



Why come back home? Breeding-site fidelity varies with group size and parasite load in a colonial bird



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Fidelity to a past breeding site is widespread among animals and may confer both costs and benefits. Colonial species occur at specific sites that can accommodate multiple breeders, and the choice of whether to return to last year's site or disperse elsewhere can affect colony site use, the colony size distribution and individual fitness. For the colonial cliff swallow, *Petrochelidon pyrrhonota*, which occupies colonies of widely different sizes, we used a 30-year field study in western Nebraska to investigate how the extent of infestation by ectoparasites and colony size affected breeders' colony site fidelity between years. We compared philopatry at colonies where parasitic swallow bugs, *Oeciacus vicarius*, had been removed by fumigation with that at nonfumigated sites exposed to natural levels of ectoparasites. About 25% of birds at nonfumigated colonies returned to their previous year's site, whereas about 69% of birds at fumigated colonies did so. Site fidelity was greatest at nonfumigated sites that changed the least in size between years. Birds were less likely to return to a nonfumigated site as the colony there became increasingly larger. Individuals philopatric to both nonfumigated and fumigated sites resided in colonies more similar in size between years than did dispersing birds. Most cliff swallows settled within 6 km of their previous year's site, indicating that many nonphilopatric birds still may have had some familiarity with the local landscape surrounding the site to which they moved. Removal of ectoparasites at a site allows large colonies to persist there perennially, probably contributing to higher philopatry because such large colonies are rare and would have been difficult to find had the residents dispersed. Cliff swallows are likely to be sensitive to both colony size and general familiarity with a given site or landscape region, and probably integrate these with other cues to select breeding colonies.

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Most iteroparous animals that are to any degree migratory or nomadic face the annual choice of whether to return to a breeding site used in the past or disperse to a new one. The consequences of philopatry versus dispersal can profoundly affect gene flow, average relatedness, demography, disease spread, mating success and social behaviour (Clobert, Danchin, Dhondt, & Nichols, 2001; Greenwood & Harvey, 1982; Johnson & Gaines, 1990; Walter, Firebaugh, Tobin, & Haynes, 2016). Ecological and behavioural correlates associated with site fidelity have been explored in many species (e.g. birds and pinnipeds; Bried & Jouventin, 2002; Kokko, Harris, & Wanless, 2004; Pomeroy, Twiss, & Redman, 2000; Shutler & Clark, 2003; Stacey & Ligon, 1991; Wolf & Trillmich, 2007). The advantages associated with philopatry include

increased familiarity with physical space (Piper, 2011), which can often increase fitness through greater experiential knowledge of the whereabouts of food or shelter or the habits of local predators (Brown, Brown, & Brazeal, 2008; Hoogland, Cannon, DeBarbieri, & Manno, 2006; Isbell, Cheney, & Seyfarth, 1993; Metzgar, 1967; Stamps & Swaisgood, 2007), while the disadvantages can include increased competition (sometimes with kin) for resources or a greater likelihood of inbreeding (Greenwood, 1980; Handley & Perrin, 2007; Hoogland, 2013; Lambin, Aars, & Pieltney, 2001).

For colonially breeding species, the choice of whether to be site-faithful between years must be superimposed on a simultaneous decision about what size group to occupy. Some animals are known to prefer certain colony sizes (Brown & Brown, 2000; Brown, Covas, Anderson, & Brown, 2003; Møller, 2002; Serrano & Tella, 2007) or levels of sociality (Charmantier, Keyser, & Promislow, 2007; Goodson, Evans, Lindberg, & Allen, 2005; Goodson, Schrock, Klatt, Kabelik, & Kingsbury, 2009), because of either heritable

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performance-based preferences or phenotypic specialization for certain social environments (Brown, 2016). Thus, individuals must integrate information on physical site suitability (e.g. parasite load that may change over time; Boulinier, McCoy, & Sorci, 2001; Danchin, 1992), past familiarity with the habitat around a site, and the number of conspecifics potentially or actually present (the colony size expectation with the associated costs and benefits of grouping; Brown & Brown, 1996) in deciding whether to be philopatric or disperse to a new colony site (Bonte et al., 2012). Knowing how colonial individuals make the decision to stay or go is critically important, both for understanding the metapopulation dynamics of colony occupancy (which may explain population-wide colony size variation; Johst & Brandl, 1997; Matthiopoulos, Harwood, & Thomas, 2005; Russell & Rosales, 2010) and for understanding how colonial species of conservation concern become 'trapped' in a subset of available colony sites (Cook & Toft, 2005; Kenyon, Smith, & Butler, 2007; Schippers, Stienen, Schotman, Snep, & Slim, 2011) due to their reluctance to disperse to new sites.

Relatively few studies have explored the role of site fidelity in animals' choice of colony size (Fasola, Hafner, Kayser, Bennetts, & Cezilly, 2002; Grandi, Dans, & Crespo, 2008; Serrano, Forero, Donazar, & Tella, 2004; Serrano, Tella, Forero, & Donazar, 2001; Shields, 1984). We do not know in general whether individuals predisposed to philopatry (perhaps because of past experience at a colony site; Brown et al., 2008; Serrano et al., 2001) are likely to remain site-faithful regardless of the colony size at the site in the subsequent year. If not, is dispersal contingent on whether the colony is smaller or larger than it was the previous year? Because some colonial animals are attracted to a site solely by the presence of others (Dittmann, Zinsmeister, & Becker, 2005; Serrano et al., 2004; Serrano, Tella, Donazar, & Pomarol, 2003; Ward et al., 2011), individuals might be more likely to be site-faithful if the colony at their previous site increases in size (through, for example, the recruitment of first-time breeders). How do other characteristics of a colony site, such as the extent of infestation by ectoparasites or residents' reproductive success, influence site fidelity? Some colonial species seem to be sensitive to the reproductive success of conspecifics in the preceding year and use that information as a guide on where to settle in the current year (Danchin, Boulinier, & Massot, 1998; Danchin & Wagner, 1997; Frederiksen & Petersen, 1999; Switzer, 1997). In these cases, the expectation of success at a site might lead to higher philopatry (Switzer, 1997) than would be predicted based on colony size alone. In other cases, continued occupancy of a site over several successive years can increase the number of ectoparasites present in or on the nesting substrate (Brown, Brown, & Roche, 2013; Calabuig, Ortego, Cordero, & Aparicio, 2010; Danchin, 1992), and dispersal away from a site may increase over time as individuals seek to avoid parasites (Brown & Brown, 1992) regardless of social environment or familiarity with a site.

In this study, we explored fidelity to particular colony sites in colonial nesting cliff swallows, *Petrochelidon pyrrhonota*, integrating results on philopatry with what is already known about colony choice in this species (Brown & Brown, 2000; Brown, Brown, & Danchin, 2000; Brown, Brown, Raouf, Smith, & Wingfield, 2005). Using long-term mark–recapture data, we examined how site fidelity varies with individual characteristics, such as sex and age, and with colony level characteristics, such as size and frequency of site occupancy. We investigated the colony sizes occupied by birds that were philopatric versus those that dispersed to new sites, asking whether site fidelity/dispersal can, to some degree, reflect individuals seeking colonies of particular sizes. By manipulating parasite load at certain colony sites through fumigation, we examined specifically how long-term absence of parasites at sites affected birds' decisions to be site-faithful versus to disperse.

Finally, for dispersing birds we examined the distances they travelled to settle elsewhere. We focused here exclusively on breeding-site philopatry among birds that had had at least 1 year of experience as breeders.

METHODS

Study Animal

The cliff swallow is a migratory, sparrow-sized passerine bird found throughout the Great Plains and westward to the Pacific coast of North America; smaller populations exist in the eastern half of the continent (Brown, Brown, Pyle, & Patten, 2017). Historically, these birds built their gourd-shaped mud nests underneath horizontal overhangs on the sides of steep cliffs, although now many cliff swallows nest under the sides of bridges and buildings or inside concrete culverts underneath roads or railways (Brown et al., 2013). The birds arrive in our study area beginning in late April, with most colony sites being occupied in May and early June, but colonies can begin as late as early July. Some colony sites are occupied synchronously by 75–100% of the eventual residents that arrive within periods as short as 4 days, while other sites (especially early-starting ones) gradually accumulate residents over a period of up to 2 weeks (Brown & Brown, 1996). Most colonies have completed nesting by late July. The species winters in southern South America, primarily Argentina (Brown et al., 2017), a one-way distance (from our study area) of approximately 9600 km between the breeding and wintering areas.

Study Site

We studied cliff swallows near the Cedar Point Biological Station (41.2097°N, 101.6480°W) in western Nebraska, U.S.A., along the North and South Platte rivers. The study area includes all of Keith County and portions of 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 defence against predators or by sharing information on the whereabouts of food (Brown & Brown, 1996). Typically, all the nests on a given bridge or road culvert constituted a colony. In rare cases, nests in different culverts that were as close as 0.1 km were considered separate colonies because adjacent residents did not interact, although most colonies were at least 0.5 km from the next nearest. Colony size varied widely, from two to 6000 nests (mean \pm SE: 404 ± 13 , $N = 2318$ colonies), with some birds also nesting solitarily. The distribution of colony sizes in the population showed some annual variability, but there was no long-term change in the annual colony size distribution over the course of our 30-year study (Brown et al., 2013). We use the term 'colony' to refer to the birds occupying a structure in a given year, whereas 'colony site' refers to the physical substrate. GPS coordinates of all colony sites were determined from Google Earth, and straight-line distances between them calculated from the coordinates using the Geographic Distance Matrix Generator software (http://biodiversityinformatics.amnh.org/open_source/gdmg/). The spatial distribution of colony sites is illustrated in Brown et al. (2013).

