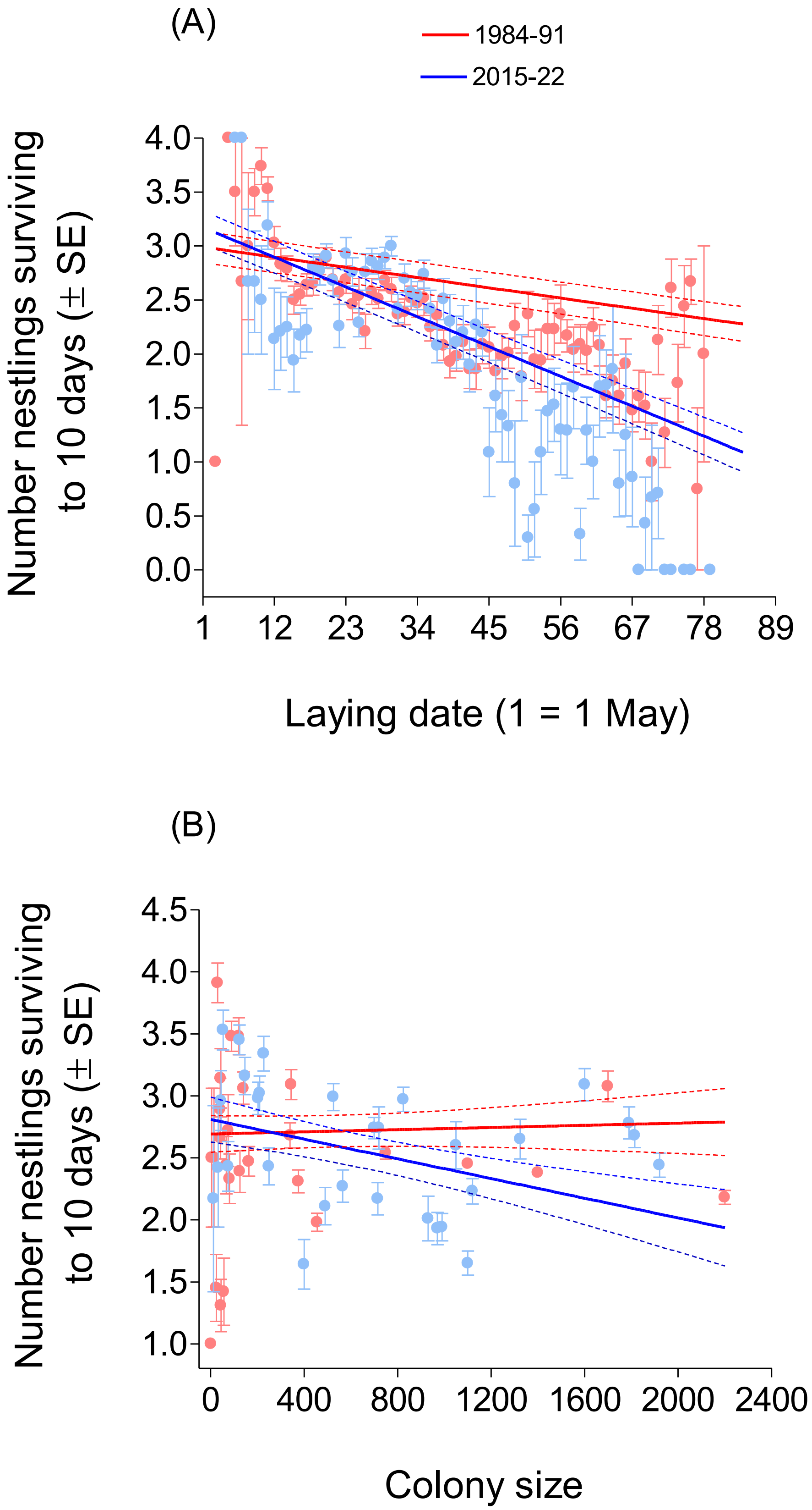

(A)
1984-91
2015-22
Number nestlings surviving to 10 days (± SE)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1
12
23
34
45
56
67
78
89
Laying date (1 = 1 May)
(B)
Number nestlings surviving to 10 days (± SE)
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0
400
800
1200
1600
2000
2400
Colony size

