

Ecological correlates of group integrity among dispersing cliff swallows

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Abstract. Breeding colonies of birds represent groups of individuals that associate during one breeding season, at least partially dissociate for the non-breeding season, and may re-associate the next year through collective settlement at another breeding site. Little is known about the extent to which colonial birds maintain group integrity when occupying different sites in different years or the benefits of long-term associations among colonial individuals. For cliff swallows (*Petrochelidon pyrrhonota*) in western Nebraska, USA, we examined ecological correlates and potential benefits associated with group integrity. Using a dataset of over 25,000 individuals, we found that associations between dispersing cliff swallows were greater than would be predicted by purely random settlement among colony sites. The extent of group integrity varied widely among sites, with birds seeming to settle together more often at sites with fewer ectoparasites and at colonies similar in size and closer in physical proximity to the one they had previously occupied. Some associations of birds lasted three years in which they used a different site each year. Successful colonies had higher levels of group integrity among their settlers than did colonies that failed completely. Cliff swallows that were known to have settled with at least one conspecific from the previous year's site had a higher survival the next year than those not known to have settled with past residents. The results are consistent with cliff swallows choosing colonies based in part on parasite load and with sorting among colonies based on the birds' preferences for colonies of certain sizes.

Key words: cliff swallow; coloniality; dispersal; familiarity; group living; habitat selection; *Petrochelidon pyrrhonota*; social behavior.

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INTRODUCTION

Breeding colonies provide many opportunities for animals to associate in both space and time and potentially develop familiarity with each other. With colony sites fixed in space and often re-occupied in successive years (McNicholl 1975, Buckley and Buckley 1980, Forbes and Kaiser 1994, Spendelov et al. 1995, Danchin and Wagner 1997, Brown et al. 2013), the colony

itself can represent a collection of individuals who may have associated together in the past at either that site or another one. Particularly in cases where colonies represent non-random sorting of individuals based on phenotypic characteristics such as age, propensity to be parasitized, or personality traits (Spottiswoode 2007, Pruitt et al. 2011, Dardenne et al. 2013, Brown 2016), perennial associations among group members may facilitate collective selection of

either a physical breeding site and/or a social group of similar phenotypic composition. When reliable cues to a site's quality (e.g., old nests, prior experience, conspecific presence; Brown 2016) are unavailable, individuals might more likely trust the collective wisdom of the group (Conradt and Roper 2005, Pinter-Wollman et al. 2009) if some members are familiar to them. Because most colonial vertebrates are relatively long-lived, many colonial birds and mammals potentially have opportunities to maintain associations with the same individuals in successive years.

The dissolution of colonies at the end of each nesting season and the re-formation of colonies the next year represent a fission–fusion system of social organization that has been well studied in primates and bats and (to a lesser extent) in a few birds (Aureli et al. 2008, Popa-Lisseanu et al. 2008, Silk et al. 2014). Most of the existing work has been done on foraging groups or other aggregations not tied to a specific place (Byrne 2000, Greenberg 2000, Strandburg-Peshkin et al. 2015), and we know almost nothing about the extent to which breeding colonies remain together from year to year, especially among individuals not philopatric to the previous year's colony site. Anecdotal evidence showed that in three species of North American terns (*Sterna* spp.), individuals from one colony site settled together at another colony site the next year, sometimes nesting in close proximity to each other (Austin 1951, Haymes and Blokpoel 1978, Gochfeld 1979, Massey and Fancher 1989, Spindel et al. 1995). In the only systematic study of group integrity in a colonial species, groups of slender-billed gulls (*Chroicocephalus genei*) that had nested together and presumably had some familiarity with each other often settled together at a new site the next year, and groups were more likely to stay together if reproduction had been successful at the previous year's site (Francesiaz et al. 2017).