Field Methods

We used mark–recapture data collected over a 30-year period, 1983–2013, in which we banded 229 167 cliff swallows and had 407 900 total bird captures in mist nets during that time at up to 40 different colony sites each year (Brown, Brown, Roche, O'Brien, &

Page, 2016). Birds were captured by putting nets across the entrance of highway culverts or along the sides of bridges that contained swallow colonies, or by dropping nets over a bridge from above. Swallows were caught as they exited their nests. We rotated among the accessible colony sites, netting at each several times each season (Brown, 1998; Brown & Brown, 2004b; Roche, Brown, Brown, & Lear, 2013), and over the summer, we typically captured 10–60% of the residents at a colony. In some cases, birds were caught at multiple colony sites within a single season. We used the pattern of multiple recaptures to assign each individual as a resident breeder at a given colony site (Roche, Brown, & Brown, 2011). For birds caught at multiple colony sites within a season, we categorized a bird as resident at a colony if (1) it was caught at the same colony multiple times prior to 20 June or (2) it was caught previously at a different colony but switched to its resident colony prior to 20 June and was caught at least twice there. Cliff swallows caught at multiple colonies after 20 June were not assumed to be residents at any of those colonies. Additional details and rationale for using the 20 June cutoff date are given in Roche et al. (2011).

Birds were sexed by the presence or absence of a brood patch or cloacal protuberance, and all received a USGS numbered band for permanent identification. Each bird was given a relative age score that denoted the minimum number of years it was known to have been alive at the time of capture. An adult bird that was unbanded upon first capture was at least 1 year old and assigned a relative age of '1'. Comparison of annual survival and recapture probabilities for birds of relative age (as defined here) and those of actual known age (obtained from banding of nestlings and juveniles) showed similar results, indicating that relative age is a useful index of true age (Roche et al., 2013). Because our focus here is on breeding dispersal, cliff swallows banded as nestlings or juveniles were not included in this study unless also caught as adults (in which case we knew their exact age).

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 (from inspecting nest contents) or by estimation based on nest counts of portions of a colony site or the number of birds present at a site (Brown & Brown, 1996; Brown et al., 2013).

Some colony sites in the study area were fumigated each year to remove ectoparasitic swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*) as part of other research (Brown & Brown, 1986, 1996, 2004a). Swallow bugs are the major nest parasite of cliff swallows. At 7–10-day intervals throughout the breeding season, nests were lightly sprayed with a dilute solution of Dibrom, an organophosphate insecticide that is highly effective against swallow bugs (Brown & Brown, 2004a; Runjaic, Bellovich, Brown, & Booth, 2017). Fumigated colonies were considered separately in all analyses, and comparison of site fidelity in fumigated and nonfumigated colonies was used to investigate the effect of ectoparasites on site fidelity.

Ethical Note

Birds were captured, handled, banded and released under authority of the Bird Banding Laboratory of the United States Geological Survey (permit 20948) and a series of Scientific Permits from the Nebraska Game and Parks Commission (most recently, permit 1033). All animal use was approved by a series of Institutional Animal Care and Use Committees of Yale University, the University of Nebraska-Lincoln, and primarily the University of Tulsa (most recently, under protocol TU-0020).

Multiple Regression Analyses

We performed multiple regression analyses of site fidelity for individuals and for colony sites. Both types of analyses used

instances in which a bird caught as a breeder at a colony site in one year was captured again as a breeder somewhere in the study area the next year. If a bird was captured in more than 2 successive years, all of its pairs of consecutive years were used and treated as independent observations. Our total data set consisted of 45 219 observations of 36 375 different individual birds. While an analysis that treated the individual as a random effect would have been ideal (Dingemanse & Dochtermann, 2013), such models were too computationally intensive (Cam et al., 2013) to be practical for a data set as large as ours.

We did not try to incorporate survival, recapture or movement probabilities into estimates of site fidelity due to the statistical complexity of the resulting models (these parameters can each vary with a specific colony site). Birds present in the first year but not found the second year were assumed to have died during the intervening year, dispersed out of the study area or were present but not detected at a colony within the study area. Estimating the fraction of individuals in these categories was beyond the scope of this study. In general, the likelihood of recapturing a cliff swallow that was present in the study area in a given year was about 15–50%, depending on the year, site, annual recapture effort and method of netting (Roche et al., 2013), and annual apparent survival was 0–80% depending on year and colony size (Brown et al., 2016). Here we use the terms site fidelity and philopatry synonymously, referring generally to the return of birds to a specific colony site, although capitalized PHILOPATRY is a colony level measure specifically of the percentage of the previous year's residents that returned to that colony site the next year (Table 1).

For individual level analyses, we modelled factors affecting whether a cliff swallow exhibited site fidelity (i.e. returned to the colony site where it was captured and presumably bred the previous year) or whether it was known not to have returned because we captured it somewhere else. We used return or not as a dependent categorical variable (MOVE) in a logistic regression and a set of independent variables (Table 1) as fixed effects. To control for nonindependence of observations from a given colony site, the site the bird used in its first year (FSITE) and to which its return was measured the subsequent year was treated as a random effect. Logistic regression was performed with Proc GLIMMIX in SAS (SAS Institute Inc., Cary, NC, U.S.A.).

The analysis of whether an individual returned to the same site used only birds that occupied in the first year a site that was again active (at least one active nest) the next year. Birds from sites that were completely vacant the next year were deemed to not have been potentially able to choose their previous year's site, possibly because of unknown factors that rendered it grossly unsuitable for any occupancy. However, for analyses of factors affecting the distance moved by dispersing birds (DIST), we used all individuals that did not return to their previous colony site, including those from sites unused the second year (but included occupancy status of the previous site as a fixed effect; SITEUSED; Table 1), and again modelled the colony site in the first year (FSITE) as a random effect. Analyses involving distance were performed with Proc MIXED in SAS.

A colony level analysis was used to explore site-related features that might cause some colony sites to attract more site-faithful birds than others. The dependent variable (PHILOPATRY; Table 1) was the percentage of past residents returning to a site the second year among all those from that site recaptured anywhere the second year. The extent to which a site changed in colony size between years, CHANGE, was defined as the colony size in the second year at the site divided by the size the first year (Table 1). If the site was unchanged in size between the 2 years, the CHANGE value was 1.0, if smaller the second year, <1.0; and if larger, >1.0. Our measure of how much a colony site had been recently used was the number of consecutive years a site had been occupied by cliff swallows (i.e. at

Table 1
Variables used in studying colony site fidelity in cliff swallows

Variable	Description
Individual level analyses	
FSITE: colony site the first year	Physical site a bird used during the first year of its 2-year capture history and the reference site to which site fidelity was measured
MOVE: whether a bird returned to the site it used the previous year	Categorical variable (yes/no) and the dependent variable denoting site fidelity, measured only for birds recaptured somewhere in the study area the second year
SEX: sex	Male or female
AGE: minimum age	A measure of relative age, defined as the minimum number of years the bird was known to be alive at the time of each capture. Adult birds banded upon first capture were age class 1
FSIZE: colony size the first year	Colony size (no. of nests) during the first year of a 2-year capture history
FFUM: fumigation status the first year	Whether a site was fumigated (yes/no) in the first year of a 2-year capture history
SSIZE: colony size the second year	Colony size (no. of nests) during the second year of a 2-year capture history
YEAR: year	First year of a bird's 2-year capture history
DIFF: difference in colony size	Second-year colony size minus first-year colony size (no. of nests)
SITEUSED: status of a site the second year	Whether the site was used by any birds (yes/no) the second year
FUMMOVE: fumigation and movement status	Categorical variable denoting (yes/no) the fumigation status of the colony the second year and whether a bird moved to that site; e.g. a bird moving to a nonfumigated site would be N_Y
DIST: distance moved by dispersers	Straight-line distance (km) between sites a bird used both years; denoted as 0 for birds returning to the same colony site
Colony level analyses^a	
PHILOPATRY: percentage of recaptured birds from a site that returned to that same site	Measure of site fidelity for a colony site (dependent variable). The numerator was the number of birds recaptured the next year at the same site, and the denominator was all birds from that site recaptured anywhere the next year
CHANGE: change in colony size at a site between the first and second years for a site active both years	Calculated as the size of the colony in the second year divided by the size in the first year; a site with no change in size was 1, those declining in size were <1 and those increasing were >1
YRSUSED: number of consecutive years a site had been occupied by cliff swallows in the years immediately prior to the first year	Measure of how traditionally a site was used; larger numbers indicated more consecutive years of use prior to when PHILOPATRY was measured
DATE: date a colony was initiated in the second year	The date when birds were first observed at a site in the spring; see Brown and Brown (2014)

^a FSITE and YEAR, as defined in the individual level analyses, were also used in the colony level analyses.

least one active nest present) prior to the first (the focal) year (YRSUSED; [Table 1](#)). If a site had been unused the previous year, it received a 0; the number of consecutive years a site had been previously occupied varied from 0 to 30. Only sites that were active both years and were netted both years were included in the colony level analysis. Colony site the first year (FSITE) was modelled as a random effect to account for nonindependence of the same site between years, and Proc MIXED was used for this analysis. In all individual and colony level linear and logistic regression analyses (see above), we used all biologically reasonable combinations of independent predictor variables in constructing the candidate set of models, from which the best-fitting one was selected based on the lowest Akaike information criterion (AIC) value. That model is presented and used for inference.

