Spatial and temporal unpredictability of colony size in Cliff Swallows across 30 years

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Abstract. Most colonially breeding animals occupy colonies that range in size from a few pairs to thousands of individuals, but the causes of colony size variation are largely unknown. Three general hypotheses are: (1) that variation in colony size is maintained by fluctuating selection via spatial and temporal changes in fitness associated with different colony sizes; (2) that colony formation reflects heterogeneity in habitat, with some sites having resources to support more individuals than others; and (3) that individuals assess the presence or annual reproductive success of current colony residents at each site and aggregate preferentially at high-quality sites. These hypotheses make predictions about how consistent colony size should be across sites and among years. We examined temporal and spatial variability of colony size for >200 Cliff Swallow (*Petrochelidon pyrrhonota*) colony sites in western Nebraska across a 30-year period. A colony's substrate type, annual population size in the study area, and whether the nesting season was relatively warm or cool, influenced average annual colony size. While some Cliff Swallow colony sites hosted perennially large colonies and others perennially small ones, between-year variability in colony size at most sites was high. Annual colony size distributions were relatively stable over 30 years and provided no evidence for long-term directional changes in colony size. The only ecological characteristic that was strongly associated with Cliff Swallow colony size at a site was the type of nesting substrate, with bridges tending to have larger colonies and being more frequently occupied than other substrates. Some sites showed annual changes in colony size consistent with the birds' basing their choice of colony on the presence or success of conspecifics, but many sites did not conform to a pattern expected if coloniality is a by-product of traditional aggregation. Colony size in Cliff Swallows was temporally and spatially unpredictable when viewed across the 30 years of this study. Each of the three hypotheses to explain size variation may have applied at certain sites, but the pattern of colony size variability leant the most support to the hypothesis that fluctuating selection on group size maintains colonies of widely different sizes.

Key words: Cliff Swallow; colonial nesting; colony size; fitness; group living; group size; habitat selection; Nebraska, USA; Petrochelidon pyrrhonota; social behavior; sociality.

INTRODUCTION

One of the central challenges in behavioral ecology is explaining why group size varies extensively in almost all animals that live in groups. Many species of colonial birds, for example, breed in colonies ranging from only a few pairs to thousands of individuals at a single site (Crook 1965, Brown et al. 1990). From the first studies on the costs and benefits of coloniality (Lubin 1974, Hoogland and Sherman 1976, Snapp 1976, Veen 1977, Hoogland 1979) to more recent work on genetic influences on sociality (Brown and Brown 2000a, Møller 2002, Serrano and Tella 2007, Spottiswoode 2009), colony size has emerged in many cases as either a key determinant of fitness or an indicator of local resource availability, breeding-site quality, or the phenotypic composition of groups (Wittenberger and Hunt 1985,

Siegel-Causey and Kharitonov 1990, Danchin and Wagner 1997, Brown and Brown 2001). Recently, efforts have been made to model group-size distributions to better describe and understand the patterns we observe in the field (Bonabeau et al. 1999, Sjöberg et al. 2000, Jovani et al. 2008a, Russell and Rosales 2010). Yet despite numerous field studies on various taxa over the last 50 years and suggestions that explaining variability in group size may ultimately help us better understand the evolution of sociality more generally (Brown et al. 1990, Brown and Brown 2001, Safran et al. 2007), we still know almost nothing about the factors causing animal groups to vary in size in the first place.

Our focus here is on avian breeding colonies and on three major ways that variation in colony size can be generated. Evolutionary processes (EVO) work through fitness expectations associated with particular colony sizes. Many of the costs and benefits of settling near conspecifics vary systematically with colony size (Hoogland and Sherman 1976, Møller 1987, Hoogland 1995,

Brown and Brown 1996, Serrano et al. 2005), and this allows us to predict the group size affording highest fitness (Wiklund and Andersson 1994, Avilés and Tufiño 1998, Brunton 1999). When spatial and temporal differences in selection pressures promoting coloniality cause fitness expectations to vary among group sizes, a given colony size may confer highest fitness in some locations or in some years, but another size may do better at other sites or in other seasons. Over the long term, fluctuating selection (Siepielski et al. 2009, Bell 2010) will maintain an equilibrium range of colony sizes as long as selection pressures do not permanently shift in one direction along the colony size distribution (Wittenberger and Hunt 1985, Møller 2002, Serrano and Tella 2007). Alternatively, polymorphisms in individuals' ability to perform in different social environments will promote adaptive variation in colony size across a population as each individual seeks to settle in a group where it does best (Brown and Brown 2000a, 2001, Spottiswoode 2007, 2009). Both of the EVO processes describe ultimate causation and posit that group size is under selection.

Ecological processes (ECO) are those in which colony size distributions are driven primarily by heterogeneous local ecological conditions that can support variable numbers of individuals (Fretwell and Lucas 1970). The most obvious example is cases where breeding substrate is limited and colony size is constrained to a size that matches the substrate's carrying capacity, but other requisite resources or environmental constraints (such as amount of food, parasite load, or numbers of predators) may also vary locally and lead to differing colony sizes in different places or at different times (Smith 1985, Gibbs et al. 1987, Cairns 1989, Brown and Rannala 1995).

Variation in colony size can be generated through behavioral processes (BEH), in which individuals are attracted to the presence of others at a specific site and aggregations form in relation to the extent of a site's social attractiveness. Individuals may cue on simply the presence of other individuals (conspecific attraction [Burger 1988, Podolsky and Kress 1989, Forbes and Kaiser 1994]), indirect indications of a site's suitability, such as existence of old nests from a previous season (Shields et al. 1988, Safran 2004), or a settler's direct observation of the reproductive success of other residents (Danchin and Wagner 1997, Brown et al. 2000). When individuals are reluctant to settle until a site's suitability is demonstrated in one or more of these ways, traditionally used sites tend to grow in size, but others that are appropriate may be small or unused simply because few or no birds happen to have tried them (Forbes and Kaiser 1994, Russell and Rosales 2010). The joining of existing groups by incoming settlers (either singly or in groups) and consequent dynamic changes in colony size can also create a size distribution that fluctuates, depending on the settlement options available to (and underlying fitness consequenc-

es for) individuals at different times (Sibly 1983, Pulliam and Caraco 1984, Higashi and Yamamura 1993, Rannala and Brown 1994). Both the ECO and BEH hypotheses are proximate drivers for colony size variation, although individuals' ability to choose sites appropriately based on resource availability or presence of conspecifics has ultimately been shaped by fecundity and/or survival selection.

Each of the processes that generate variation in group size leads to predictions about how consistent or predictable colony size should be both at a single site among years or among sites in a single year. (1) Spatiotemporal variation in fitness should lead to relatively stable size distributions over time with no group size(s) increasing or decreasing in frequency over the long term (EVO). (2) Sites with small and large colonies should differ in predictable ways with respect to substrate size or resources (e.g., local food availability), and thus colony sizes at any given site should remain roughly similar from year to year as long as local conditions are unchanged (ECO). (3) Attractive sites in one year will tend to draw individuals into them the next, leading to cyclical increases in colony size (at least in the short term) at some sites and declines or extinction at others, as local conditions or resource availability deteriorates (BEH). These predictions assume that individuals are relatively mobile and thus have the capacity to move among sites and actively choose one. While this may be true of many birds, more sedentary species, such as some colonial rodents, may not have frequent chances, and thus not be as likely, to move between colonies and potentially assess them (Sherman and Morton 1984, Hoogland 1995).

While colony size distributions have been reported for a variety of species, primarily of birds (Brown et al. 1990, Deerenberg and Hafner 1999, Jovani and Tella 2007, Jovani et al. 2008a), few studies have addressed the temporal or spatial dynamics of colony size for given populations. Most of what we know about colony size variation comes from single-year studies or aggregate distributions of colony sizes over multiple years from multiple geographic regions (Jovani et al. 2008a). A notable exception was Jovani et al.'s (2008b) study of a Spanish population of kestrels over eight years, in which they documented changes in average colony size and colony size distributions in relation to overall population size.

In this study, we use 30 years of data on colony size in Cliff Swallows (*Petrochelidon pyrrhonota*) from >200 colony sites of a well-studied population in western Nebraska to explore how colony size changes both temporally and spatially, and to determine to what extent colony size dynamics can be predicted by environmental conditions. Here, we (1) describe Cliff Swallow colony size distributions across years and examine how both average colony size and the size distributions change annually in response to ecological factors such as climate and variability in total popula-
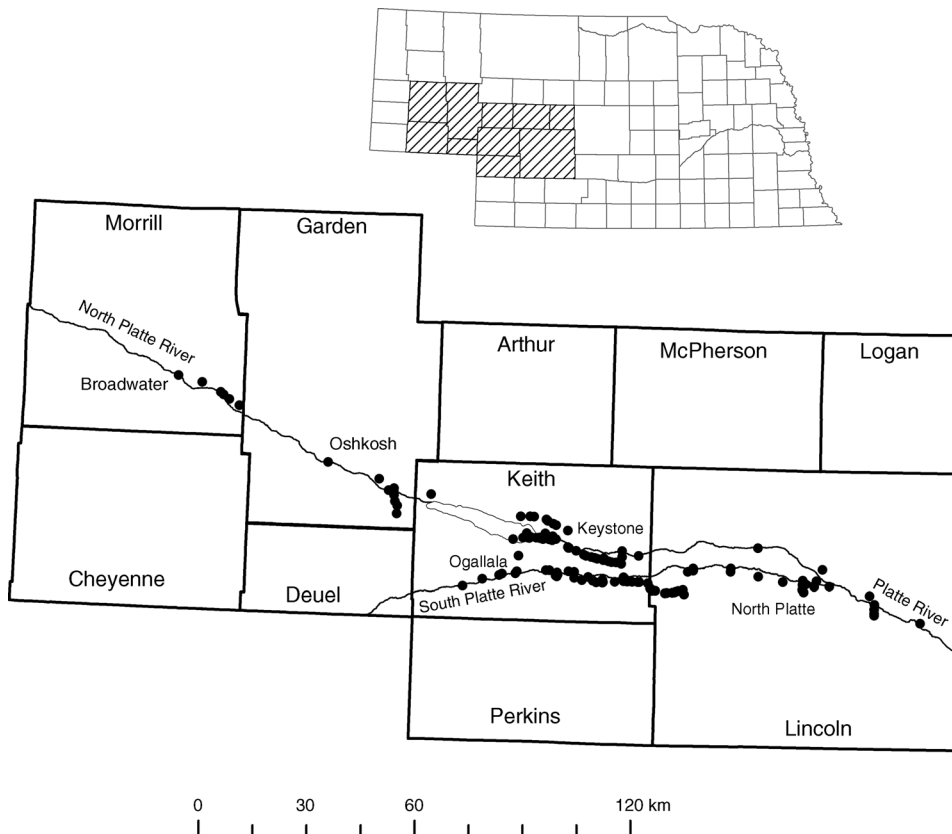
Fig. 1. Study area in southwestern Nebraska, USA, with locations of all Cliff Swallow colonies monitored in this study shown with solid circles. Some sites were close enough to each other that they are represented by the same circle.

tion size; (2) examine how site characteristics such as substrate type and surrounding habitat potentially influence Cliff Swallow site use and colony size across sites; and (3) investigate patterns in colony size variability within sites over time and ecological variables potentially associated with these size changes. Our goal is to determine whether Cliff Swallow colony size varies in predictable ways in accordance with the general hypotheses (EVO, ECO, BEH) that may account for the evolution of group living in this species.