As part of a comprehensive effort to understand colony choice in highly social cliff swallows (*Petrochelidon pyrrhonota*; Brown and Brown 2000, Brown et al. 2002, 2005, 2013, 2016, 2017a), here we explore the extent to which groups of individuals from one colony site remain together at another colony site in successive years. Our study focuses solely on individuals that settled at

a colony site different from the one that they occupied the previous year. We recognize that by using only birds dispersing away from the previous year's colony site, we are using a subset of birds that potentially differ (e.g., with respect to past reproductive success; Brown and Brown 1996) from ones that are philopatric to last year's site. However, because we were interested in the determinants and potential advantages of group integrity, we elected to confine our analyses only to birds that moved physical locations. While philopatric individuals may also benefit in various ways from being with familiar group members, there are important advantages associated with site familiarity per se (McNicholl 1975, Isbell et al. 1993, Hoogland et al. 2006, Brown et al. 2008, Piper 2011) that complicate analysis of group integrity among site-faithful birds. Correlates associated with philopatry at the individual level have been explored previously for cliff swallows (Brown et al. 2017a), and in this study, we test whether the same factors (and others) predict group integrity among dispersing birds. Because so many colony sites of different sizes and characteristics (>200) are available each year to cliff swallows in our population (Brown et al. 2013), individuals have multiple opportunities to either settle with or without birds from their previous year's site.

Cliff swallows are sensitive to both colony size and extent of parasite load at a colony site in making settlement decisions (Brown and Brown 1996, 2000, Brown et al. 2005, 2017a, Roche et al. 2011), and thus, we emphasize these variables in studying group integrity. Our objectives are to ask whether individuals settle at other colony sites non-randomly with respect to other birds from their previous colony, and whether the extent of group integrity among dispersing birds is related to factors such as the size or the extent of parasite load at either the origin or destination colonies and the distance between colony sites. We also explore whether broad measures of reproductive success at a site influence the extent of group integrity, and whether group integrity is correlated with annual survival or with colonies that are ultimately more successful. Our study is unique in that it uses a large dataset of over 25,000 marked individuals recaptured in at least two successive years at different colony sites.

METHODS

Study animal and study site

The cliff swallow is a migratory, sparrow-sized passerine bird found commonly throughout the Great Plains and westward to the Pacific coast of North America (Brown et al. 2017b). In its ancestral habitat, the species built its gourd-shaped mud nests underneath horizontal overhangs on the sides of steep cliffs, but now many cliff swallows nest under the sides of bridges and buildings or inside concrete culverts underneath roads (Brown et al. 2013). The birds arrive in our study area beginning in late April, with most colony sites being 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 d, while other sites (especially early-starting ones) gradually accumulate residents over a period of up to two weeks (Brown and Brown 1996). Most colonies have completed nesting by late July. The species winters in southern South America, primarily Argentina (Brown et al. 2017b), a one-way distance (from our study area) of approximately 9600 km between the breeding and wintering areas.

We studied cliff swallows near the Cedar Point Biological Station (41.2097°N, 101.6480°W) in western Nebraska, USA, along the North and South Platte rivers. The study area includes portions of Keith, Garden, Deuel, Lincoln, and Morrill counties. Our work was done primarily at cliff swallow colonies on highway bridges and box-shaped culverts underneath roads or railroad tracks (Brown et al. 2013). Colonies were defined as birds from groups of nests that interacted at least occasionally in defense against predators or by sharing information on the whereabouts of food (Brown and Brown 1996). Typically, all the nests on a given bridge or 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, ranging from 2 to 6000 nests (mean \pm SE: 404 ± 13 , $n = 2318$ colonies), with some birds also nesting solitarily. 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. Global Positioning System (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/).

Field methods

We used mark–recapture data collected over a 30-year period, 1984–2013, in which we banded ~229,000 cliff swallows with United States Geological Survey bands and had ~405,000 total bird captures in mist nets during that time at up to 40 different colony sites each year (Brown et al. 2016). As swallows exited their nests, they were captured by putting nets across the entrance of highway culverts or along the sides of bridges that contained swallow colonies. In order to achieve roughly equal recapture probability across the study area, we shifted our recapture efforts among accessible colony sites, netting at each several times each season (Brown 1998, Brown and Brown 2004b, Roche et al. 2013). Over the summer, we typically captured 10–60% of the residents at a colony, as inferred from a colony’s capture total and the colony size. Most colonies netted were in a region of about 15×15 km in Keith County (Fig. 1), although the total study area over which netting occurred was about 20×125 km, from near Paxton, Nebraska, to near Broadwater, Nebraska, USA.