For a subset of nonfumigated colony sites in which annual colony initiation date (when the site was first occupied; sensu [Brown & Brown, 2014](#)) was known, we included initiation date (DATE) in the model to explore whether the extent of philopatry at a site changed between colonies that started relatively early or late within a season. Dates refer to the time when the colony at a site was initiated in the second year. We did not have precise initiation dates for enough fumigated colonies to analyse DATE for them.

For another subset of colonies for which we knew average reproductive success, defined as the number of cliff swallow nestlings surviving to 10 days of age per nest ([Brown & Brown, 1996](#); [Brown et al., 2000](#); [Brown, Roche, & Brown, 2015](#)), we explored whether the extent of philopatry was related to overall nesting success at a site. This analysis was done at the colony level only, because we did not have extensive data on which adults occupied which nests. Because of a relatively small number of colonies for which reproductive success was known, we used a univariate Spearman correlation test for this analysis (Proc CORR SPEARMAN) and did not include this variable in any multivariate models.

Multinomial Logistic Regression

We used multinomial logistic regression to explore and visualize specifically how colony size and ectoparasitism potentially affected site fidelity in cliff swallows. Multinomial logistic regression is an extension of logistic regression in which more than two outcome events are allowed for in the dependent (i.e. response) variable and when those responses cannot be ordered in a meaningful way (e.g. low, medium or high).

In our analysis, the dependent response variable (Y) was a bird by year index (i) of the outcome event for bird $_k$ in the second year of its capture history. We allowed for four possible outcome events, depending on whether the site was fumigated the second year and whether it was the same site the individual had occupied the previous year. Each outcome event can be thought of as the result of responding to a series of two yes/no questions (outcome events = no. of answers^{no. of questions} = $2^2 = 4$; [Table 2](#)). This yielded a total of eight outcome events, with each of the four ([Table 3](#)) possible at either a nonfumigated or a fumigated site in the first year. Multinomial logistic regression requires one of the outcome events be designated the 'confrontation category', and all other outcomes are separately regressed against this designated category.

Table 2

Description of how outcome events were determined in the multinomial logistic regression used to study site fidelity in cliff swallows

Questions	Answers			
1. Was the colony site bird $_k$ occupied the second year fumigated?	No	Yes		
2. Was the colony site bird $_k$ occupied the second year different from where it resided the first year?	No	Yes	No	Yes
Outcome event:	NN	NY	YN	YY

Table 3

Sample sizes (number of unique birds by year) for outcome events (Table 2) by the site's fumigation status in the first year (FFUM)

Outcome event	Was the colony site bird _k occupied the first year fumigated (FFUM)?	
	No	Yes
NN	4194	155
NY	12 454	6622
YN	17	18 947
YY	6964	2359

We designated outcome event 'NN' (Table 3) to be the confrontation category.

We assumed that the probability of each of the four outcome events could be influenced by three independent variables: (1) the fumigation status of the colony site that bird_k occupied the first year (FFUM; Table 1); (2) the size of the colony that bird_k occupied the first year (FSIZE; Table 1); and (3) the difference in colony size between the sites that bird_k occupied during the first and second years (DIFF; Table 1). We incorporated an additive association between the response variable and each independent variable and an interactive effect between DIFF and FSIZE. The multinomial logistic regression model was built using package 'nnet' in program R (Venables & Ripley, 2002).

$$\ln \frac{\Pr(Y_i = \text{YN})}{\Pr(Y_i = \text{NN})} = \beta_1 \times \text{FFUM}_i + \beta_2 \times \text{DIFF}_i + \beta_3 \times \text{FSIZE}_i + \beta_4 \times \text{DIFF}_i \times \text{FSIZE}_i \quad (1)$$

$$\ln \frac{\Pr(Y_i = \text{YY})}{\Pr(Y_i = \text{NN})} = \beta_1 \times \text{FFUM}_i + \beta_2 \times \text{DIFF}_i + \beta_3 \times \text{FSIZE}_i + \beta_4 \times \text{DIFF}_i \times \text{FSIZE}_i \quad (2)$$

$$\ln \frac{\Pr(Y_i = \text{NY})}{\Pr(Y_i = \text{NN})} = \beta_1 \times \text{FFUM}_i + \beta_2 \times \text{DIFF}_i + \beta_3 \times \text{FSIZE}_i + \beta_4 \times \text{DIFF}_i \times \text{FSIZE}_i \quad (3)$$

We did not include effects of sex, age, or year in the multinomial regression. Doing so would have made these models computationally burdensome and difficult to present in a coherent way. Furthermore, because effect sizes of these variables were generally small (see Results), inclusion of them in the more complex multinomial regressions would probably not have yielded much additional insight.

Bootstrapping and Cross-validation

The large sample size ($N = 45\,219$) meant that the error associated with any of the parameter estimates was small. Under these circumstances, the standard error estimate indicates how well the model may fit this specific data set, but does not allow conclusions about the variability resulting from sampling. Additionally, the error reported may be underestimated if any assumptions are violated when building the models. To better capture the true sampling variability surrounding the parameter estimates, we conducted a nonparametric bootstrapping analysis. We sampled the real data set with replacement 1000 times, fitted the multinomial regression to each nonparametric bootstrapped sample, and approximated 95% confidence intervals (CIs) for each parameter estimate using the bootstrap percentile method. To explore the

relationship between the model covariates and the probability of bird movements, we generated prediction curves based on each model fit for the bootstrapped data solved at mean parameter values (Table 4), and approximated 95% CIs for the predictions using the bootstrap percentile method.

The predictive accuracy of the multinomial logistic model was assessed with a k -fold ($k = 10$) cross-validation analysis on the bootstrapped data. We randomly divided each bootstrapped data set into k subsets. For each of $k = 10$ iterations, we combined $k - 1$ of the subsets and treated this as the 'training' data with which we fitted the multinomial logistic regression. We then generated fitted response values using this model and the remaining k th 'test' subset. We compared the fitted response values to the actual values from the test data set using the 'effects' package in program R (Fox, 2003) and computed accuracy as $1 - [\text{the mean number of times fitted response values failed to match actual values}]$. The mean accuracy across each iteration of the k -fold cross-validation analysis was computed and then computed again for each of the 1000 bootstrapped samples. The 95% CIs for model accuracy were approximated using the bootstrap percentile method.

RESULTS

The overall observed site fidelity for cliff swallows occupying nonfumigated sites was 24.6% ($N = 17\,325$ individuals) and for fumigated sites, 68.5% ($N = 27\,894$). Overall male philopatry at nonfumigated sites was 26.4% ($N = 10\,164$) and female philopatry was 22.0% ($N = 7161$). At fumigated sites, overall male philopatry was 68.4% ($N = 15\,682$) and female philopatry was 68.7% ($N = 12\,212$).

Effects of Sex, Age and Year

Whether an individual returned to its breeding colony site or dispersed elsewhere in the study area was significantly influenced by sex, year and age for nonfumigated sites, although effect sizes of year and age were small (Table 5). Site fidelity at fumigated sites was significantly predicted by year and age but did not vary with sex (Table 5). Individuals generally showed decreasing philopatry over time, which seemed to be the case for both sexes and at both nonfumigated and fumigated sites (Fig. 1). There was a significant curvilinear relationship between site fidelity and year at nonfumigated sites (Table 5), with the lowest levels from about 1996 to 2006 (Fig. 1).

Site Level Effects

For nonfumigated sites that were active and sampled by us in successive years ($N = 315$), the percentage of residents that were

Table 4

Mean parameter estimates with SE, used to generate prediction curves in the multinomial regression analysis of how site fidelity varied with colony size and ectoparasitism in cliff swallows

Variable	Outcome event		
	NY	YN	YY
FFUM (No)	0.817 (± 0.0412)	-9.67 (± 0.375)	-2.26 (± 0.0558)
FFUM (Yes)	3.38 (± 0.124)	1.51 (± 0.139)	1.19 (± 0.135)
DIFF	9.34×10^{-4}	2.44×10^{-3}	4.69×10^{-3}
FSIZE	$(\pm 6.69 \times 10^{-5})$	$(\pm 1.11 \times 10^{-4})$	$(\pm 8.33 \times 10^{-5})$
	4.37×10^{-4}	3.95×10^{-3}	2.28×10^{-3}
DIFF * FSIZE	$(\pm 8.89 \times 10^{-5})$	$(\pm 1.11 \times 10^{-4})$	$(\pm 1.05 \times 10^{-4})$
	-4.31×10^{-7}	1.86×10^{-6}	-1.06×10^{-6}
	$(\pm 7.18 \times 10^{-8})$	$(\pm 1.03 \times 10^{-8})$	$(\pm 8.49 \times 10^{-8})$

Each parameter estimate reflects the change in log-odds relative to the baseline outcome event (NN).