METHODS

Study animal and study sites

Cliff Swallows are migratory passerines that build gourd-shaped mud nests and attach them to a vertical wall beneath a horizontal overhang. They breed commonly throughout western North America and are increasing in areas east of the Great Plains (Brown and Brown 1995). Cliff Swallows winter in southern South America. They first arrive in our study area in late April and complete nesting by late July (Brown and Brown 1996).

Our study area was centered at the Cedar Point Biological Station (41°12.591′ N, 101°38.969′ W) in Keith County, western Nebraska, and extended from

near Brady in Lincoln County on the east to Broadwater in Morrill County on the west (Fig. 1). Within this area, there were 222 different Cliff Swallow colony sites (as of 2011) that had been used by the birds in at least one year and that were included in this study. Colonies were defined as groups of swallows using the same nesting structure (or in the case of natural cliff colonies, occupying discrete clusters of nests) that at least occasionally interacted during foraging or in predator avoidance (Brown and Brown 1996). In rare cases, birds nesting on separate but closely spaced structures (e.g., parallel bridges on divided interstate highways) clearly interacted with each other and were considered to belong to the same colony. Colony sites were generally separated from the next nearest site by 1–10 km (Fig. 1). Throughout this paper, a colony site refers to a physical structure at a particular locale where birds nest, whereas a colony refers to a collection of individuals breeding at a given site.

Cliff Swallow colony sites in the study area were of four general substrate types (Fig. 2). Bridge sites (Fig. 2a) were relatively long spans over rivers, railroad tracks, or interstate highways. Most were characterized by relatively extensive substrate for nest attachment, and the birds' semi-regular alternation in successive years between use of nests on either side or at either end
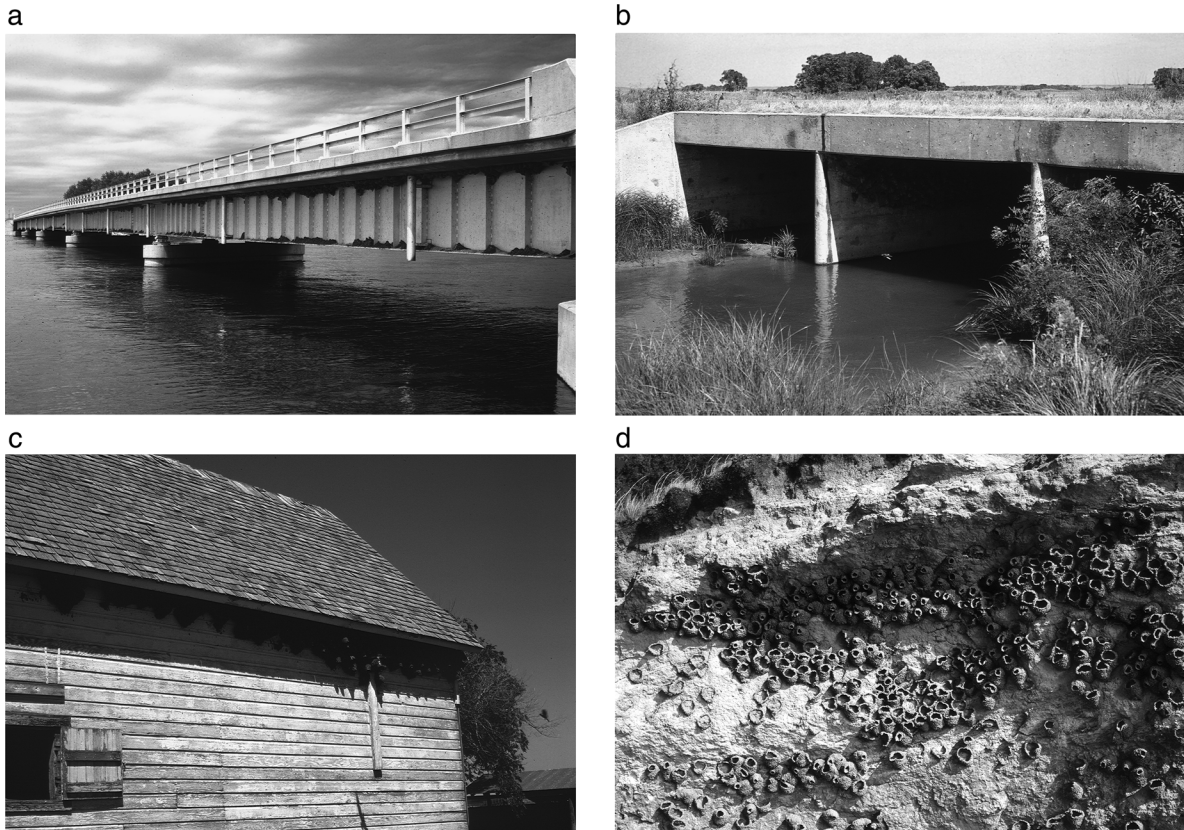
Fig. 2. Examples of the four major substrates of Cliff Swallow colony sites in southwestern Nebraska: (a) bridge, spanning the North Platte River; (b) culvert, underneath county road; (c) building, barn in farmyard; (d) cliff, on south side of Lake McConaughy.

(although many nests on bridges were reused in consecutive years). Most nests tended to be placed underneath the outside eaves (Fig. 2a), but some nests could be on inner beams not readily visible or on the concrete support pilings. Because bridges were often tall, relatively exposed to wind, and did not have earthen embankments around them, nests on bridges likely experienced greater temperature extremes throughout the year than those at other types of colony sites.

Culverts were relatively small, box-shaped, concrete structures typically built for drainage underneath roads or railroad tracks (Fig. 2b). They tended to be relatively well insulated with earthen embankments above and on either side, staying cool inside even in summer. Some culverts had multiple sections separated by concrete walls; birds from different tunnels of a site typically interacted and were considered part of the same colony. Many culverts had flowing or standing water inside them, at least occasionally, although some were completely dry. Culverts had less total nesting substrate available than did bridges, but in all cases substantial unused portions remained.

Buildings were not frequently used by Cliff Swallows in the study area. Among those the birds selected were old farmhouses, awnings and carports, and barns (Fig.

2c); nests tended to be placed under outside eaves and never inside a structure. Nests on buildings were relatively well protected from the elements. Cliff nesting sites (Fig. 2d) in the study area were on limestone outcroppings along the North Platte River near Lewellen, Garden County, and primarily on the southeastern shore of Lake McConaughy, Keith County. Nests were clustered in somewhat irregular groupings, depending on the availability and distribution of suitable horizontal overhangs. Cliff sites tended to be relatively high above the ground or water surface (>5 m), and generally all the birds occupying nests within sight of each other functioned as the same colony. Further details and illustrations of the four major types of colony sites are presented in Brown and Brown (1996).

The study population experienced a major mortality event in 1996, in which large numbers of Cliff Swallows starved to death in late May due to lack of flying-insect food during a six-day period of cold and rainy weather (Brown and Brown 1998, 2011). Less severe weather-related mortality events also occurred in 1988, 1992, and 2004; further descriptions are provided in Brown and Brown (1998, 2000b, 2011).

Some culvert colony sites in the study area were fumigated perennially to remove infestations of hematophagous swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*), a major cost of coloniality for Cliff Swallows (Brown and Brown 1986, 1996, 2004*a*). Those sites were not included in the analyses presented here; in this paper, we focus entirely on unmanipulated colony sites exposed to natural numbers of ectoparasites.

Field methods

Colony size in all cases refers to the maximum number of active nests at a site, with an active nest defined as one in which one or more eggs were laid. Colony sizes were determined by direct counts of all active nests or by estimation based both on nest counts of portions of a colony site and on the number of birds present at a site. Direct counts of active nests were made at sites where other research (Brown and Brown 1996) required periodic nest checks, done by inserting a dental mirror and small flashlight through each nest's mud neck to view nest contents. At sites where nests were inaccessible for nest checks or colonies too large to check all nests, we estimated the number of active nests in the colony by counting all the nests in sections of the colony where birds had settled and multiplied those counts by the number of sections (with similar nest densities) that were obviously active. We also counted or estimated the number of birds present at a colony site during prolonged alarm responses (to us) when presumably most of the birds living there appeared. Estimates of colony size and subsequent direct counts based on nest contents agreed closely for a sample of colonies where both methods were used (Brown and Brown 1996).

Colony sizes were typically determined for all sites in mid- to late June (occasionally early July, in late-nesting years), after eggs had been laid and before fledging had started. The few late-starting colonies each year were usually surveyed in mid-July, early enough to include the relatively large number of active nests that often failed during incubation in the late colonies.

From 1982 to 1989, we collected colony size data on ~40–60 colony sites in Keith and Garden Counties, centered roughly at the Cedar Point Biological Station, and chosen (for other research) to represent the size range seen in the population. From 1990 to 2011, we surveyed colony sizes at all potential sites (where birds had been known to nest in the past or whose substrate suggested they were suitable for Cliff Swallows) within the entire study area each year (Fig. 1). Some analyses used all years and others only 1990–2011, depending on the data set required. Breeding population size was estimated by summing the total number of active nests in all colonies in a year and done only for 1990–2011, when colony surveys were comprehensive across the study area. In analyzing colony site use, any site that had Cliff Swallows at least once during the study was considered an available colony site and included in the total number of potential sites each year (including in

years before it was first used). In some cases, a site was rendered unavailable in later years, either by removal of a building, falling of overhangs on cliffs, or the growth of vegetation that obscured the birds' approach. The number of available colony sites generally increased over time as more culverts or bridges were constructed in the study area. In analyzing the percentage of years a colony site was occupied, only sites with at least 10 years of size and use data were included.