We used the pattern of recaptures to assign each individual as a resident breeder at a given colony site (Roche et al. 2011). Individuals caught at only a single colony in a given year were assumed to be residents of that site. For any bird caught at more than one colony site within a season, we categorized it as a resident at a given colony if it was caught at that colony site at least twice prior to 20 June. Cliff swallows caught at multiple colonies after 20 June were not assumed to be residents at any of those sites, due to widespread colony visitation by non-breeding and post-breeding birds later in the summer (Brown 1998). Additional details and rationale for using the 20 June cutoff date are given in Roche et al. (2011).

Colony size in all cases refers to the maximum number of active nests at a site in a season, with

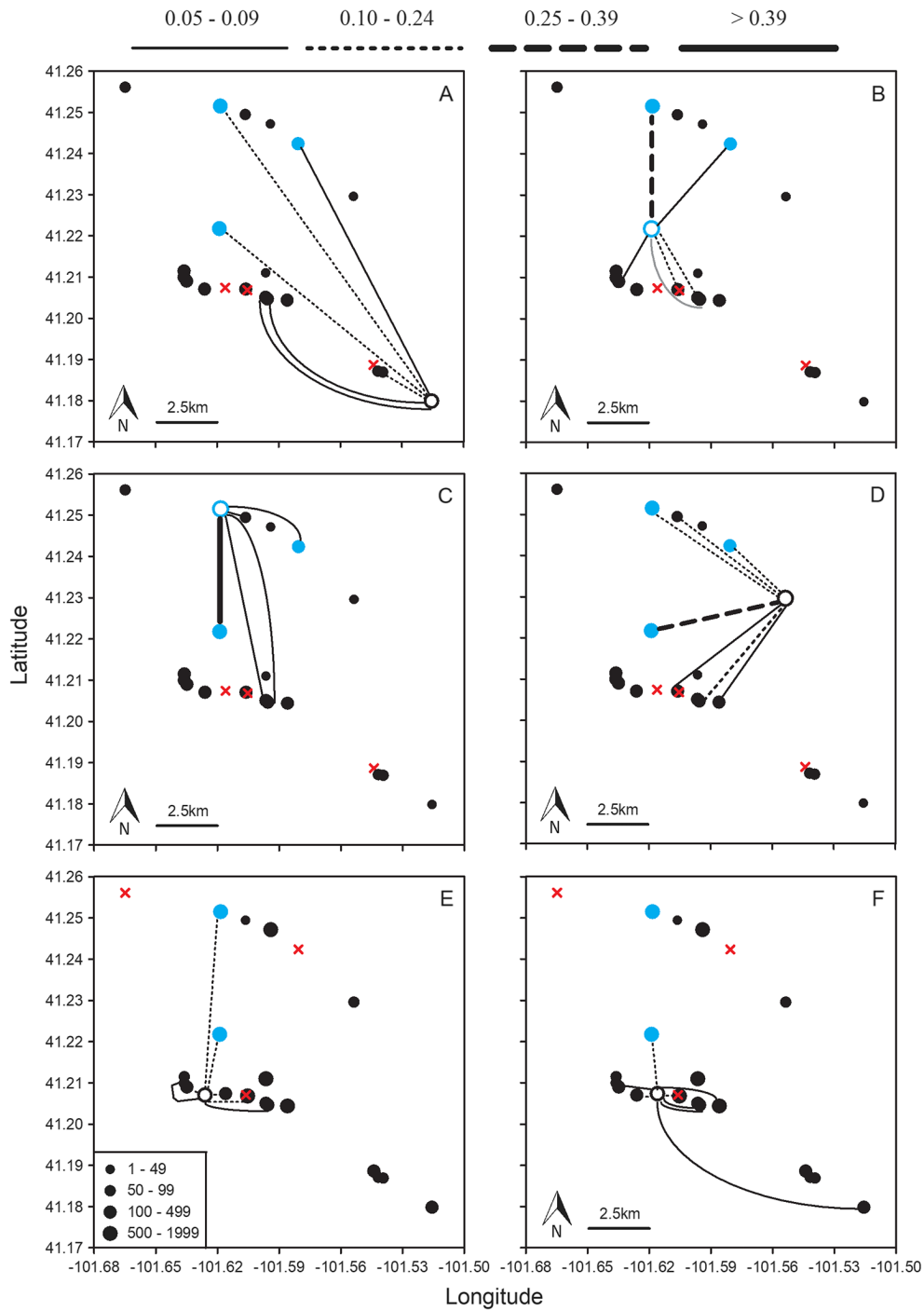


Fig. 1. Spatial positions of cliff swallow colony sites and extent of group integrity for birds moving among them (GRPINTEG) for six representative sites (A–F). Position of the origin colony site is shown with an open circle; the proportion of birds dispersing to each destination site the next year (year $t + 1$) by four different line weights; relative size of each colony (number of nests) by circle size; fumigated sites in blue; and sites unused in year $t + 1$ by a red x.

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 both on nest counts of portions of a colony site and on the number of birds present at a site (Brown and Brown 1996, Brown et al. 2013). Colony reproductive success was measured as whether at least some nests were known to have successfully fledged young (success = yes) or that none was known to have been successful (success = no). Colonies that failed completely were obvious, with all residents completely vacating the site over periods of 2–3 d during the nestling period.

Some colony sites in the study area were fumigated each year to remove ectoparasitic swallow bugs (Hemiptera: Cimicidae: *Cimex vicarius*) as part of other research (Brown and Brown 1986, 1996, 2004a). Swallow bugs are the major nest parasite of cliff swallows. At 7- to 10-d 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 and Brown 2004a, Runjaic et al. 2017). Two colony sites were fumigated each year of this study, while 12 additional ones were fumigated in subsets of one to five years. In analyses, sites were treated as either fumigated or non-fumigated in a given year depending on whether they were sprayed that year, and no lag effects of fumigation were considered. This was justified because only a single spraying at a colony site can effectively eliminate bugs there for the entire season (Runjaic et al. 2017), whereas bugs can rapidly re-colonize a site the year after fumigation (C. R. Brown, *personal observation*).

General statistical methods