Table 5

Logistic regression analysis of whether an individual cliff swallow exhibited site fidelity between years (MOVE) in relation to potential predictor variables at non-fumigated and fumigated colony sites in the first year

Variable	β (\pm SE)	P	Odds ratio (95% CI)
Nonfumigated sites (N=17 325 birds)			
SEX ^a	-0.243 (\pm 0.041)	<0.0001	0.784 (0.724, 0.849)
AGE	0.0839 (\pm 0.0147)	<0.0001	1.087 (1.057, 1.119)
YEAR	-18.284 (\pm 2.016)	<0.0001	1.005 (1.004, 1.006)
YEAR ²	0.00457 (\pm 0.00050)	<0.0001	
DIFF	-0.00115 (\pm 0.00004)	<0.0001	0.944 ^b (0.940, 0.947)
Fumigated sites (N=27 894 birds)			
SEX ^a	0.0374 (\pm 0.0268)	0.162	1.038 (0.985, 1.094)
AGE	0.342 (\pm 0.0120)	<0.0001	1.409 (1.376, 1.442)
YEAR	-0.0295 (\pm 0.0023)	<0.0001	0.971 (0.967, 0.975)

All models with other combinations of variables were poorer fits (≥ 6.0 AIC). Colony site the first year (FSITE) was modelled as a random effect. No interaction terms remained in the final model.

^a In relation to male as baseline.

^b 50 units offset from the mean; all others, 1 unit.

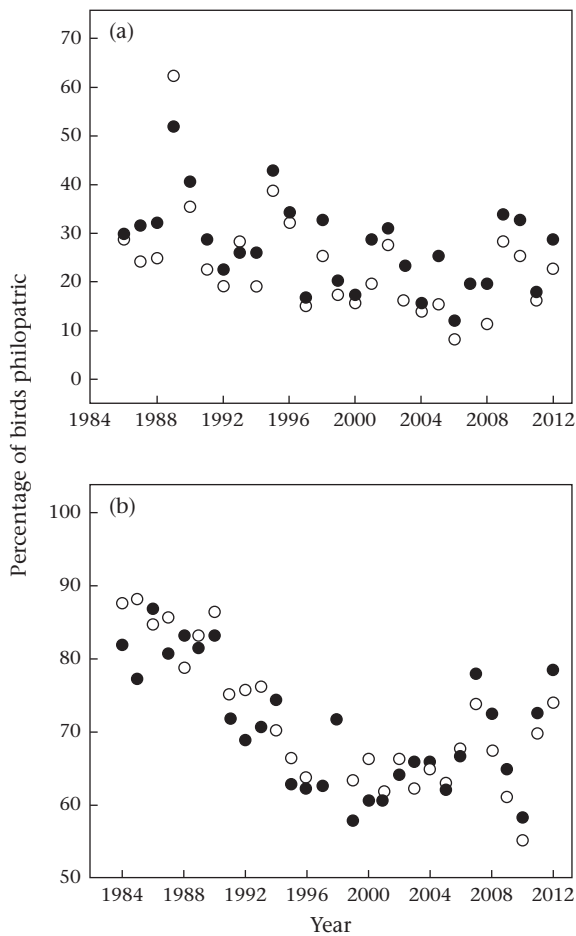


Figure 1. Percentage of individual cliff swallows exhibiting site fidelity (MOVE = no) between years for each season, males (●) and females (○), at (a) nonfumigated and (b) fumigated colony sites. Only birds occupying a site the first year that was also active the second year were included in this analysis.

site-faithful the next year was significantly predicted by both the colony size change (CHANGE) at a site and year, with the best model incorporating a quadratic effect of both variables (Table 6). For size change, the nonlinear coefficient was negative (Table 6), indicating the highest level of philopatry at nonfumigated sites that changed the least in size between the 2 years (Fig. 2a). The nonlinear

Table 6

General linear model analysis of the percentage of the recaptured residents from a site that exhibited fidelity to that site the next year (PHILOPATRY) in relation to potential predictor variables at nonfumigated and fumigated colony sites

Variable	β (\pm SE)	P
Nonfumigated sites (N=315 colonies)		
CHANGE	3.72 (\pm 0.983)	0.0002
CHANGE ²	-0.170 (\pm 0.0573)	0.003
YEAR	-318.47 (\pm 90.15)	0.0005
YEAR ²	0.0795 (\pm 0.0225)	0.0005
Fumigated sites (N=61 colonies)		
CHANGE	24.70 (\pm 6.77)	0.0007
CHANGE ²	-7.59 (\pm 1.77)	<0.0001
YEAR	-302.69 (\pm 70.61)	<0.0001
YEAR ²	0.0751 (\pm 0.0177)	0.0001
YRSUSED	1.789 (\pm 0.985)	0.076

All models with other combinations of variables were poorer fits (≥ 6.0 AIC). Colony site the first year (FSITE) was modelled as a random effect. No interaction terms remained in the final model.

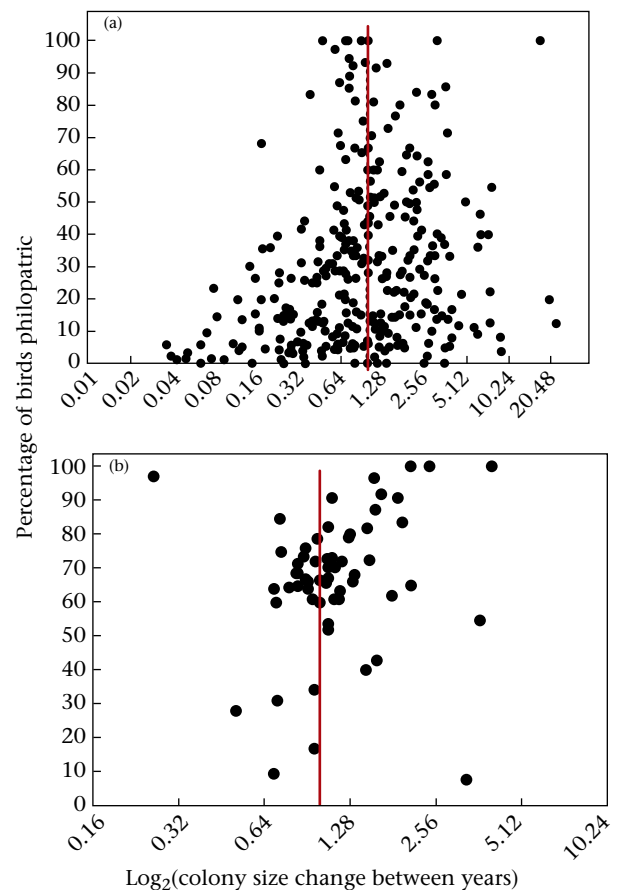


Figure 2. Percentage of a colony site's residents that returned to that site the next year (PHILOPATRY) in relation to the change in colony size (CHANGE) between years (see text) for (a) nonfumigated and (b) fumigated colony sites. Sites that did not change in size between years had a change of 1.0 (denoted by red line), sites that decreased, <1.0 and sites that increased, >1.0. Change is presented on a log₂ scale for clarity.

coefficient for year was positive (Table 6), showing some support for the curvilinear effect at nonfumigated sites that was suggested by the individual level analysis (Fig. 1a). We found the same statistical result for fumigated colonies (Table 6), although the pattern was less obvious (Fig. 2b), probably because the sample of fumigated sites ($N = 61$) was smaller. The frequency of a site's previous use (YRSUSED) had no effect on the extent of philopatry observed at nonfumigated colonies: an identical model but including YRSUSED

had an AIC 24.4 higher than the best model (Table 6). Similarly, at fumigated colonies, the number of previous years of use had no significant effect on the extent of philopatry (Table 6).

Using the subset of sites for which annual colony initiation date was known in the second year, we found similar effects of colony size change and year, and initiation date was also a significant predictor of the extent of philopatry ($\beta = -0.212$, $SE = 0.0927$, $N = 255$, $P = 0.023$). Nonfumigated sites that started earlier in the year had higher site fidelity than those beginning later in the season.

There was no evidence that the extent of site fidelity was related to average annual reproductive success at a colony for either non-fumigated sites ($r_s = 0.28$, $N = 9$ colonies, $P = 0.46$) or fumigated sites ($r_s = 0.20$, $N = 17$ colonies, $P = 0.44$), using only sites that the birds used and that we netted at both years.

Effects of Colony Size and Ectoparasitism

Averaged across all nonfumigated sites, the mean (\pm SD) colony size (FSIZE) for birds in this study was 533 (\pm 506) nests (range 2–3500), and the mean difference in colony size a bird occupied between years (DIFF) was 243 (\pm 732) nests (range -2920–2965).