Climate data were taken from an automated weather reporting station at Arthur, Nebraska, about 45 km north of the center of our study area (Brown and Brown 1996). Hourly and daily temperature and rainfall measurements at the site were collected by the High Plains Regional Climate Center of the University of Nebraska-Lincoln. We used climate data for the period 1 May to 15 June each year, as that was the portion of the Cliff Swallow's nesting season when most birds settled and thus when weather conditions were most likely to affect choice and formation of groups of different sizes.

Colony size classes

Some analyses required the creation of colony size classes, as use of the entire range of actual colony sizes was statistically or graphically impractical. We designated 10 different colony size classes of 0 (not used), 1, 2–9, 10–49, 50–99, 100–249, 250–499, 500–999, 1000–1999, and ≥2000 nests. These categories were based on our extensive experience with this species and chosen to reflect groups of colonies that each represented a distinct social environment, in which the birds had patterns of interaction with colony members that were clearly different from other classes of colonies (Brown and Brown 1996). Thus, we believe the colony size categories used here reflect differences in selection pressures experienced by the birds occupying them.

Descriptive statistics, correlations, linear regressions, and mixed-model analyses were performed with SAS (SAS Institute 2004).

Categorizing habitat of colony sites

Habitat surrounding colony sites was quantified from high-resolution aerial photographs taken in 1993 by the Aerial Photography Unit of the U.S. Department of Agriculture. The photos were overlaid with a transparent acreage grid centered on each colony site. Because Cliff Swallows generally forage within a 1-km radius from the colony site (Brown et al. 1992, Brown and Brown 1996), we designated a circular buffer of 2-km diameter centered at the colony site in which to classify habitat. The entire buffer was considered to represent potential foraging space at each site (Brown et al. 2002). Within each colony site's foraging range, we used the acreage grid to determine the total coverage of the following eight habitat types, defined as "flowing water," the surface area of rivers and creeks; "standing water," the surface area of lakes and ponds; "roads and

buildings," the surface area of asphalt roads and all artificial structures; "bare earth," the surface area of dirt roads, sand pits, sand bars, plowed fields, or other un-vegetated ground; "trees," the surface area of deciduous and evergreen (*Juniperus* spp.) tree cover; "marsh," the surface area of aquatic wetlands; "grassland," the surface area of prairie vegetated with noncultivated grass (often grazing land); and "crops," the surface area of cultivated fields (usually wheat [*Triticum*] or corn [*Zea mays*]; Brown et al. 2002). We had habitat data for 114 of our colony sites.

As an integrative measure of land use diversity within a colony site's foraging range, we used Simpson's index of diversity. The Simpson index is the most appropriate diversity measure when all members of a community are censused (Ludwig and Reynolds 1988), which was the case here because all acreage within the 2-km diameter buffer was categorized. Values of the Simpson index vary inversely with diversity; thus, lower values indicate higher diversity. Further details on categorizing habitat near colony sites are provided by Brown et al. (2002).

Estimating probabilities of colony size change

We quantified the probability of colony size at a site changing between successive years using multistate mark–recapture methods (Barbraud et al. 2003). Multistate models are designed to estimate the probability that an individual changes attributes (such as location or breeding status) between sampling events while control-ling for differences in survival (S) and detection (p) probabilities (Nichols and Kendall 1995, Lebreton and Pradel 2002). For our study, an individual corresponded to a given colony site. Each site received a multistate recapture history, denoting its size state each year with states corresponding to the 10 colony size classes defined previously. Because we knew the existence of each colony site and monitored each one annually once it entered our data set, survival (S) and recapture (p) probabilities approximated 1.0. We estimated the probability (ψ) of a site transitioning from one size class to another or of remaining the same size between successive years. We had data for 222 colony sites, with the maximum number of encounter occasions (years) being 30. Program MARK (White and Burnham 1999, White et al. 2006) was used to fit models and generate estimates of colony size transition probabilities. The data set met the variance assumptions of mark–recapture analysis, with a $\hat{c}$ of 1.19, as calculated by the median $\hat{c}$ test in MARK.

Preliminary model fitting showed that the best model structure for these analyses was one that treated survival and recapture probabilities as constant across states and years, and each state-to-state transition unique but not varying by year. A null model with only three parameters (constant survival, constant recapture, and constant transition) was a much poorer fit, with an AIC$_c$ that was 6218.3 greater than the one with state-dependent transitions.

Because colony size transitions may be influenced by substrate type (see the following section), we fit a model that considered each of the four substrate types as a separate group, with state-to-state transitions varying by group (substrate type). The model with a group effect (187 parameters) was a better fit to our data, with an AIC$_c$ value 357 less than that of the equivalent model without a group effect (80 parameters). However, because many of the transitions for buildings and cliffs were inestimable due to relatively small sample sizes for those substrate types, we present results for only bridge and culvert sites.

Measuring within-site variability in colony size

We used the index of population variability (PV) described by Heath (2006) to quantify the extent of annual colony size variability at each site. Although earlier analyses of colony size in Cliff Swallows relied on metrics such as the coefficient of variation for a colony site (Brown and Brown 1996), the PV is less biased by zero counts (which occur when sites are unused) or cases when the colony size is well above or below its typical value. The PV compares all possible pairs of occurrences (colony sizes) over a time series (years of data) and standardizes variability relative to the maximum colony size (rather than the mean) seen at the site. A PV score of 0 indicates complete stability in colony size among years, whereas a value of 1 is approached as differences in colony size near infinity (Heath 2006). PVs here are calculated on actual colony sizes rather than size classes.

RESULTS

Overview of colony size

Across all colonies and years, Cliff Swallow colony size (mean ± SE) was 404.3 ± 13.3 nests ($n = 2318$ colonies), and ranged from 1 to 6000. Mean and maximum colony sizes in a given year were significantly positively correlated ($r_S = 0.81$, $P < 0.0001$, $n = 30$ years), so we used mean colony size in exploring yearly trends. Mean colony size increased with total breeding-population size of the study area each year (Fig. 3a), with some of the variation in population size attribut-able to the major weather-related mortality event of 1996 and the population's subsequent recovery (Fig. 3b). The overall population size was larger in the 5–15 years after the kill than in the 6 years immediately preceding the weather event (Fig. 3b; 2001–2011 vs. 1990–1995, $Z = 3.27$, $P = 0.001$, Wilcoxon test), as was mean colony size (459.4 ± 16.0 nests vs. 379.1 ± 14.1 nests; $Z = 2.66$, $P = 0.008$). Overall, even with the effects of the 1996 weather event during the middle of the study, there was evidence for an increase in mean colony size over time ($r_S = 0.35$, $P = 0.06$, $n = 29$ years). Mean colony size each year increased with the average annual high temperature for the 1 May–15 June period (Fig. 3c). There was no significant effect of rainfall, measured as the cumulative amount during 1 May to 15 June each year ($r_S = -0.25$,

$P = 0.19$, $n = 29$ years.) The year 1982 was excluded because of incomplete climate data.

Using colony site as a random effect in a linear mixed model, we found that colony size varied significantly with both substrate type (bridge, culvert, building, or cliff; $F_{3,2064} = 12.73$, $P < 0.0001$) and year ($F_{29,2064} = 4.66$, $P < 0.0001$). Colony size for bridge colonies (mean ± SE) was 714. 4 ± 30.3 nests, range 1–6000 nests ($n = 861$); for culvert colonies, 242.1 ± 9.3 nests, range 1–2350 nests ($n = 1270$); for building colonies, 84.3 ± 17.3 nests, range 1–550 nests ($n = 45$); and for cliff colonies, 75.1 ± 8.2 nests, range 1–735 nests ($n = 142$).

Habitat of the foraging area surrounding a Cliff Swallow colony site had relatively little effect on the typical colony size at a site. Using the mean colony size over all years a site was occupied, only the extent of standing water ($F_{1,103} = 11.08$, $P = 0.001$, ANCOVA) in a site's foraging area was a significant predictor of mean colony size after controlling for substrate type ($F_{3,103} = 13.33$, $P < 0.0001$); all other habitat types were nonsignificant ($P \geq 0.16$). The regression coefficient for standing water was positive, indicating that larger sites tended to occur in areas with greater acreages covered by lakes or ponds. The Simpson index of habitat diversity within a site's foraging area was not a significant predictor of mean colony size ($F_{1,109} = 0.44$, $P = 0.51$, ANCOVA) after controlling for substrate type ($F_{3,109} = 10.1$, $P < 0.0001$).

Colony size distributions

Colony size distributions by size class for each year of the study revealed that intermediate colony sizes tended to be most frequent, but the modal colony size class varied (Fig. 4; all 30 years are presented in Appendix: Fig. A1). One-nest colonies were least common when pooled across years (3.1%, $n = 2318$), followed by colonies with ≥ 2000 nests (4.5%) and colonies with 2–9 nests (8.2%). Over all years, the most common colony size class was 250–499 nests (19.7%), followed by 100–249 nests (17.3%) and 10–49 nests (16.1%). The shapes of these distributions (Fig. 4) varied from strongly modal, in which almost a third of all colonies were in a single size class (1999), to relatively uniform size-class distributions (2000). Colonies of 10–49 nests were the most common in the 1980s, compared to the 2000s, in which colonies of 250–499 were most common (Appendix: Fig. A1), consistent with the significant increase in mean colony size after 2001 (see *Overview of colony size*). The 1990s showed the most between-year variability in colony size distributions, perhaps in part because of the 1996 mortality event. The most obvious effect of this event was the elimination of all ≥ 2000-nest colonies that year and the next year. The minor mortality events of 1988, 1992, and 2004 had no dramatic effects on the colony size distribution in those years (Appendix: Fig. A1).