Our analyses only used instances in which a breeding bird was captured in two successive years at two different colony sites. For individuals caught in more than two successive years (except for those in the analysis of extended group integrity; see below), we used only the first 2-year capture history to avoid non-independence. This resulted in a total sample size of 25,245 individual birds.

From the two-year capture histories, we identified settlement groups, defined as the birds from

a given origin site in year t that settled at a destination site in year $t + 1$. A given origin site could produce several settlement groups, depending on how many colonies to which its residents dispersed. The number of birds in each settlement group (which ranged from 1 to 130) divided by the number of birds from a given origin site that dispersed anywhere that year (GRPINTEG) was a relative index of group integrity, measuring the extent to which the birds from a given colony remained together at another site the next year.

In analyses of extended group integrity, defined as that extending to three consecutive breeding seasons, we used a subset of birds in which we had records of their colony choice in three successive years and in which they were non-philopatric in each successive pair of years. In these cases, we termed the first colony site in the capture history the origin site and the third colony the destination site. For birds that had dispersed from a site in year t to the same colony site in year $t + 1$, we calculated the proportion that subsequently stayed together to settle at a given destination site in year $t + 2$ (T2INTEG) as a measure of extended group integrity. We could not address group integrity beyond three consecutive seasons due to relatively few non-philopatric birds caught for four or more years in a row.

Modeling random settlement

Following Francesiaz et al. (2017), we calculated the coefficient of variation (CV; standard deviation/mean) of GRPINTEG for each year of the study to examine whether group integrity was non-random among colony sites within the study area. Low CV values represent approximately equal-sized groups of birds dispersing from a given origin site to all available colonies in year $t + 1$, which would suggest that settlement is largely random with respect to birds from the previous year's colony. High CV values represent many birds settling at a particular colony and not at others, suggesting that birds stay together in a non-random way. To test whether the CV values significantly deviated from random, we built a null model comprised of 10,000 randomized versions of our data in which birds randomly settled among active colony sites (Farine and Whitehead 2015, Francesiaz et al. 2017). We calculated a P -value as [the number of times the observed CV value was $>$ the expected CV

value]/10,000, in which $P < 0.05$ was considered to significantly deviate from random (Francesiaz et al. 2017). Coefficient of variation analyses were performed using the raster package (Hijmans 2017) in R 3.4.4 (R Core Team 2017).