For birds from fumigated sites, the mean colony size was 1428 (\pm 465, range 5–2350), and the mean difference in colony size was -216 (\pm 582; range -2343–3160).

For nonfumigated sites, the difference in size between the colonies a bird occupied between years was significantly associated with whether it was site-faithful (Table 5). As the size difference became greater, a bird was less likely to be philopatric. The odds ratio indicated that for each increase in 50 nests in the size difference, a bird had a 5.6% less chance of being philopatric (Table 5). However, for fumigated sites, the best model did not include any colony size metric (Table 5).

The multinomial regression modelled the choices birds made (the outcome events; Table 3) explicitly in relation to the colony size the first year (FSIZE), the extent of size change between years (DIFF) and fumigation status of colonies in both years. There were very few instances where a cliff swallow stayed at the same colony site between years and the site switched from being nonfumigated to fumigated, and vice versa (Table 3). Thus, here we disregard these cases and focus on the six (of the possible eight) outcome events (Table 3) where we had relatively large sample sizes.

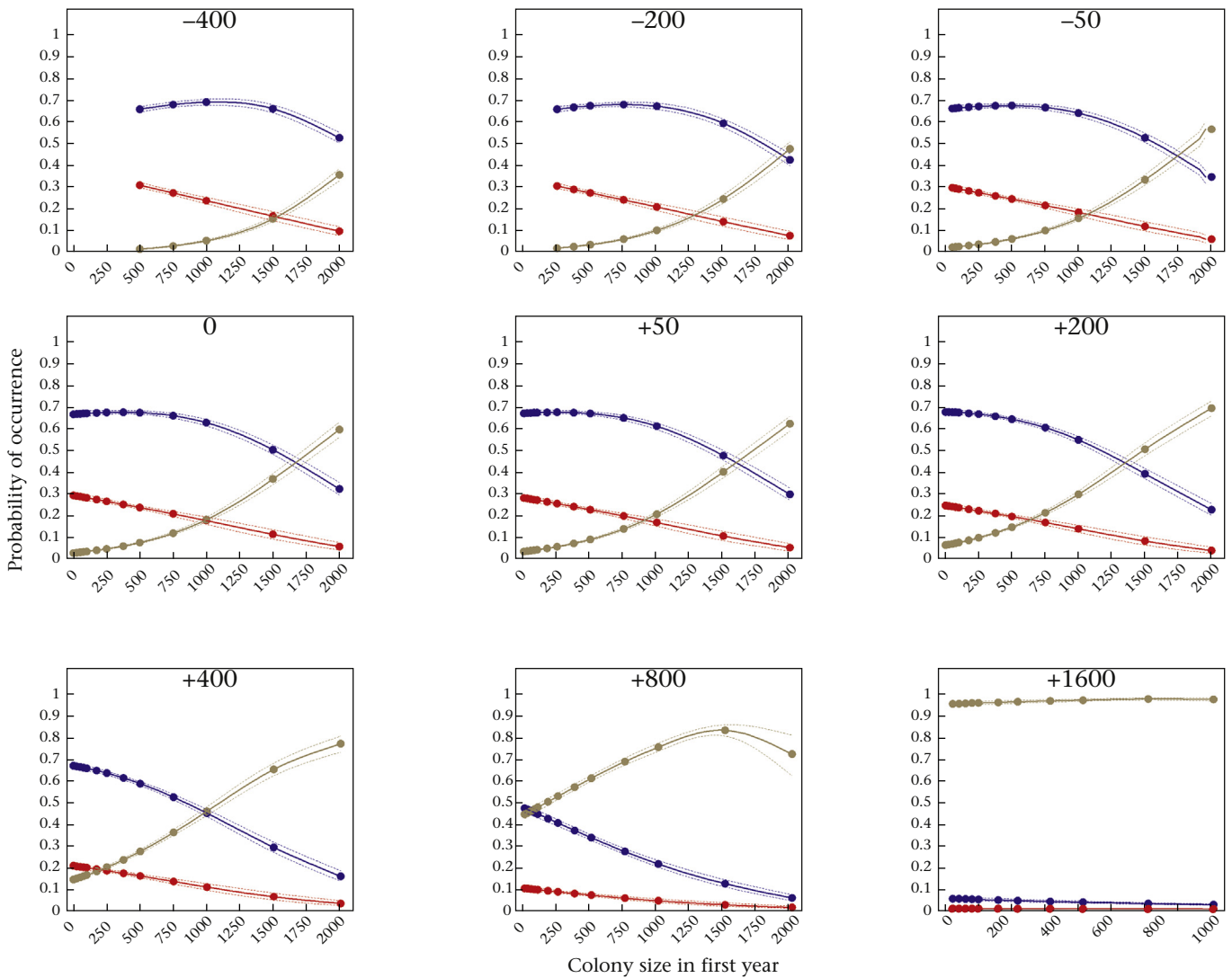


Figure 3. For individuals making colony size changes of from -400 to +1600 nests between years, the predicted probability (from multinomial regression) that the given size change occurs when a bird remains at the same nonfumigated site (red), moves to another nonfumigated site (blue), or moves from a nonfumigated to a fumigated site (gold) in relation to colony size in the first year (number of nests). Sexes were combined. Solid lines show predicted probabilities, dotted lines the 95% confidence intervals of the predicted probabilities.

The results of the k -fold cross-validation analysis indicated that the multinomial logistic regression model accurately predicted the correct responses for the test data sets with a probability of 0.788 (95% CI: 0.784–0.791). Thus, we used the predicted results to explore the probability of the three possible outcome events, respectively, for colonies of different sizes that were either non-fumigated or fumigated in the first year. We used nine different representative colony size changes between years (DIFF) to reflect the range of size changes possible and for which we had enough birds to estimate the outcomes (–400, –200, –50, 0, +50, +200, +400, +800, +1600). For colonies of different sizes and fumigation status in the first year, the model generated predicted probabilities of the three possible outcomes for individuals that made a given size change between years (Figs 3, 4).

Among birds at nonfumigated sites, regardless of whether birds were changing colony sizes by –400 to +200 nests between years, the probability of philopatry for that outcome declined in approximately linear fashion with the first-year colony size (red curves in Fig. 3). The probability of movement to other nonfumigated sites that differed from –400 to +200 nests was about the same for birds

in colony sizes up to about 750 nests the first year, then declined for larger colonies (blue curves in Fig. 3). The probability of birds moving from a nonfumigated to a fumigated site between years (regardless of size change) increased dramatically with the first-year's colony size (gold curves in Fig. 3). In general, for birds changing colony sizes by +400 to +1600 nests, few such birds were philopatric, and the probability of site fidelity in such instances clearly declined with the first-year's colony size (Fig. 3). The probability of a size change of +400 to +1600 nests even for birds moving to other nonfumigated sites was low, and thus most instances in which cliff swallows chose much larger colonies the next year involved birds moving to fumigated colonies.

Among birds at fumigated sites, those that were in relatively small colonies the first year (up to about 250 nests) that changed sizes by –400 to +200 nests the next year were most likely to have moved to a nonfumigated site (blue curves in Fig. 4). Moving out of a fumigated colony to a nonfumigated site of any colony size was unlikely if the first-year's fumigated colony was large (>1000 nests). The converse was true for site fidelity: birds in large fumigated sites the first year tended to stay there, regardless of how the