The percentage distribution of Cliff Swallows in the different colony size classes was heavily skewed toward
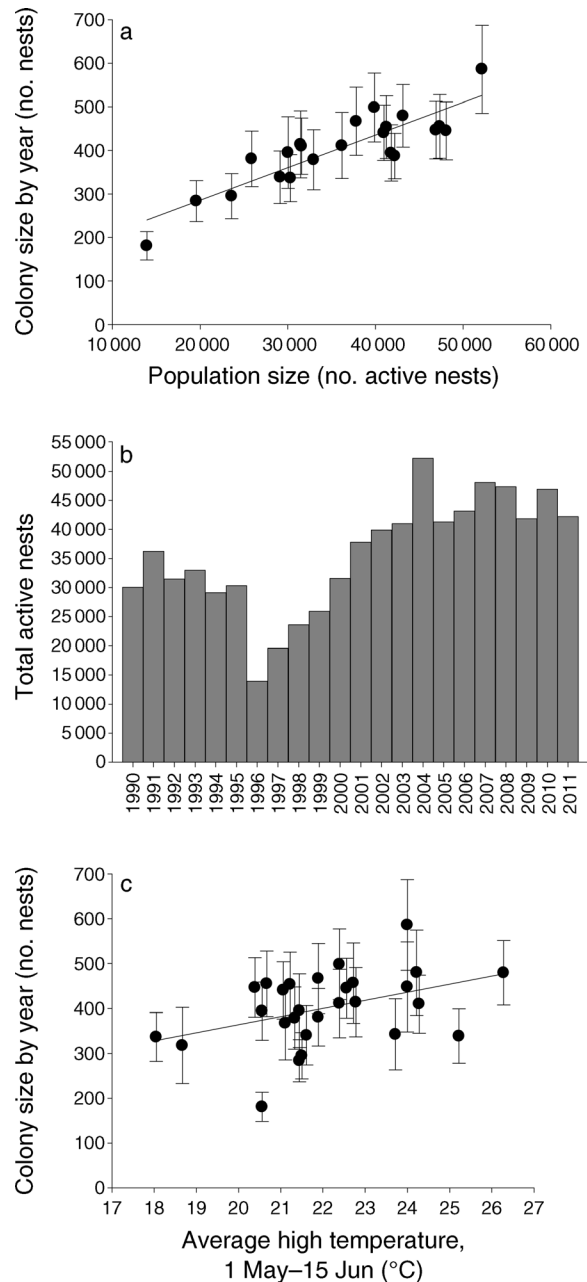

FIG. 3. (a) Cliff Swallow colony size (mean ± SE) each year in relation to total breeding-population size (defined as the number of active nests in all colonies that year). The line indicates best-fit least-squares regression. Mean colony size increased significantly with yearly population size ($r_S = 0.78$, $P < 0.0001$, $n = 22$ years). (b) Total active Cliff Swallow nests in all colonies by year, 1990–2011. A major weather-related mortality event occurred in 1996. (c) Cliff Swallow colony size (mean ± SE) in relation to average high temperature (°C) for the period 1 May–15 June each year. The line indicates best-fit least-squares regression. Mean colony size increased significantly with temperature ($r_S = 0.41$, $P = 0.025$, $n = 29$ years).
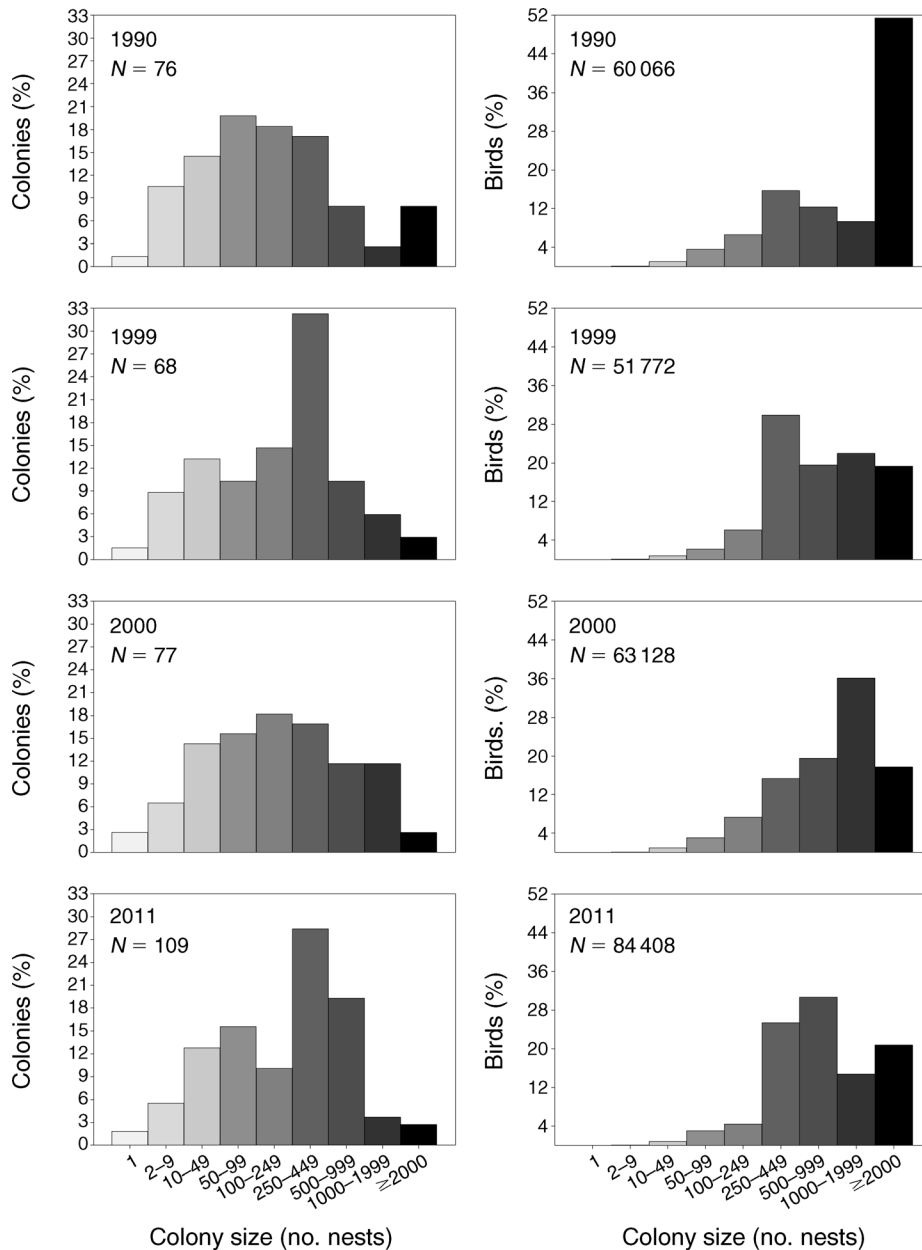
Fig. 4. Examples of Cliff Swallow colony size distributions by size class (left column) and the percentage distribution of individuals in each colony size class (right column) for four years. The total number of colonies and total number of individual birds each year are shown within the graphs. All 30 years are shown in the Appendix: Fig. A1.

the largest colony sizes in most years (Fig. 4; Appendix: Fig. A1). Across all years, 0.008% of the total nests ($n =$ 1 874 184) were in 1-nest colonies, 0.095% in 2–9 nest colonies, 1.03% in 10–49 nest colonies, 2.17% in 50–99 nest colonies, 6.75% in 100–249 nest colonies, 17.3% in 250–499 nest colonies, 19.2% in 500–999 nest colonies, 22.8% in 1000–1999 nest colonies, and 30.6% in ≥2000 nest colonies. The distributions varied from strongly modal (1990) to relatively uniform (1999), but birds in

larger colonies always numerically predominated. The colony size class containing the most birds in a given year ranged from size class 250–499 (in one year, 1999; Fig. 4) to the ≥2000 class (in 16 of 30 years; Appendix: Fig. A1). The largest colony size class tended to have the highest percentage of birds consistently each year from 1987 to 1994, but this was not the case following the mortality event of 1996. In the later years of the study (2005–2011), the percentage of birds was not always

greater in the largest colony size class, and in 2011 the largest size class contained only the third highest percentage of birds (Fig. 4; Appendix: Fig. A1).

Transitions between colony sizes

Using a multistate model with transition dependent on colony size class and substrate type, we estimated the probabilities of specific colony size class transitions in successive years for colonies situated on bridges and culverts (Fig. 5). We also estimated the probability of colony size declining to or remaining at zero in successive years (localized extinction). All colony size classes showed substantial unpredictability in the colony size to which they transitioned the next year. The highest probabilities were for sites to remain unused between years and for bridge sites with colonies $\geq$2000 nests to remain at that size (Fig. 5). Sites harboring relatively small colonies were generally more likely to stay small (or unused) the next year, but some sites still occasionally showed dramatic size changes between years; for example, bridge colonies of 2–9 nests had a 0.06 ± 0.03 probability of transitioning to one of 500–999 nests the next year. Sites with the largest colony size classes similarly were more likely to contain relatively large colonies the next year than to transition to a small colony or be unused, although even sites as large as $\geq$2000 nests (at culverts) had a 0.29 ± 0.17 probability of being unused the next year. Larger culvert colonies (250–999 nests) were in general more likely to transition to 0 (be unused) the next year than were bridge colonies of similar size (Fig. 5).

Colony size variability by site

Population variability (PV) metrics describe the temporal predictability of colony size at a given colony site. Across all sites ($n = 213$), PV ranged from 0.067 (colony sizes most stable across years) to 0.833 (least stable), averaging 0.493 ± 0.014 (mean ± SE). Examples of yearly size variation for 10 representative colonies with relatively high PVs of 0.72–0.78 and 10 with relatively low PVs of 0.34–0.44 are shown in Fig. 6. Colony sites could have relatively similar PVs even when the average colony size at the site varied from relatively small to relatively large. Sites with higher PVs were characterized by dramatic annual size changes and periodic local extinction events (colony size falling to 0), regardless of size, whereas lower PVs were associated with large colonies' rarely falling to 0 and many small colonies' routinely being unused (Fig. 6). There was a weak but statistically significant trend for PV at a site to increase with the mean colony size at the site in the years it was used ($r_S = 0.20$, $P = 0.004$, $n = 213$), indicating that sites traditionally supporting larger colonies were slightly more variable in size.