Because varying distances between colony sites could result in non-random group integrity if birds are simply more likely to disperse to (or be detected at) colony sites near the origin site, for the CV analysis we used a subset of 22 colony sites located within 15.5 km of each other (Fig. 1). This distance is easily traversed by cliff swallows and is that over which most between-year dispersal typically occurs (Brown et al. 2017a). By using only this group of sites, we minimized the effect of dispersal distance on the detected settlement patterns (Barrowclough 1978, Koenig et al. 1996).

Analyzing group tenacity, colony success, and recapture

We examined ecological factors affecting the measures of group integrity (GRPINTEG, T2INTEG) using mixed models with a set of biologically reasonable independent predictor variables as fixed effects. These variables were identified a priori as likely to be relevant (e.g., Brown et al. 2017a), and we used them to construct a global model for each analysis. Inference was based on the global model, and we did no model selection. A curvilinear effect was investigated for two variables: year, which was known to affect philopatry in a non-linear way (Brown et al. 2017a), and the difference in colony size between the origin and destination sites, because a curvilinear effect would be predicted if birds preferred to settle at sites similar in size to the one they had occupied previously. Biologically plausible interactions among covariates were also included initially, but those that were not significant ($P > 0.05$) were dropped. All continuous predictor variables were standardized ($[x - \bar{x}]/SD$). Because GRPINTEG and T2INTEG were proportions, we logit-transformed these variables in order to fulfill linear modeling assumptions (Warton and Hui 2011). To control for non-independence of observations from a given colony site, the origin site was treated as a random effect in all models involving GRPINTEG or T2INTEG as dependent variables, and the destination site was treated as a random

effect in the analysis of how reproductive success at a destination site varied with GRPINTEG. Mixed-model regression was performed with Proc GLIMMIX in SAS (SAS Institute 2004). Pairs of colony sites in a given year had to have had at least one instance of a bird moving between them to be included (i.e., GRPINTEG = 0 were discarded).

We examined whether group integrity potentially affected individual fitness by modeling the reproductive success of the destination colony as the dependent variable in a mixed model with a set of independent predictor variables as fixed effects (including the average GRPINTEG for all settlement groups at the destination site). A recapture analysis was used to determine whether individuals that had collectively settled with at least one other individual were then re-caught anywhere the following year (i.e., in year $t + 2$). For birds caught in more than two consecutive years, we used only their first two year-pairs in the recapture analysis, because using more than two year-pairs might have introduced a bias toward an overrepresentation of older individuals who could have been more or less likely to be re-caught in more than two years. We restricted our analysis to recaptures only and did not estimate actual survival (sensu Lebreton et al. 1992).

RESULTS

Across all sites and years, group integrity (GRPINTEG) for cliff swallows ranged from 0.002 to 1.000 (mean 0.147, SE \pm 0.003, $n = 4372$ settlement groups). About 58% of settlement groups contained a proportion of all dispersing birds that was less than 0.10, although about 9% of groups had proportions ≥ 0.4 , and 2% of settlement groups consisted of all birds (1.0) detected as dispersing from that colony (Fig. 2). Group integrity varied widely, with some colonies near an origin site attracting relatively large numbers of birds from other sites, while others drew none (Fig. 1), but the overall pattern was one in which most colony sites were connected by at least limited dispersal (Fig. 3, top row). Some sites perennially attracted relatively large proportions of birds from other colony sites, with GRPINTEG > 0.25 (Fig. 3, bottom row). The most attractive colonies were at fumigated sites