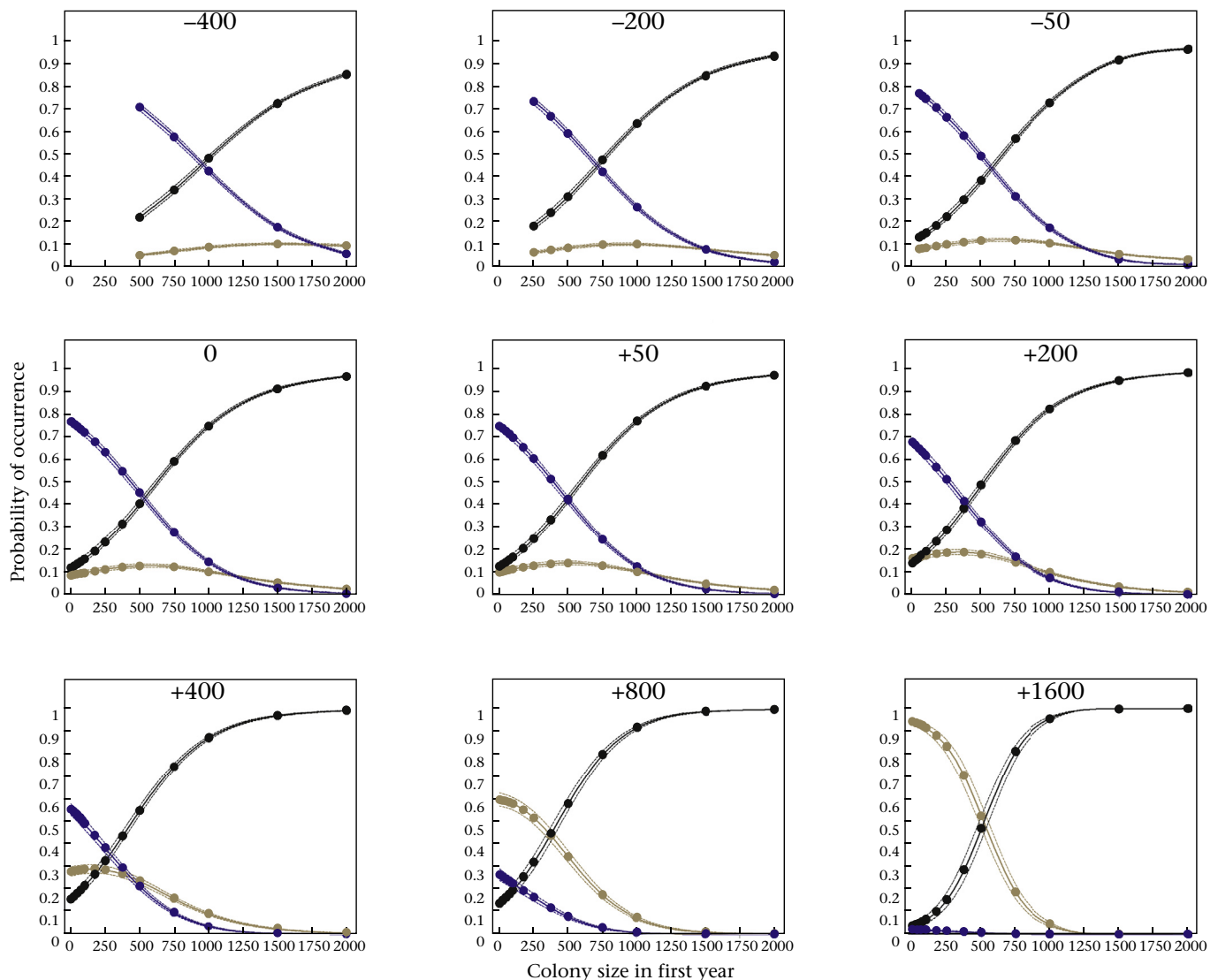


Figure 4. For individuals making colony size changes of from –400 to +1600 nests between years, the predicted probability (from multinomial regression) that the given size change occurs when a bird remains at the same fumigated site (black), moves to another fumigated site (gold) or moves from a fumigated to a nonfumigated site (blue) in relation to colony size in the first year (number of nests). Sexes were combined. Solid lines show predicted probabilities, dotted lines the 95% confidence intervals of the predicted probabilities.

size may have changed between years (black curves in Fig. 4). The probability of moving from a fumigated site to a different fumigated site was low for all size changes, except for ones involving a large size change, in which case those birds tended to mostly be ones moving from small fumigated colonies (gold curves in Fig. 4).

At nonfumigated sites, colony sizes in the 2 years for birds that were site-faithful were strongly correlated (males: $r_s = 0.58$, $N = 2682$, $P < 0.0001$; females: $r_s = 0.63$, $N = 1578$, $P < 0.0001$). The correlation was weaker (although still significant, probably due to the large sample size) for birds that were nonphilopatric between years (males: $r_s = 0.16$, $N = 11059$, $P < 0.0001$; females: $r_s = 0.17$, $N = 8286$, $P < 0.0001$). Fumigated sites showed a similar result, with site-faithful birds exhibiting significant and much stronger correlations in colony size between years (males: $r_s = 0.66$, $N = 10727$, $P < 0.0001$; females: $r_s = 0.66$, $N = 8392$, $P < 0.0001$) than those that moved to another site (males: $r_s = 0.01$, $N = 5026$, $P = 0.52$; females: $r_s = -0.02$, $N = 3881$, $P = 0.26$), in which the correlations were not significant.

Distances Moved

Cliff swallows whose previous year's (nonfumigated) site was unused the second year ($N = 6286$) moved a mean (\pm SE) 3.28 (± 0.049) km, compared to 3.44 (± 0.037) km for birds whose previous year's site was active ($N = 13072$); the difference was not significant (Wilcoxon test: $Z = -1.02$, $P = 0.31$). In addition, the variable denoting whether a site was used the second year (SITEUSED; Table 1) was not included in the final model for DIST (Table 7). Thus, we used all birds dispersing from their previous year's site, regardless of its active status the second year, for the distance analyses.

Birds not philopatric to their previous year's colony site tended to move to sites generally within 6 km of the previous year's site (Fig. 5). For those moving from nonfumigated sites ($N = 19346$), 87.4% settled <6 km from their previous year's site, and 88.7% of those from fumigated sites ($N = 6602$) chose nonfumigated sites within 6 km. No birds moved between fumigated sites within 1 km of each other, because no fumigated colony had a neighbouring colony site that close to it. The longest distances that we detected a bird dispersing between years within the study area were two males moving 107 km (both from the same colony to the same colony in the same year) and a female moving 104.5 km, all from nonfumigated to nonfumigated sites. One female moved 63.5 km from a nonfumigated to a fumigated site. The overall distributions of settlement distances for nonphilopatric birds were largely the same regardless of whether their previous year's site was fumigated or not (Fig. 5).

Table 7

General linear model analysis of the distance between colony sites occupied by a nonphilopatric cliff swallow in consecutive years (DIST) in relation to potential predictor variables at nonfumigated and fumigated colony sites in the first year

Variable	β (\pm SE)	P
Nonfumigated sites (N=19 342 birds)		
SEX ^a	0.0922 (± 0.0502)	0.066
AGE	-0.0944 (± 0.0208)	<0.0001
FUMMOVE ^b	-1.32 (± 0.0057)	<0.0001
Fumigated sites (N=8907 birds)		
AGE	-0.279 (± 0.0354)	<0.0001
YEAR	-0.0272 (± 0.0076)	0.0003
FUMMOVE ^b	0.662 (± 0.0963)	<0.0001

All models with other combinations of variables were poorer fits (≥ 3.1 AIC). Colony site the first year (FSITE) was modelled as a random effect. No interaction terms remained in the final model.

^a In relation to male as baseline.

^b In relation to birds moving to a fumigated colony (YY).

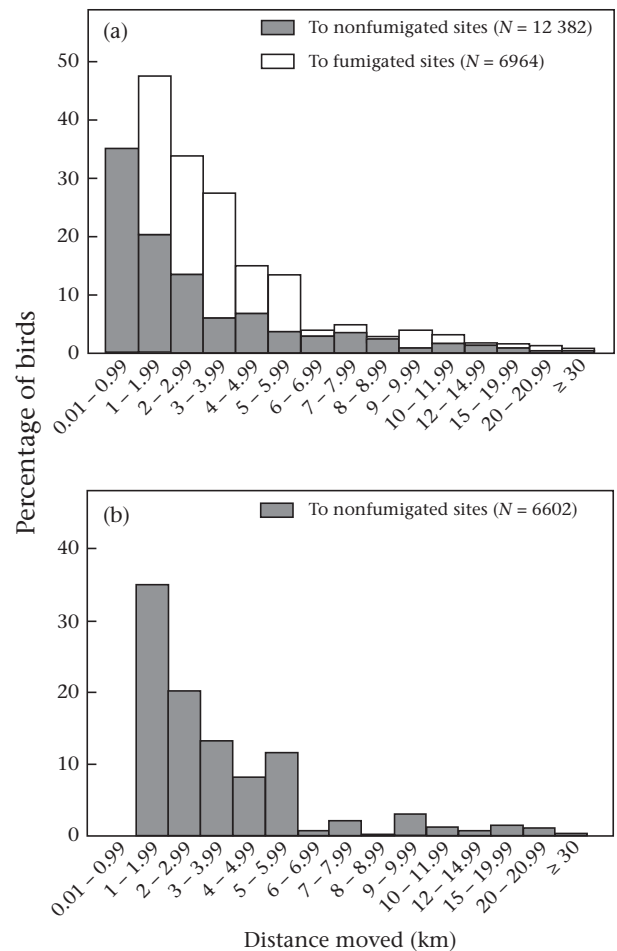


Figure 5. Percentage distribution of distances (km) between the pair of colony sites a cliff swallow occupied in successive years for (a) those moving from a nonfumigated site to another nonfumigated site (grey bars) and from a nonfumigated site to a fumigated site (light bars); and (b) those moving from a fumigated site to a nonfumigated site. Birds moving between two fumigated sites are not shown due to a small number of such sites. Sexes were combined.

For nonfumigated sites and using only nonphilopatric birds, the distance moved the next year was significantly affected by an individual's age and the fumigation status (FUMMOVE) of the colony moved to (Table 7). The age effect was largely due to birds of the first age class ($N = 15898$) moving further (3.16 ± 0.035 km) than birds of all other age classes ($N = 7732$) combined (1.98 ± 0.031 km). Birds dispersing to other nonfumigated sites ($N = 12391$) did not move as far (3.05 ± 0.039 km) as those ($N = 6966$) going to fumigated sites (3.98 ± 0.044 km). Neither colony size (of the first-year's site) nor the difference in colony sizes between the sites chosen was included in the final model for distance moved (Table 7).