Substrate type influenced PV. Culvert colony sites ($n = 106$) had the highest (mean ± SE) PV, 0.569 ± 0.018, followed by bridge sites ($n = 51$), 0.491 ± 0.182, buildings ($n = 16$), 0.389 ± 0.053, and cliffs ($n = 40$),
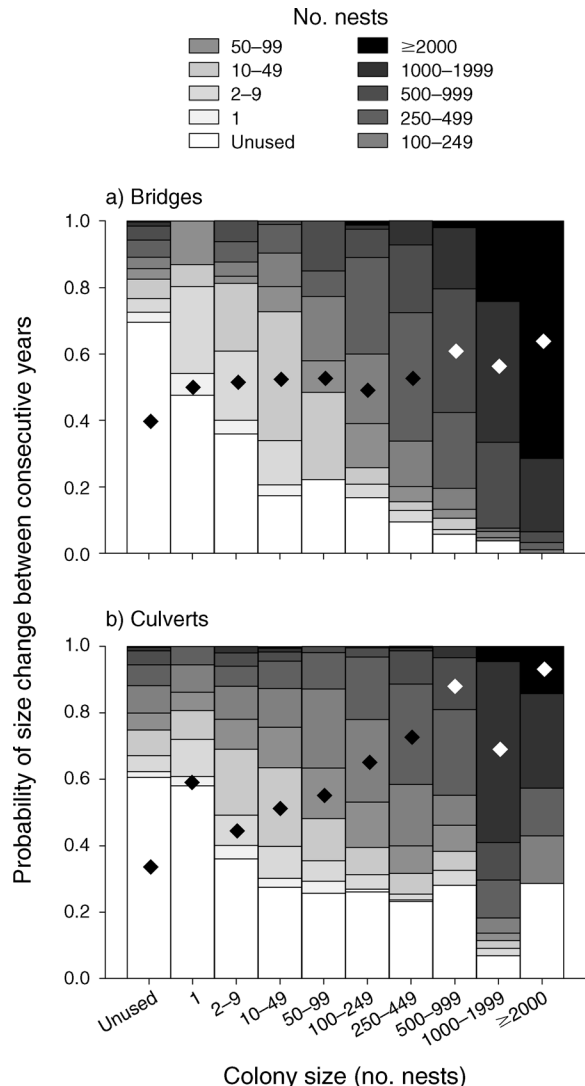

FIG. 5. Cliff Swallow colony size transition probabilities between successive years (ψ), as estimated from a multistate model with program MARK, for each colony size class on (a) bridge colony sites and (b) culvert sites. Transition probabilities from each size to all others collectively sum to 1.0. The probability of a site remaining the same size between years is highlighted with a diamond symbol.

0.335 ± 0.027; these differences were significant ($\chi_3^2 = 43.5$, $P < 0.0001$; Kruskal-Wallis ANOVA).

Diversity of the habitat in the birds' foraging area at a colony site was also related to PV. A site's Simpson index of habitat diversity was a significant predictor ($F_{1, 107} = 4.30$, $P = 0.04$) of its PV when controlling for substrate type ($F_{3, 107} = 14.58$, $P < 0.0001$, ANCOVA), with less diverse habitat (higher Simpson indices) associated with more variable colony sizes (higher PVs; Fig. 7). Of the different habitat types, extent of standing water ($F_{1, 101} = 6.03$, $P = 0.016$) and extent of urbanization (roads and buildings; $F_{1, 101} = 4.86$, $P = 0.030$) in a foraging range were the only significant
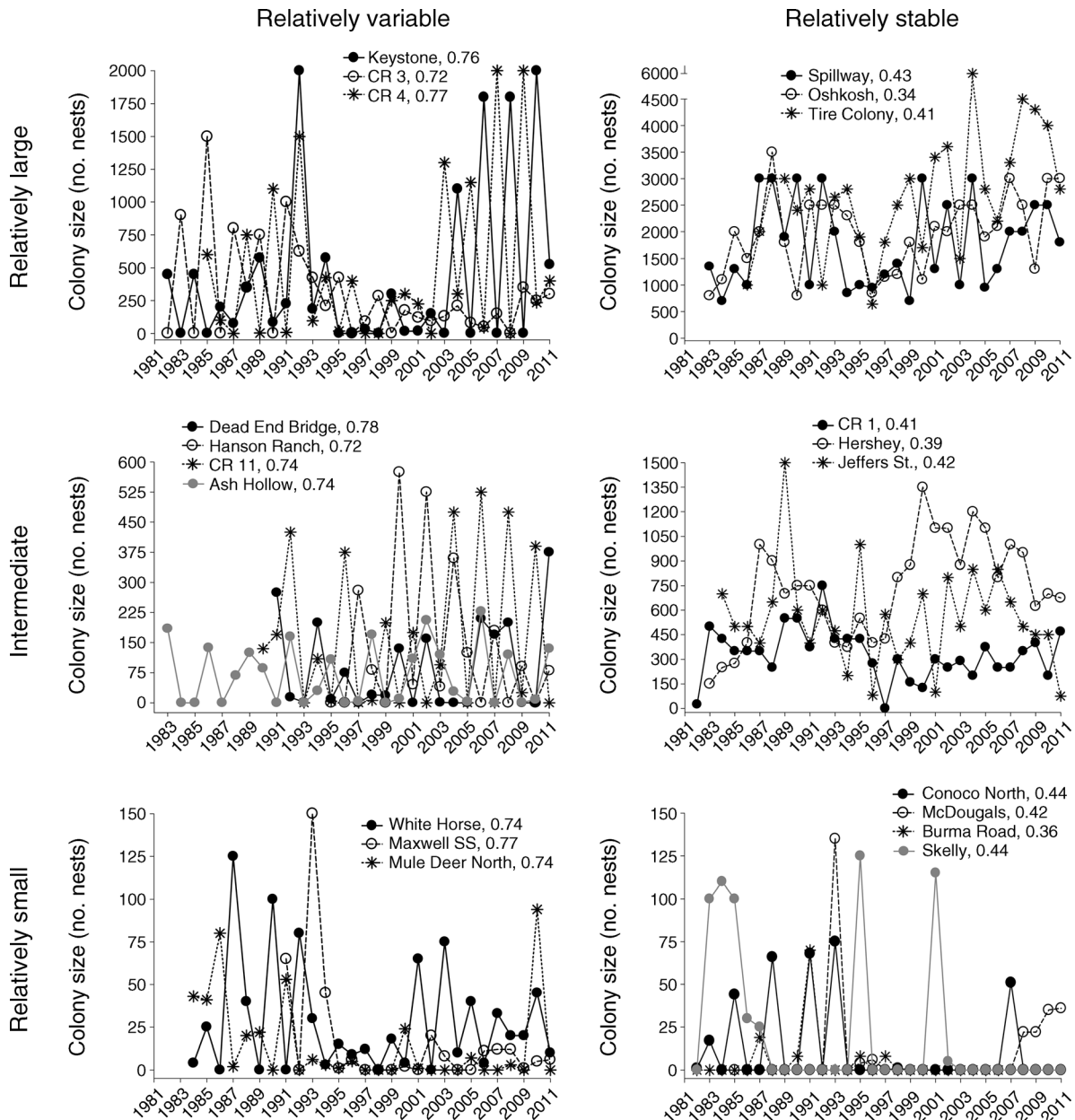
FIG. 6. Examples of annual size changes at 10 representative Cliff Swallow colony sites where population variability metrics (PV; numbers follow site names) were 0.72–0.78 (relatively variable sizes across years; left column) and 10 colony sites where PVs were 0.34–0.44 (relatively stable sizes across years; right column). Sites that were relatively large, intermediate, and small in size when used are shown in the upper, middle, and lower rows, respectively.

predictors of PV when controlling for substrate ($F_{3, 101} =$ 7.38, $P < 0.001$, ANCOVA). In both cases, the regression coefficients were negative, indicating that sites with greater colony size stability tended to occur in habitats with more standing water and greater anthropogenic modifications. This may have reflected the fact that most cliff colonies in the study area, which had lower PVs, in part because they were often unused, were on the shore of a large lake, and that large colonies

situated on highway bridges within towns tended to be perennially large and did not fluctuate widely in size.

Colony size of first-time sites

Colony size of 39 sites during the first year they were used averaged (mean ± SE) 238.8 ± 36.6 nests. These ranged from 1 to 1000 nests in size; 35.9% were <100 nests; 46.1% were 100–499 nests; and 18.0% were ≥500 nests. Of the 38 sites that were monitored the following year, 44.7% were unused the next year, 26.3% increased

in size the next year, 26.3% decreased in size, and one (2.6%) stayed the same. Only three were used for only one time. These colonies were known to be in the initial year of a site's occupancy because each was at a bridge or culvert that was first installed during the study or was an existing site that had not been occupied for at least 15 years and had no evidence of prior nesting (nest remnants).

Colony site use

Averaged across all years, about 55% of Cliff Swallow colony sites were occupied in a given season. While the number of available colony sites in the study area remained roughly the same over 1991–2011, there was a trend, though not significant, for the percentage of those sites that were used each year to increase with time ($r_S = 0.41$, $P = 0.06$, $n = 22$ years; Fig. 8, "all sites"). Use of sites fell below 50% during the 1996 mortality event and remained there until the population recovered (2003); beginning in 2007, site use increased to >60% each year (Fig. 8). Sites that were more often used were larger than were sites used less often; mean colony size at a site in the years it was active increased significantly with the percentage of years it was used by Cliff Swallows (Fig. 9).

Colony site use varied by substrate type. For bridges ($n = 51$ sites with ≥10 years of use data), the percentage of years occupied (mean ± SE) was 72.1 ± 4.5 years; for culverts ($n = 85$), 60.2 ± 3.3 years; for buildings ($n = 12$), 25.6 ± 5.0 years; and for cliffs ($n = 37$), 18.5 ± 1.8 years. The percentage of years used did not differ statistically for buildings compared to cliffs ($Z = 1.12$, $P = 0.26$, Wilcoxon test), but use of bridges differed significantly from culverts ($Z = 2.74$, $P = 0.006$), and both bridges ($Z = 6.80$, $P < 0.0001$) and culverts ($Z = 6.79$, $P < 0.0001$) differed significantly from buildings and cliffs collectively. Of 40 colony sites monitored each of the 30 years and deemed at least grossly suitable for Cliff Swallows each year, only 8 (20.0%) were occupied by the birds in all years. Of these eight sites, seven were large bridges over rivers, and the other was a massive metal water-control structure on the edge of a large lake (and considered a bridge site).

Use of cliff nesting sites declined over the course of the study, with the decline beginning in about 1989 and continuing to the present (Fig. 8). The other substrate types remained largely constant in the percentage of years occupied over time, although use of building sites dropped in the aftermath of the 1996 mortality event before recovering somewhat in the late 2000s.