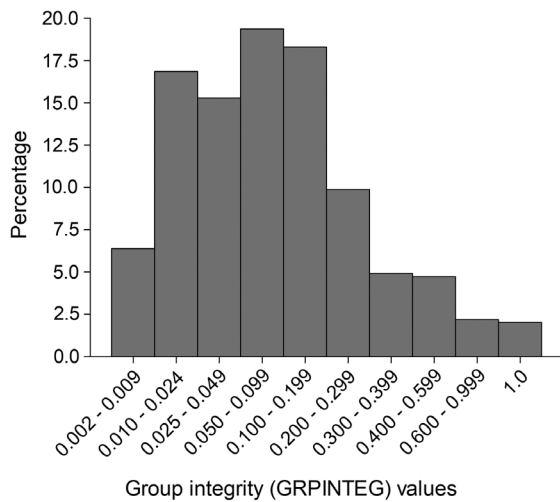


Fig. 2. Percentage distribution of GRPINTEG values (defined as the proportion of all cliff swallows dispersing from an origin site in year t that settled at a given destination site in year $t + 1$). Total settlement groups were 4372. Note different bin sizes on x -axis.

(Fig. 3). Observed CV values (Table 1) were significantly larger than what would be expected by purely random settlement.

Correlates of group integrity

The extent to which the cliff swallows from a given origin site settled together elsewhere the next year (GRPINTEG) was affected most by the fumigation status of the origin and destination site, the distance and difference in size between the origin and destination colonies, the reproductive success of the origin colony in year t , and whether the origin site was used in year $t + 1$ (Table 2). The effect of year was curvilinear (year²), such that the lowest levels of group integrity occurred during the middle years of the study (Table 2). Fumigated destination sites generally had larger values of group integrity than non-fumigated destination sites: Mean (\pm SE) group integrity was 0.124 (\pm 0.003, $n = 3645$ settlement groups) at non-fumigated sites and 0.262 (\pm 0.008, $n = 727$ settlement groups) at fumigated sites.

The extent of group integrity declined as distance between the origin and destination sites increased (Table 2). Group integrity also varied in a curvilinear way with the difference in colony sizes between the origin and destination sites

(Table 2). Group integrity tended to be higher at destination colonies that differed least in size from the origin colony (Fig. 4), with actual colony size at the destination site not having an effect on extent of group integrity (Table 2). There was a significant decrease in group integrity for birds dispersing from sites that were inactive in year $t + 1$ (Table 2). Group integrity increased significantly when the origin site experienced total colony failure the previous year and when a destination colony consisted of a greater proportion of immigrants from the focal colony (Table 2).

Extended group integrity

The proportion of birds from a site that had settled together in both years t and $t + 1$ that subsequently settled together again in year $t + 2$ (T2INTEG) was significantly predicted by whether the sites chosen in both year t and year $t + 2$ were fumigated and the size difference between the colonies chosen in years $t + 2$ and t (Table 3). There was a significant interaction term for the fumigation status of the colony in year $t + 2$ and whether it was the same site the birds had used in year t . For fumigated destination colonies, the mean (\pm SE) proportion of birds associated in years t and $t + 1$ that settled together in year $t + 2$ (T2INTEG) was 0.516 (\pm 0.0357, $n = 37$ settlement groups) when the destination site was the same one as in year t , and 0.298 (\pm 0.0351, $n = 34$ settlement groups) when the site was a different one. For non-fumigated destination colonies, the mean (\pm SE) proportion of birds associated in years t and $t + 1$ that settled together at the same destination site in year $t + 2$ was 0.355 (\pm 0.0696, $n = 20$ settlement groups) when the site was the same one as in year t , and 0.170 (\pm 0.0119, $n = 195$ settlement groups) when the site was a different one.

The magnitude of extended group integrity seemed to be highest when the colonies chosen in year t and $t + 2$ were most similar in size (Fig. 5), although a curvilinear effect of size difference was not significant (Table 3).

Effects of group integrity on colony success and recapture

The reproductive success of a destination colony was significantly predicted by the extent of group integrity of birds dispersing to that site, as