We found similar results for birds dispersing from fumigated sites, except there was also an effect of year (Table 7). Birds of the first age class ($N = 6593$) moved $4.05 (\pm 0.052)$ km, and those of the older age classes ($N = 2485$) combined moved $3.22 (\pm 0.052)$ km, from fumigated sites. Birds dispersing to nonfumigated sites ($N = 6617$) from fumigated colonies moved $4.04 (\pm 0.053)$ km, while those going to other fumigated colonies ($N = 2301$) moved $3.47 (\pm 0.035)$ km.

DISCUSSION

While this study identified a number of socioecological correlates of site fidelity in cliff swallows, three main conclusions

emerge: (1) individuals that were philopatric were more likely to reside in a colony more similar in size to the one they used the previous year than were birds dispersing to other colony sites; (2) cliff swallows occupying parasite-free colonies were more likely to be site-faithful than those at sites exposed to natural numbers of ectoparasites; and (3) despite these generalizations, there remained extensive variation in individuals' propensity to be site-faithful between years.

Colony Size

Because cliff swallows (especially yearling birds) show heritable preferences for colonies of certain sizes (Brown & Brown, 2000; Roche et al., 2011), individuals should be more likely to be philopatric between years when the colony size at a site was similar to what it had been the previous year. This prediction had some support: birds returning to the same site exhibited less of a between-year difference in colony size than those dispersing; the rank-order correlation between colony sizes in successive years was much stronger for philopatric than for nonphilopatric individuals; and at the colony level, the percentage of residents that returned from the previous year was often greatest at sites that changed the least in size.

However, the direction of any causality between site fidelity and colony size is potentially unclear. Does site fidelity per se determine colony size, or does colony size affect site fidelity? If many birds chose not to reoccupy a colony site in a given year, because it was unsuitable in some way, then we would automatically find a lack of fidelity at sites that were much smaller (or unused) the next year. We attempted to control for this possibility by including in most of our analyses only sites that were occupied by at least some birds both years and thus excluding any birds avoiding sites that were grossly unsuitable. Yet the fact remains that in some cases in which colony size at a site declined drastically between years, we may have seen low philopatry there because birds chose to settle elsewhere to start with and not because the smaller colony size itself deterred them.

Cases in which the colony size at a site was much larger the next year provide a better test of how philopatry might depend on colony size. In these instances, the site was clearly attractive the next year (and there is always unused substrate available at cliff swallow colony sites; Brown & Brown, 1996), yet those sites in general tended to have lower percentages of philopatric individuals. Increases in colony size that are not associated with a higher likelihood of site fidelity (1) argue against increased philopatry causing the size increase, (2) suggest that past residents are not using the same cues to select a breeding site as site-naïve birds (Brown et al., 2000) and (3) are consistent with cliff swallows' avoidance of colonies that differ too much in size from what they occupied in the previous year.

Site fidelity being lower at sites that host much larger colonies the next year suggests that past residents are not using the presence of others (sensu 'conspecific attraction'; Stamps, 1988; Safran et al., 2007) to select sites. Conspecific attraction mechanisms assume that larger colonies should be more attractive, but our analyses show that larger colonies are not necessarily preferred by residents familiar with a site from an earlier year and especially if the colony size there had been small. Past residents have potentially more and/or better information about a site than naïve settlers, and might use this knowledge to reject a site. Larger colonies could still be most attractive to uninformed individuals that rely more on collective decision making (Forbes & Kaiser, 1994; Giraldeau, Valone, & Templeton, 2002; Russell & Rosales, 2010). There is evidence that cliff swallows exhibit some level of conspecific attraction (Brown & Rannala, 1995), reflected in part in larger colonies

having greater percentages of yearling birds than do the smaller colonies (Brown, Roche, & Brown, 2014). That site-naïve birds gravitate to larger colonies is also consistent with our finding here of dispersing, nonphilopatric individuals tending to choose (or be attracted to) colonies larger than the one they used the previous year.

In addition to conspecific attraction, individuals may assess the performance of conspecifics, probably by monitoring their reproductive success at a site the year before, and use that to select breeding sites in the current year (Danchin et al., 1998; Danchin & Wagner, 1997; Safran et al., 2007). Sites that are more successful one year thus attract more birds the next. Patterns of colony size change between years in relation to reproductive success suggested this mechanism might apply to cliff swallows (Brown et al., 2000).

However, the earlier analysis (Brown et al., 2000) did not include information on whether marked birds based their site choice on reproductive success. Our current analysis of philopatry suggests little effect of reproductive success on site choice: the percentage of philopatric residents did not vary significantly with average colony reproductive success, and sites that grew the most in size between years (presumably the most successful ones the year before) had relatively low levels of individual site fidelity. Because past residents should also be likely to return to sites that were successful and that thus grew in size between years (Danchin et al., 1998), our results do not suggest that these birds are relying on past performance per se at a colony site in their habitat selection.

Ectoparasitism

The most striking result in our study was the higher percentage of birds (by about 2.8 times) that were site-faithful between years to fumigated sites where ectoparasites were removed. These sites also changed less in size between years than nonfumigated sites. Cliff swallows assess the presence of swallow bugs in nests and use that information to select existing nests within a colony to occupy (Brown & Brown, 1986) and which nests to brood-parasitize (Brown & Brown, 1991). The results reported here suggest that birds also use the presence/absence of bugs to select colony sites and more readily reuse sites from the previous year when bug numbers there are low. This difference in site fidelity between fumigated and nonfumigated sites suggests that the lower philopatry in general among nonfumigated colony sites may be directly related to the presence of ectoparasites at those sites.

Previous work on other populations suggested that cliff swallows are sensitive to ectoparasites and avoid colony sites when they become infested (Chapman & George, 1991; Earle, 1985; Emlen, 1986; Grinnell, Dixon, & Linsdale, 1930; Loye & Carroll, 1991). Usage histories of some Nebraska sites are also consistent with this scenario (Brown et al., 2013). However, other colony sites are used by cliff swallows perennially despite the presence of swallow bugs each year; some are vacant even when bugs have declined to almost total absence; and still others show unpredictable annual use. If bugs have an important role in determining the extent of site fidelity at nonfumigated sites, we would predict a negative relationship between the frequency of consecutive year use and philopatry. As a site is used in successive years, swallow bug populations increase (Page, 2016), and thus cliff swallows should be less likely to return the more a site has been continually occupied. Yet, we found that the extent of prior year use (a proxy for ectoparasitism) had no effect on site fidelity at the colony level for nonfumigated sites.

Fumigated sites possibly had higher levels of philopatry in part because they varied less in size between years than most nonfumigated colony sites. Philopatric birds at fumigated colonies experienced an average change in colony size of only about -9

nests, compared to about –95 nests for philopatric individuals at nonfumigated sites. If these birds are sensitive to colony size in making settlement decisions, as we argued above, sites with a predictable colony size from year to year may be especially attractive to past residents.

The fumigated sites also tended to be larger, on average, than nonfumigated sites. By reducing the number of deleterious bugs (which tend to increase in larger colonies; Brown & Brown, 1986, 1996) and thus preventing continually increasing bug infestations that can eventually lead to complete colony collapse, the fumigation may have allowed the fumigated sites to perennially collect large numbers of cliff swallows that were ‘large colony’ phenotypes (sensu Brown & Brown, 2000). Being a predictable rallying point for such individuals, birds were more likely to return there each year. In such a scenario, individuals would be responding to the perennially large colonies present there (i.e. to colony size) and not to the presence/absence of bugs per se. Cliff swallows predisposed to colonies of this size (>1000 nests) would also have fewer sites to choose from and might have to travel further, on average, to find them, since such colonies are disproportionately rarer than the smaller colonies (Brown, 2016). Increased philopatry could thus reflect the difficulty in resettling at other very large colonies and the fact that perennial fumigation allowed such sites to retain stable large colonies on a regular basis. The same constraints may have applied to birds from nonfumigated sites that sought very large colonies (for whatever reason) the next year: these birds tended to switch to one of the fumigated sites and not to other nonfumigated colonies. The relatively few birds dispersing from fumigated colonies tended to choose ones much smaller, on average, perhaps in part because those individuals were not suited to large colonies (Brown, Brown, Raouf, Smith, & Wingfield, 2005).

Other Correlates of Site Fidelity

For colony sites under natural conditions (i.e. nonfumigated colonies), only about 25% of birds, on average, were site-faithful, and colony sites with a similar extent of size change between years often had widely different proportions of philopatric residents. Had we included birds from sites that were completely vacant the second year, the overall percentage of site-faithful residents would have been even lower. Thus, site fidelity was subject to extensive variation, and more cliff swallows changed sites between years than did not. One cause of this pattern could be the unpredictability of colony size at a given site from year to year (Brown et al., 2013), especially if colony size figures into settlement decisions (see above).