Fig. 8

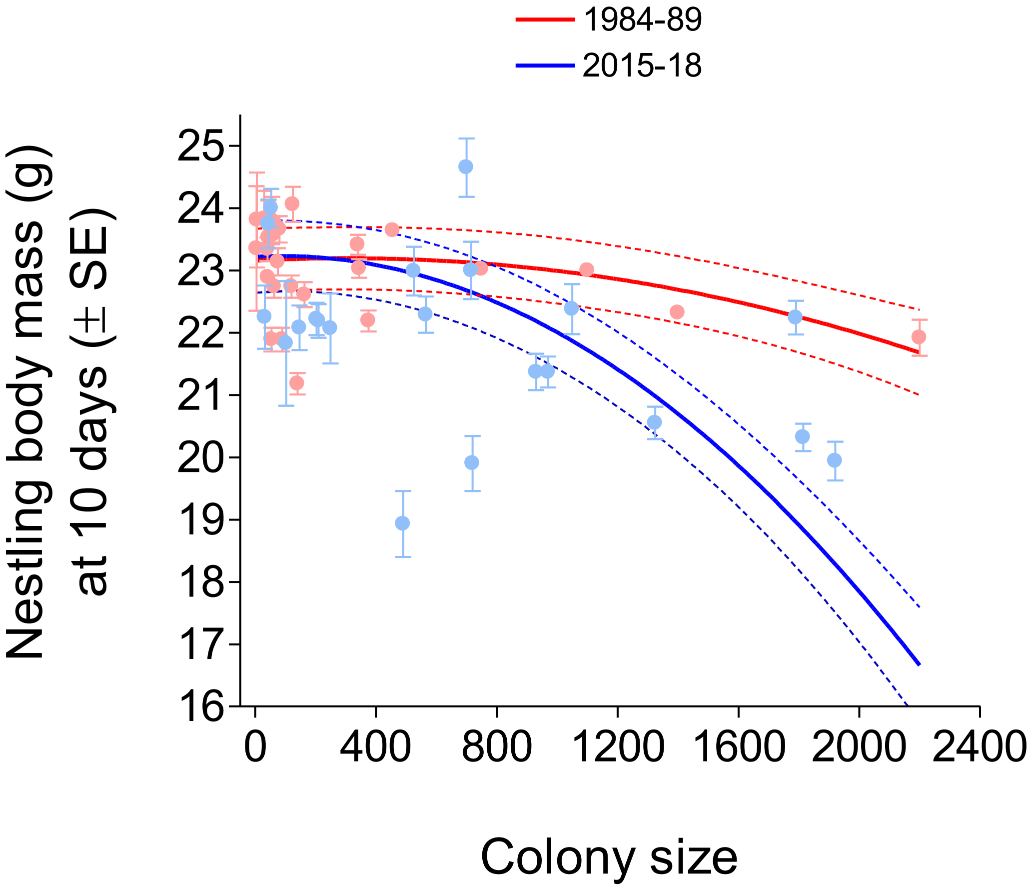
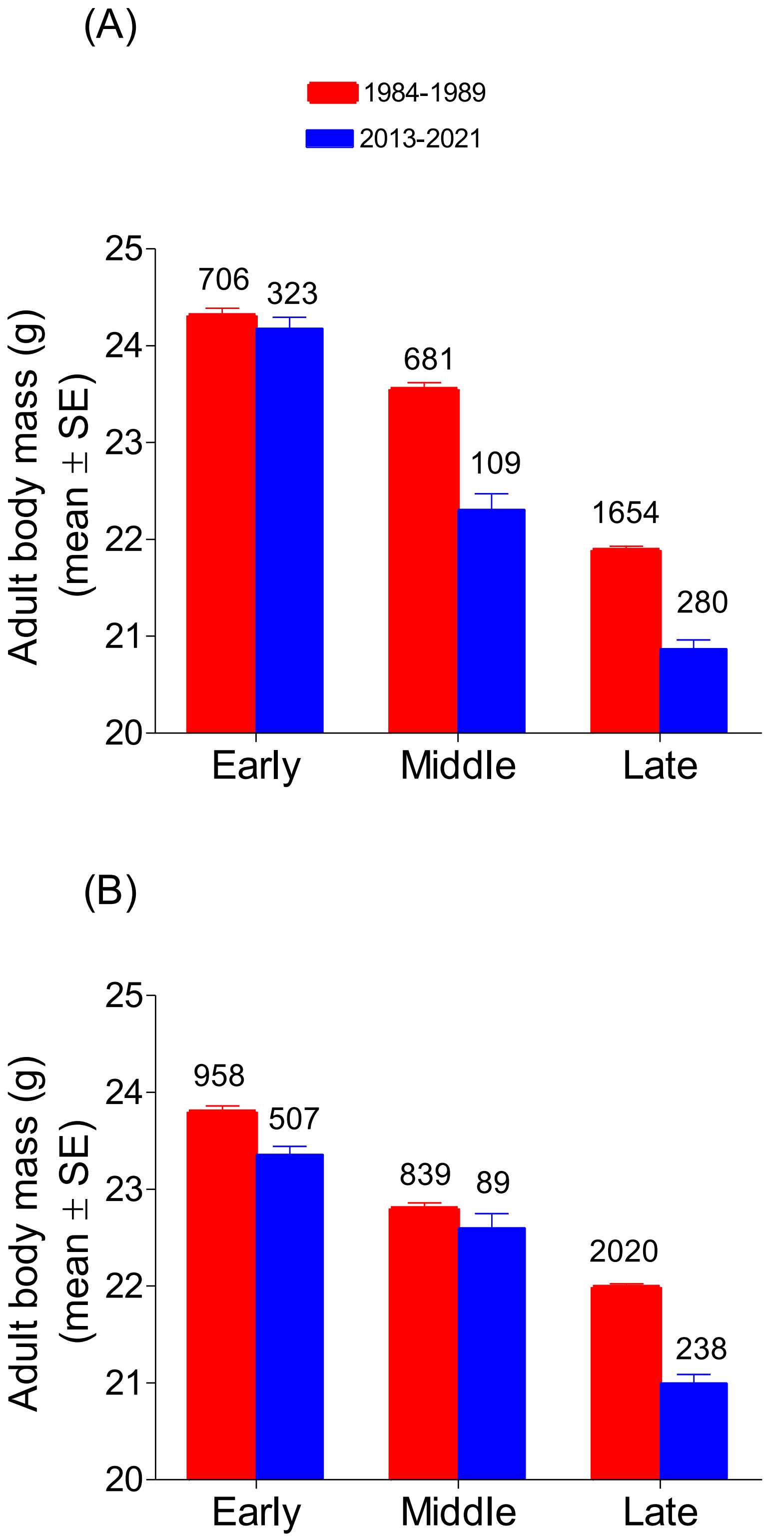

1984-89
2015-18
Nestling body mass (g) at 10 days (± SE)
25
24
23
22
21
20
19
18
17
16
0
400
800
1200
1600
2000
2400
Colony size

Fig. 9


(A)
🟥 1984-1989
🟦 2013-2021
Adult body mass (g) (mean ± SE)
25
24
23
22
21
20
706
323
681
109
1654
280
Early
Middle
Late
(B)
Adult body mass (g) (mean ± SE)
25
24
23
22
21
20
958
507
839
89
2020
238
Early
Middle
Late