Habitat in the surrounding foraging area seemed to have little effect on the probability of colony site use in a given year. After controlling for substrate type ($F_{3, 105} = 35.3$, $P < 0.0001$, ANCOVA), the Simpson index of habitat diversity was unrelated to the percentage of years a site was occupied ($F_{1, 105} = 1.62$, $P = 0.21$). Individually, none of the specific habitat types was a significant predictor of the percentage of years a site was
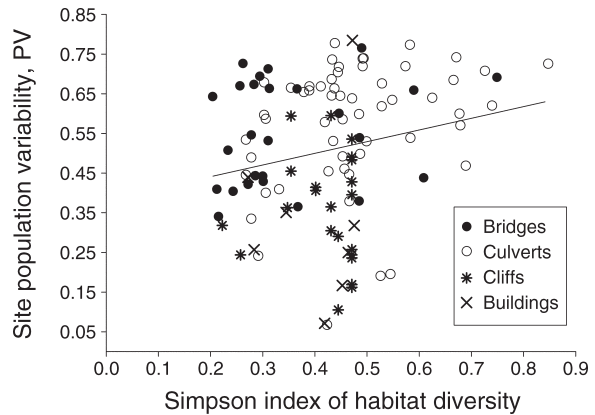

FIG. 7. Population variability (PV) metric for each Cliff Swallow colony site of different substrate types in relation to the Simpson index of habitat diversity for a colony site's foraging range. Lower values of the Simpson index indicate greater habitat diversity. The line indicates the best-fit least-squares regression. PV increased significantly with the Simpson index ($r_S = 0.22$, $P = 0.019$, $n = 112$ sites), meaning that sites with more variable colony sizes occurred in less diverse areas.

used ($P \geq 0.07$ on all) after controlling for substrate type ($F_{3,99} = 17.0$, $P < 0.0001$, ANCOVA).

DISCUSSION

Colony size in Cliff Swallows varied extensively among sites and among years. A colony's substrate type, annual breeding-population size in the study area, and whether the nesting season was relatively warm or cool appeared to influence to some degree average colony size and, to a lesser extent, the colony size distribution in a given year. Colony sizes at some sites were more unpredictable from year to year than at other sites, but only a colony's substrate type (and perhaps to a lesser extent, habitat diversity of the birds' nearby foraging range) was strongly associated with the probability of size change or site occupancy. While the colony sizes and the distribution of individuals among colony sizes showed variability among years, and there was a trend for mean colony sizes to increase in later years, the annual distributions of colony sizes did not show strong directional changes over the 30 years of the study. Thus, our overall conclusion is that Cliff Swallow colony size is temporally and spatially unpredictable both at the level of a single site and across the population, and that variation in colony size is not easily explained by known environmental correlates.

Mean annual colony size in Cliff Swallows during the 30 years varied by >400 nests if the year 1996 was included (the year the population was reduced by the mortality event) and by ~300 nests in more normal years. The only temporal correlates associated with mean colony size were population size and early-season temperature, and these effects may be related to each other. This Cliff Swallow population contains large numbers of nonbreeding, transient individuals each year
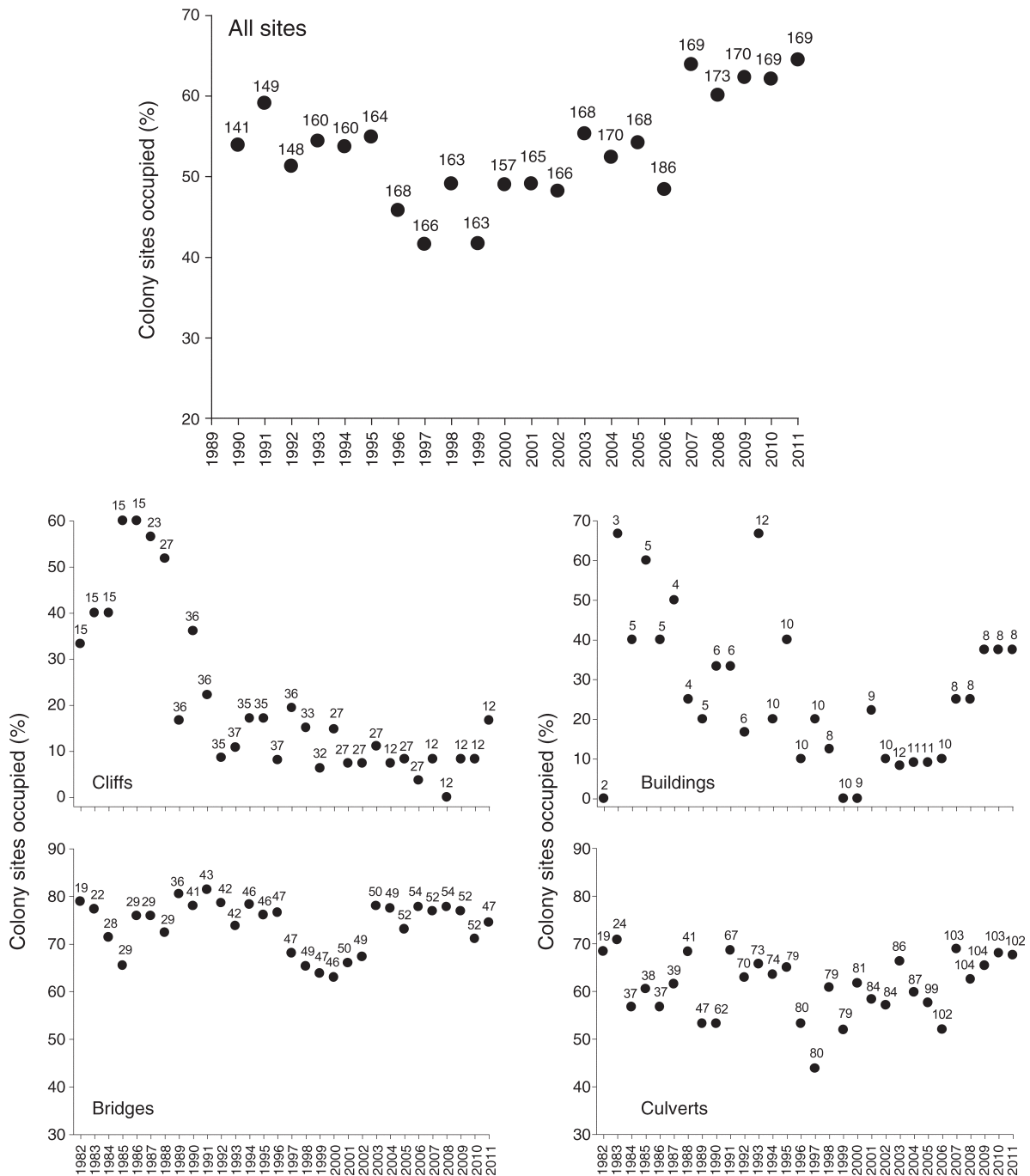
Fig. 8. The percentage of occupied Cliff Swallow colony sites in the study area each year, 1990–2011 (center), together with the percentage occupied for the different substrate types over the entire study period. Occupied sites were those with one or more active nests. Above each circle is the number of sites monitored each year.

(Brown 1998, Brown and Brown 2004a, Brown et al. 2007). In warm years when insect food is more abundant, possibly more transients are able to get into breeding condition and establish nests. Because the proportion of colony sites being occupied was largely constant across years, our results suggest that annual increases in the breeding population are absorbed by crowding at existing colonies and not by expansion to unused or new sites.

Predictability of colony size distributions across years (EVO)

A common approach to studying the evolution of coloniality in Cliff Swallows and other species (Hoog-

land and Sherman 1976, Snapp 1976, Hoogland 1981, Brown and Brown 1996, Serrano et al. 2005) has been to use the natural variation in colony size seen in most populations to infer directly how the costs and benefits associated with group size lead to differences in fitness among individuals in the different social environments. Many short-term studies have documented significant correlations between colony size and annual reproductive success (Brown and Brown 2001). Depending on the species, this work has revealed both increases and decreases in apparent fitness with colony size, and in other cases an "optimal" intermediate size where annual success appears to be highest. Yet despite these short-term directional trends in the fitness–colony size link, natural variation in colony size has been maintained in most populations without apparent selection against the group sizes where individuals have lower success. This conundrum has been explained by spatiotemporal fluctuations between fitness and group size (sensu Siepielski et al. 2009, Bell 2010), perhaps brought about by unpredictable changes in the risk of predation or parasitism in different social environments (Wittenberger and Hunt 1985, Møller 2002, Serrano and Tella 2007) or by environmental variability that changes the consequences (e.g., payoffs to be gained from social foraging [Brown and Brown 1996]) of living in different-sized groups from year to year. This hypothesis predicts that there is no "best" colony size, and that over the long term one should not see directional change in colony size.

Our study is one of the few with long-term data on colony size distributions across years for the same population. There were clear annual differences, with some years showing many colonies of similar sizes and other years a broader range of colony sizes. The population-wide fluctuations in the colony size distribution among years are broadly consistent with the hypothesis that payoffs associated with different colony sizes vary over time. In particular, the shift toward larger colonies in warmer years illustrates how relative payoffs for certain colony sizes could vary depending on environmental conditions (e.g., with foraging conditions). The trend for an increase in mean colony size, especially since the 1996 weather event, could be driven largely by the summers becoming warmer, perhaps a result of global climate change.

Some evidence indicates that the largest Cliff Swallow colonies may in fact reach a threshold that constrains continued colony growth. Each colony size has certain costs (such as ectoparasitism and interference among conspecifics) and benefits (such as transfer of information about food and enhanced vigilance for predators) associated with it (Brown and Brown 1996). While costs increase linearly or exponentially with colony size, benefits in general tend to asymptote at smaller colony sizes (Brown and Brown 1996). The consequence can be that costs of coloniality become substantially greater than the benefits above a threshold colony size, and that
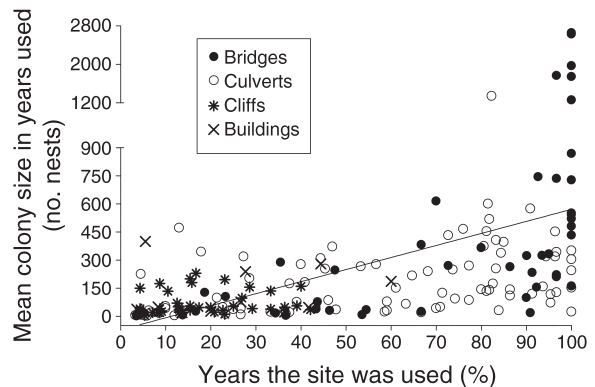

FIG. 9. Mean Cliff Swallow colony size in the years a colony site was used in relation to the percentage of years during the study that the site was occupied for different substrate types. Only sites with use data for ≥ 10 years were included. The line indicates the best-fit least-squares regression. For all substrates combined, a site's mean colony size when active increased significantly with the percentage of years the site was occupied ($r_S = 0.64$, $P < 0.0001$, $n = 182$ sites).

fewer colonies above that size form. The size distributions suggest that this threshold might be in the vicinity of 1000 nests. Perhaps only a relatively few sites can support colonies above that size where individuals can still realize benefits equal to or greater than the costs, because of relatively unique local ecological conditions. In addition, the disappearance of the largest colonies immediately following the mortality event seems to suggest that colonies at the upper end of the size range are most sensitive to environmental extremes.