Relatively high philopatry might be expected in general, given that Brown et al. (2008) detected within-year survival advantages during the nesting season for cliff swallows occupying the same site they had used the previous year, and survival was lowest for naïve immigrants using a site for the first time. The survival results (Brown et al., 2008) imply an advantage associated with being familiar with a specific locale, probably a common benefit for site-faithful animals (Bonte et al., 2012; Piper, 2011). However, most birds dispersing from their previous year's site settled within 6 km, and at least on a landscape level, they may still have been using habitat (e.g. for foraging; Brown, Sas, & Brown, 2002) with which they were generally familiar. For example, during bad weather when insect food is scarce, cliff swallows sometimes forage up to 4 km from their colony site (Brown & Brown, 1996), implying that they probably have some familiarity with the habitat that contains most of the colony sites to which between-year dispersers move. If site fidelity is defined at the landscape level, rather than solely by return to a given nesting structure, adult cliff swallows could be considered to show relatively high philopatry, which would also be

the case for natal philopatry in first-year birds (Brown & Brown, 1992, 2000; Roche et al., 2011).

Spatially restricted dispersal to neighbouring sites may also facilitate the maintenance of associations between the same individuals between years. Such nonrandom associations may have important but still largely unknown consequences for understanding population dynamics and habitat selection in general. In slender-billed gulls, *Chroicocephalus genei*, which show very low philopatry to certain colony sites, the same individuals stay together more than expected by chance when moving to a new site (Francesiaz et al., 2017). We have not yet analysed associations among dispersing birds in cliff swallows. However, one benefit of being with the same individuals across years could be that all members of the group have similar colony size preferences and thus they can more easily form a colony of the preferred size without size fluctuations caused by the frequent comings and goings of others with different preferences. Stable colony membership across years and sites can result in higher reproductive success than in groups with more strangers (Francesiaz et al., 2017).

Male cliff swallows showed slightly but consistently higher philopatry than females at nonfumigated sites. This may reflect the fact that males arrive earlier than females in the study population (Brown & Brown, 1996). While males may thus have greater choice in sites to occupy (including their previous year's site) by virtue of being among the first to settle, they may also not have as good information on the eventual colony size at their chosen site. Colonies can fluctuate in size over several days after initial settlement, and a definitive colony size may not be established for a week or more. Females, coming later, may have better information on a site's likely colony size (if only by judging the number of males there). They are likely to be choosing sites not only by colony size but also by assessing nest sites and male quality, and females spend more days selecting colony sites than do males (Brown & Brown, 1996). For these reasons, females may be more likely to find a site other than the one they previously occupied that better meets their needs. That there was no sex-related difference in philopatry at fumigated sites is consistent with birds at such sites being more inherently limited in finding other similarly large colonies.

Over the course of our 30-year study, we found evidence for a curvilinear relationship between year and the percentage of philopatric birds. A potential explanation is that the period of lowest site fidelity (from about 1996 to 2006) was in the aftermath of a major weather-related mortality event in the study area in 1996 (Brown & Brown, 1998) that reduced the population by at least 53%. The population did not fully recover in size until about 2001 (Brown et al., 2013). During this time, colony sizes averaged smaller. Site fidelity may have been lower as more birds sought the larger colonies, which were few, and this may have forced more birds to move away from last year's site.

Despite the curvilinear relationship, there was still evidence for a slight overall decline in site fidelity in cliff swallows during the study. This may reflect both an increasing number of potential colony sites over time and an increasing percentage of those sites that are occupied each year (Brown et al., 2013). The number of sites has increased as new bridges or culverts have been constructed throughout the study area. An increase in cliff swallow population size over the 30 years in western Nebraska (Brown & Brown, 2013; Brown et al., 2013) and the Great Plains more generally has led to colonization of many sites and an increase in mean colony size over time. A consequence has been that an individual now probably has a greater choice of nearby active sites, and possibly more large ones, than were available when our research began. Studies on other species have shown that availability of nesting (or roosting) sites is a key determinant of philopatry (Grandi et al., 2008; Kokko et al., 2004; Lewis, 1995; Lucia et al., 2008), and a similar decline in site

fidelity with increasing colony size over time was found in storks, *Ciconia ciconia* (Itonaga, Köppen, Plath, & Wallschläger, 2011).

Dispersal Distance

The distances moved by nonphilopatric cliff swallows to the next year's colony site show a typical sort of dispersal distance curve (Koenig, Van Vuren, & Hooge, 1996; Wiens, 2001), with a strong bias towards short dispersal distances and then a declining tail of very far distances. In many species, this pattern reflects researcher effort at locating dispersers, which often tends to be centred in a localized (finite) study area, as well as an increasing number of potential occupancy sites (which cannot all be monitored) as one moves further away from a given point (Baker, Nur, & Geupel, 1995; Barrowclough, 1978).

In our case, for two reasons the dispersal distance distribution is likely to reflect less detection bias than in other studies. (1) For colonial birds like cliff swallows, all potential breeding sites (i.e. bridges, culverts) in any given area can be identified, and our long-term work in the study area (Brown & Brown, 1996; Brown et al., 2013) and in regions adjacent to it has led us to knowing where virtually all potential colony settlement sites are located. There were no additional sites where birds might have gone undetected regardless of distance moved within the study area. (2) We regularly netted at 75% of the colony sites throughout the western two-thirds of the study area (a region of about 50 × 125 km), and thus we were as likely to detect the longer range dispersal events as the shorter ones within that portion of the study area.

If we assume no severe dispersal distance bias, at least within most of the study area, our results suggest that cliff swallows in fact often settle at or near (<6 km) their previous year's site. As noted earlier, this may reflect fitness advantages associated with familiarity with the landscape near last year's colony site (Brown et al., 2008) or the facilitating of associations among the same individuals between years. What causes the rarer, longer distance movements, however, is less clear. One possibility is that long-distance dispersers are seeking colony sites they could not find closer to the previous year's site. For example, the two birds dispersing the furthest (107 km) both moved from a 175-nest colony in 2008 to a 31-nest colony in 2009. That year, there were only two similarly sized colonies (both 30 nests) closer to the previous year's site than the one chosen, and there were only two additional colonies within 10 nests (20–40) in size that were closer. If these individuals had relatively stringent size requirements in 2009, they may have had relatively little choice but to move far. This could be modulated in part by stress hormones, if these birds had been in the 'wrong' colony size (i.e. one too large) the first year (Brown et al., 2005).

Conclusions

Theoretical work on colony size dynamics has suggested that selection for philopatry may be a key driver in maintaining long-term use of particular colony sites (Matthiopoulos et al., 2005; Schwager, 2005). When dispersal to another breeding site is constrained (e.g. because of being rare and hard to find, too far away or risky to reach), philopatric individuals may concentrate at a few perennially used sites even though fitness there is reduced (Kildaw, Irons, Nysewander, & Buck, 2005; Matthiopoulos et al., 2005; Russell & Rosales, 2010; Schippers et al., 2011; Schwager, 2005). Varying the costs of dispersal by changing the distances between potential colony sites may alter the colony distribution. The large number of cliff swallows (75%) in our study that moved somewhere else between years suggests that constraints on dispersal are unlikely at nonfumigated sites and that colony distributions probably

do not reflect difficulty in assessing and dispersing among sites under natural conditions. However, the experimental removal of ectoparasites, by perennially clustering birds into very large colonies at a few sites, may have created the sort of constraints (with respect to the very large colonies) described by Matthiopoulos et al. (2005) and Schwager (2005), and therefore support the real-world applicability of their models.

Colony choice in cliff swallows, as in other well-studied colonial birds (Brown et al., 2003; Fasola et al., 2002; Francesiaz et al., 2017; Serrano et al., 2004, 2001; Serrano & Tella, 2007), is a complex phenomenon. Its components include a heritable basis for choice of colony size for yearling breeders (Brown & Brown, 2000), advantages associated with site familiarity (Brown et al., 2008), attraction to conspecifics per se (Brown et al., 2000, 2014; Brown & Rannala, 1995), hormonal responses to stress (Brown et al., 2005), and colony size sorting based on phenotypic traits such as body size and propensity to be ectoparasitized (Brown, 2016; Brown & Brown, 1996). To these, we now add another component, site fidelity.

Because cliff swallows often return to the general vicinity of where they bred the previous year (this study) and over 60% of colony sites are occupied in consecutive years (Brown et al., 2013), many birds are faced with the choice of whether to settle at the same (active) colony site they used the previous year. Here we have identified correlates of that choice. The principal conclusion is that philopatry will often depend on whether the colony that forms there (perhaps often through collective decision making; Brown & Brown, 1996) is similar in size to last year's; if it is widely different in size, philopatry is less likely. Paradoxically, for those birds dispersing, they then often change colony sizes even more drastically. Where possible, site fidelity should be advantageous, through familiarity with the local environment around a colony site (Brown et al., 2008) and/or because colonies with certain attributes (e.g. the very large colonies at fumigated sites) are rare and hard to locate should one disperse elsewhere.

The picture that emerges suggests that cliff swallows are probably sensitive to both colony size and general familiarity with either a given site and/or a specific landscape region, and they superimpose these two factors on other cues (e.g. annual presence of ectoparasites, opportunities to reuse old nests at a site) used to select breeding sites. Individuals could value colony size versus habitat familiarity to different extents, depending on age, sex, experience or other characteristics (Brown et al., 2008; Roche et al., 2011). This variation between individuals may ultimately lead to the patterns of site fidelity observed in cliff swallows and perhaps other colonial species and help explain the variable levels of philopatry often observed in field studies.

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