The weather-related mortality event of 1996 (Brown and Brown 1998) was obviously responsible for some of the temporal variability observed in colony size distributions during this study. The breeding-population size in 1996, determined from colony sizes several weeks after the mortality event had occurred, dropped by ~53% relative to the years immediately preceding this event. The population increased steadily in the following years, and was back to pre-kill levels four years later. While the effect of the mortality event on overall breeding-population size was relatively short lived, this event apparently had a longer-term effect on the distribution of colony sizes and especially on the distribution of the population in those colony sizes.

The largest colonies disappeared entirely in the immediate aftermath of the kill, and for the following 10 years, a smaller fraction of the population occupied those largest colony sizes than in most of the years prior to the weather event. This may have reflected higher mortality of birds in the largest colonies during the kill, leading to fewer "large-colony phenotypes" (Brown and Brown 2000a) in the years following the event. If such viability selection against birds in the largest colonies occurred, it was likely mediated by competition for food during stressful conditions. There is evidence that Cliff Swallows in larger colonies sometimes deplete local food

resources (Brown and Brown 1996), a potentially costly consequence of living in large colonies, especially when insects are so scarce that information sharing about food resources (Brown 1986, 1988, Brown and Brown 2004b) cannot compensate for local food depletion. Catastrophic mortality events such as that of 1996 thus may periodically exert selection pressure on birds in different-sized colonies and lead to reshuffling of the colony size distribution, thereby maintaining population-level temporal variation in colony size (Roche et al. 2011).

We thus conclude that while variability in annual colony size distributions was often extensive, colony size distributions in this study were relatively stable over 30 years, and provide no strong evidence for directional changes in colony size in response to selection pressures. The results are thus consistent with colony size variability being maintained by fluctuating selection on group size.

Predictability of colony size in relation to local resources at a site (ECO)

If heterogeneity in local resources leads to varying numbers of individuals occupying habitat patches (colony sites), local habitat and site characteristics should determine to some degree colony size and site use. The largest contributor to among-site spatial variation in colony size and site use was the type of substrate the nests were built on. Colonies on bridges averaged about three times the size of those in culverts and 8–9 times larger than those on buildings and cliffs. The most obvious difference between bridges and the other substrate types was that bridges tended to be much larger in physical structure. For example, the largest bridge used by Cliff Swallows in the study area was 220 m long, with most of the other bridges 70–180 m long. With both outer and inner vertical beams spanning this distance, bridges offered abundant surfaces for nest attachment. In contrast, culverts in our study were usually 15 m or less in length, and while some had multiple parallel sections separated by walls that increased attachment surfaces (Fig. 2b), many consisted of a single tunnel with only two walls.

In Lesser Kestrels (*Falco naumanni*), growth of colonies above a given size threshold is regulated by despotic behavior of established residents who prevent others from settling, resulting in a truncated colony size distribution and an overabundance of smaller colonies (Jovani et al. 2008b). Cliff Swallows do not exclude others from settling, but the physical size of colony substrates may in part prevent large colonies from forming at some sites. The largest colony seen in our study was one of 6000 nests that formed at the longest and largest bridge in the study area; such a colony could not have been accommodated, for example, at a 10-m long culvert. However, overall, the total amount of concrete substrate at a bridge or culvert showed no relationship with the mean colony size recorded there,

with some culverts having over 2000 nests (Brown and Brown 1996).

Although substrate was not likely limited at most colony sites, probably only a relatively few sites (the large river bridges) could contain the largest colonies (≥3000 nests). These bridges may have also been situated in particularly rich foraging habitat that could support thousands of birds. Yet the fact that none of the largest colonies formed in the aftermath of the mortality event even when sites suitable for them were present (and occupied by some birds) indicates that these large colonies also result from social processes and may be influenced in part by breeding-population size in a given year. At other times (e.g., 1990), over half of all nesting Cliff Swallows in the study area occupied the very largest colonies at the upper end of the size range; conditions that favored this degree of aggregation remain unclear.

Bridges may have had larger colonies, on average, also because the greater substrate there allowed more unused nests to accumulate. Cliff Swallows readily reuse old nests from previous years (nests can routinely last for 2–4 years or longer), especially when the nests are not infested by ectoparasites (Brown and Brown 1986). The birds can save substantial time and energy by appropriating existing nests at the start of the season, and often compete intensely by fighting for them (Brown and Brown 1996). Bridges that supported the largest colonies typically had hundreds of unused nests in a given year, which often seemed to allow Cliff Swallows to alternate between using different ends or different sides of the bridge in successive years. This may have helped them avoid infestations of swallow bugs more effectively on bridges. With fewer nests, on average, at the other substrate types and shorter nest longevity at building and cliff sites because the nests are less sheltered or do not adhere as well, these colony sites simply offer fewer existing, potentially uninfested nests to incoming settlers at the start of each season and thus may be less attractive. Similar scenarios have been proposed for Barn Swallows (*Hirundo rustica*), which also build mud nests that can last between seasons (Shields et al. 1988, Safran 2004).

Do colonies on different substrate types experience different levels of ectoparasitism, and if so, could this account for differences in colony size among sites? Microclimate differences exist among substrates, and the bugs likely respond behaviorally to that microclimate (which in turn makes accurately estimating bug population sizes difficult [Rannala 1995]). Because of the challenges of quantifying bug parasite load on a large scale without collecting nests, we do not know whether the different substrates harbor different total numbers of parasites. Limited information suggests that bugs might overwinter more successfully in culvert environments than on the more exposed bridges, perhaps because of a more favorable winter microclimate (warmer, more humid) inside the culverts (Brown et al. 2010). If so,

culverts might have larger bug populations at the start of each nesting season, potentially influencing initial settlement by Cliff Swallows. However, because bridge colonies often become much larger in size, and because more swallow bugs are introduced into the larger colonies during the season (Brown and Brown 2004a, Brown et al. 2007), birds on bridges may not experience a net seasonal reduction in parasitism even if they start out with fewer bugs in their nests. The smaller colonies on buildings and cliffs might imply that they would have the fewest parasites (because per capita parasitism is directly related to colony size [Brown and Brown 1986, 1996, 2004a]) and therefore be most likely to be reused each year, but we found that these substrates were less likely than bridges or culverts to be reused annually.

Relatively little of the colony size variation among sites appeared related to physical features of the habitat surrounding a colony. Colony size in some animals may partly reflect the amount of food that can be found locally (Uetz et al. 1982, Rypstra 1985, Johst and Brandl 1997, Ambrosini et al. 2002), with larger colonies forming in areas that contain enough prey to support more predators. The Cliff Swallow's aerial insect food is virtually impossible to sample directly (owing to the many different taxa on which the birds feed), but an indirect index of food availability is the habitat around a colony (Brown et al. 2002). If colony size varies systematically with certain habitat features that influence insect abundance, a link between food availability and colony size is possible. However, only the extent of standing water in a colony site's foraging range was related (positively) to average colony size. The association between standing water and colony size may be partly an incidental association between big bridges (which can contain many nests) and the water that they span. Thus, there is no indication that colony size in Cliff Swallows is primarily a response to ecological availability of food in a local area. Inter-colony competition for food (Furness and Birkhead 1984, Cairns 1992, Griffin and Thomas 2000, Lewis et al. 2001) as a determinant of colony size in Cliff Swallows was ruled out earlier because colony size at a given site varies independently of the number of birds settling at sites that potentially share its foraging range (Brown and Brown 2002).

Cliff Swallows in our study area used primarily artificial nesting substrates, and use of natural cliff sites declined during the 30 years. The birds have been using bridges and culverts as nesting sites in our study area since at least 1942 and possibly as early as 1920 (Brown and Brown 1996), although extensive use of artificial nesting sites appears to have only begun in the early 1980s at about the time our study commenced (Brown and Brown 2013). While we have seen few differences in social behavior of birds on the different substrate types, undeniably substrate type has influenced colony size dynamics. Because they are more protected than on cliffs, nests on bridges and culverts survive longer and

potentially encourage site reuse and affect swallow bug populations. That the birds now occupy nesting substrates with physical properties that differ from their ancestral breeding habitat means that their colony choice may not reflect conditions under which it evolved and/or that the birds are adapting to these new environments. The species is switching to artificial sites widely throughout its range (Brown and Brown 1995), and thus soon it may not be possible to study Cliff Swallows at completely "natural" colony sites anywhere.

We thus conclude that the only local resource that was strongly associated with Cliff Swallow colony size at a site was the type of nesting substrate, with bridges tending to have larger colonies. The positive relationship between standing water and colony size may have been principally because the larger bridges usually spanned standing water.

Predictability of colony size in relation to conspecific activity (BEH)

Coloniality has been suggested to be a by-product of animals' assessing breeding habitat and simply aggregating in areas with high-quality resources where annual reproductive success is likely to be high. Although the underlying basis for some sites being more successful than others is likely related to local ecological conditions (ECO), the BEH hypothesis proposes that colony formation is driven largely by social processes resulting from selection on individuals to act on the information available to them. In some cases, incoming settlers may rely on indirect cues such as existence of old nests to infer likely success at a site (Shields et al. 1988, Safran 2004), or perhaps more commonly, potential settlers may directly observe the reproductive success of conspecifics in the previous season and recruit to sites where success had been highest (Danchin and Wagner 1997, Wagner et al. 2000). In the absence of any information on site quality, individuals that have never nested may cue directly on where others have settled as the best available indication of site suitability (Burger 1988, Podolsky and Kress 1989, Forbes and Kaiser 1994, Brown and Rannala 1995).

Only if reproductive success at a colony site one year is similar to that the next year will information on a site's past success be useful. If this assumption is correct, large colonies one year (which presumably had been successful in the past and for that reason are large currently) should continue to grow the next year. Small colonies might be ones that were previously less successful, explaining why they have few settlers in the current year. Thus, generally we should see large colonies continue to be used each year and probably grow in size, and small colonies should decline over time and eventually become extinct. When new sites are colonized or previously unused ones are reoccupied, initially colonies there should be small because the lack of public information on those sites' suitability will prevent many individuals from taking the risk of using them.

Colony sizes at some sites were consistent with these predictions, while those at others were not. Estimated transition probabilities illustrated that many unused sites remained that way between successive years, supporting the hypothesis that sites may often stay unused because potential settlers have no information to evaluate them (sensu Forbes and Kaiser 1994). Colonies of 100 nests or larger often stayed the same or grew in size the next year, consistent with the mechanism of aggregation in traditional sites (Shields et al. 1988, Danchin and Wagner 1997, Safran 2004). Furthermore, for a small subset of colonies where we had information on annual nesting success, we found that the most successful sites in one year tended to grow in size the next year, and less successful sites did not (Brown et al. 2000).

In general, sites with lower population variability (PV) scores tended to support the traditional aggregation hypothesis, while those with higher PVs (0.6–0.8, and especially those with regular oscillations between zero and 2000 nests in alternate years [Fig. 6, upper left]) did not. Culverts had higher PVs than bridges, suggesting that Cliff Swallows might rely on public information more (i.e., fitness expectations were more consistent) at bridges than at culverts. If swallow bug infestations were greater at culverts and fluctuated more between years (see the paragraph beginning, "Ectoparasitism has long been thought . . . ."), this alone might make reliance on public information from one year to the next more risky at those sites.

Colony sizes at sites used for the first time partially supported the prediction (Forbes and Kaiser 1994, Danchin and Wagner 1997) that when a site is initially colonized it should be small. Colony size at these sites averaged ~150 nests smaller than for the population of colonies at large, and the percentage of first-year colonies <100 nests in size (~36%) was larger than the comparable percentage for the population at large (~21%). On the other hand, 18% of all first-year colonies were ≥500 nests in size, with the largest being 1000 nests, indicating that sometimes new sites were colonized initially by large numbers of birds. In these cases, the birds must have been relying on cues other than past annual reproductive success to determine the suitability of the site.

We thus conclude that while some sites showed annual changes in colony size consistent with these birds' basing their choice of colony on the presence or success of conspecifics in an earlier year, many sites did not conform to a pattern expected if coloniality is a by-product of traditional aggregation.

Predictability of colony size at a site across time

The estimated colony size transitions showed that virtually all conceivable size changes were possible and in fact were observed to occur, although some were rare. Yet the factors causing these annual size shifts at a site were far from clear. PV metrics differed consistently

only by substrate type, with culvert sites showing the greatest degree of size change between years. The higher PVs of culvert sites may reflect, in part, their most often being of intermediate size, meaning they could shift either much larger or much smaller between years, whereas sites of the other substrate types more often could move in one direction only. The finding of sites with less diverse habitat in the surrounding foraging range having greater annual size variability may reflect more unpredictable local food resources between years. Less diverse habitat such as monoculture cropland can be associated with boom-or-bust insect outbreaks in some years but not others (Brown et al. 2002). This scenario is difficult to evaluate fully without more direct measures of insect abundance at a colony site in different years, which we lack.

Ectoparasitism has long been thought to play a prominent role in Cliff Swallow colony size and site dynamics (Grinnell et al. 1930, Earle 1985, Emlen 1986, Chapman and George 1991, Loye and Carroll 1991). The conventional wisdom has been that birds avoid sites for one or more years after a period of heavy use (several years occupancy or large colony sizes) to allow the heavy infestations of the nest-based swallow bugs to die off. Annual increases of colony size and perennial use at sites where parasites have been removed experimentally (Buss 1942, Brown and Brown 1986, 1996, Emlen 1986) are consistent with this hypothesis. Selected colonies in the study area in some years have shown patterns supporting the parasite avoidance idea: for example, some sites (Fig. 6) contain large colonies one year, drop to zero the next, and are reoccupied by many birds the following year in a predictable cycle.

But most colonies do not show a clear pattern, with use itself being erratic at some sites, and others (of all substrate types) used perennially. What keeps perennially used sites from being overrun with swallow bugs? We observed heavy infestations of bugs at some sites that led to complete colony reproductive failure; in such cases, sometimes the site was abandoned the next year as expected, but in other cases it was reused. Because we lack data on bug population abundance at sites at the start of each nesting season and do not know the conditions that promote bug population growth at a site, at present the extent to which ectoparasitism contributes to annual size variation and site use is unclear.

We thus conclude that, while some Cliff Swallow colony sites tended to be perennially large and others perennially small, between-year variability in colony size at most sites was high, and whether a site exhibited similar colony sizes from one year to the next could not be reliably predicted by features of the local environment as we currently understand them.

Predictability of colony site use

Whether a given colony site was used by Cliff Swallows in a season was variable across years and

could be best predicted by substrate type, with bridge sites the most likely to be reused in consecutive years. The same unpredictability underlying size change in this population seemed also to apply to site use per se. However, while individual colony sites were variable in use, across the population the percentage of suitable sites occupied by Cliff Swallows did not show wide temporal fluctuation (other than a slight decline in the aftermath of the 1996 kill and a upward trend in recent years for unknown reasons).

The exception was for colony sites located on cliff faces. Use of these sites exhibited a long-term decline throughout the 30 years of the study, dropping relatively dramatically after 1988. While the number of such sites also decreased during the study (Fig. 8), largely attributable to rocky overhangs falling and some sites becoming overgrown with eastern red-cedar (*Juniperus virginiana*), the decline in site use began before the number of cliff sites decreased. This pattern is consistent with historical Breeding Bird Survey data showing that Cliff Swallows began moving onto highway culverts and bridges in our study area in large numbers in the early to mid-1980s (Brown and Brown 2013). This shift may reflect the birds' having higher annual reproductive success on artificial sites, where nests are better protected from the elements and survive more intact between seasons.

Random colony choice?

Recently it has been emphasized that avian habitat occupancy can sometimes be described by largely random settlement patterns (Haila et al. 1996, Campbell et al. 2010), in which a bird's settling at any given breeding site does not depend on any attribute of that site or the individual's phenotype. Thus, could a purely random process of settlement generate the relatively unpredictable distributions of individuals among colony sites that we observed for Cliff Swallows? Russell and Rosales (2010) addressed this question in a series of simulations for populations of colonial animals that appear directly applicable to Cliff Swallows. Under a model of purely "random" choice, individuals will distribute themselves such that population densities among sites are similar and the only variation is that of white noise (Russell and Rosales 2010). In contrast, we had widely dissimilar numbers of settlers among sites, with many colony sites (~45%) having no birds in a given year and others having 2000 nests or more. This highly over-dispersed distribution of birds alone rules out purely random choice of breeding sites. On the other hand, as the tendency of individuals to actively choose sites (based on undetermined cues) increases and when sites have unequal capacities to accommodate settlers, one begins to see colony dynamics similar to those we observed with Cliff Swallows: some sites have large numbers of birds and are used perennially, others have none, and still others show wide oscillations in size as individuals switch en masse between sites among years

(Russell and Rosales 2010). This is the expected result if we assume birds are basing colony choice on different cues (EVO, ECO, and BEH) and integrating these processes in selecting colony size. The simulations do not identify what cues are being used, but they do suggest that the patterns of colony size variation we observed result from active choice of breeding site and do not reflect random settlement.

Conclusions

Our take-home message is that colony size in Cliff Swallows is temporally and spatially unpredictable when viewed across the 30 years of this study. We had expected to uncover more predictable patterns, given the large number of colony sites monitored over this long time scale. While we did find that the spatial and temporal dynamics of colony size in Cliff Swallows could be broadly predicted by substrate type, colony size among sites and among years varied widely and frequently did not show an obvious pattern.

Had our study been restricted to a smaller subset of colony sites within the study area, it is probable we might have inferred patterns of colony site use and size change that would not have been representative of the study area at large. For example, six colony sites near the Cedar Point Biological Station that have been studied each year since 1982 have at times shown regular patterns: quite large one year and unused the next (two of these are shown in Fig. 6, upper left). If our work had been confined to these six sites (a sample size more typical of many studies on colonial birds [Brown and Brown 2001]) and only in certain years, we probably would have proposed that colony size is regulated by ectoparasite infestations and that the birds vacate sites in years after colony size at a site was large to allow parasite numbers to decline. Yet this pattern, which in some cases persisted for 8–10 years, disappeared for these particular sites as we continued to monitor them over more seasons. This illustrates the pitfalls in making conclusions from field studies that are short or even moderate-term in scope, and at the same time shows that, paradoxically, resolving patterns can be more difficult with long-term data. In many ways, this phenomenon is analogous to the problem with temporal trends in effect sizes in ecology and evolution (Jennions and Møller 2002): as more studies are published (more years of data collected), the clear results that came from earlier studies (fewer years of data) become less apparent.

The analyses reported here and elsewhere (Brown and Brown 1996, 2000a, Brown et al. 2000, 2005, 2008, Roche et al. 2011) reveal that the extensive colony size variation in Cliff Swallows is likely generated by evolutionary (EVO), ecological (ECO), and behavioral (BEH) processes working in complex and sometimes synergistic ways. Cliff Swallows may choose sites and colony sizes based in part on (1) heritable tendencies toward small or large groups that have been selected for

by (2) expected phenotypic-dependent payoffs in different group sizes (EVO), while at the same time individuals likely refine colony selection by (3) familiarity with particular sites (ECO) and (4) prior assessment of the probability of success at a colony site or by aggregating with conspecifics already settled (BEH). Superimposed on these choices are (5) physical characteristics of nesting sites that sometimes constrain colony size based on substrate size, extent of food resources, ectoparasite load, or other factors (ECO), and (6) these constraints vary across time and space to affect fitness differently in colonies of different sizes and thereby maintain diversity in group size (EVO). Our long-term study suggests that arguments that coloniality can be explained largely by a single process of habitat assessment (Danchin and Wagner 1997) are too simplistic, and that the generation and maintenance of colony size variation is complex.

Colony size distributions and patterns of site use are the outcomes of individuals' decisions (Safran et al. 2007). The next step is to determine if individuals' histories of colony choice are related to specific phenotypic traits (Brown and Brown 2000a, Brown et al. 2005, Roche et al. 2011) under different ecological scenarios. Analyses are underway to study individual choice of colony size for our population. With >225 000 marked Cliff Swallows and >400 000 captures/recaptures, we will have an opportunity to see if another long-term data set will resolve clear patterns.

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SUPPLEMENTAL MATERIAL

Appendix

A figure illustrating 30 years of Cliff Swallow colony size frequency distributions (*Ecological Archives* M083-017-A1).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.t3b18