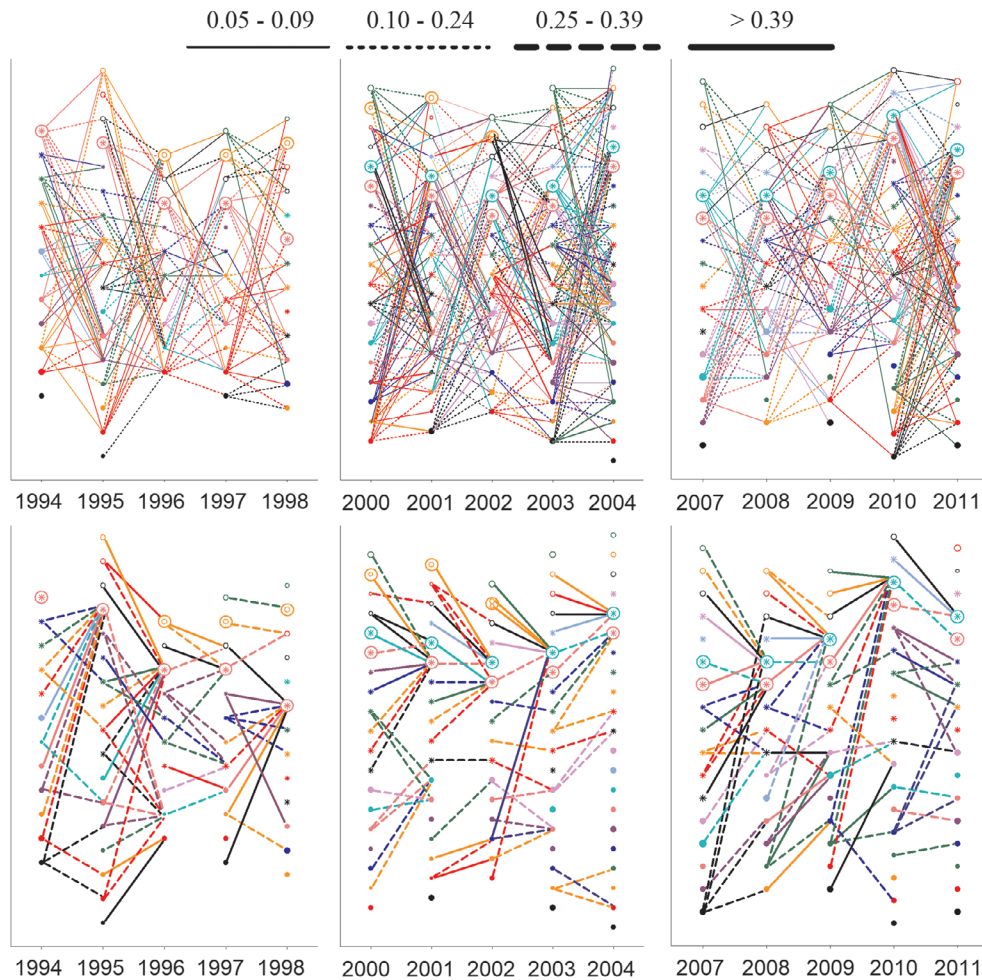


Fig. 3. Proportion of cliff swallows from each colony site settling (GRPINTEG) at each of 22 colony sites in the study area. GRPINTEG values were grouped into four classes, with the top row showing the lower two classes and the bottom row the upper two classes. Each colony site has a unique color and symbol designation; sites not active or not sampled in a given year are not depicted. Relative size of the colony at each site each year is shown by size of the symbol (as in Fig. 1), and sites that were fumigated are circled. Sites are arranged roughly by geographic proximity from east (lower end of y axis) to west (upper end). Representative 5-year blocks (1994–1998, 2000–2004, 2007–2011) from throughout the study period are illustrated.

measured by the average GRPINTEG of the settlement groups at that site; fumigation status of the colony site and year also had a significant effect on success (Table 4). Year exhibited a curvilinear effect (Table 4) opposite that found in the settlement-group analysis (Table 2). Non-fumigated sites that were successful had a greater mean (\pm SE) proportion of birds settling together (0.161, \pm 0.010, $n = 472$ colonies) than did colonies that had complete failure (0.056, \pm 0.023, $n = 37$ colonies). Successful fumigated colonies

had a higher mean group integrity (0.296, \pm 0.030, $n = 63$ colonies) than did successful non-fumigated colonies. There were no unsuccessful fumigated colonies. Colony success was unaffected by a colony's size and the total number of settlement groups (i.e., origin sites) it contained (Table 4).

The percentage of birds that were recaptured in year $t + 2$ that were known to have settled with a bird from their previous colony in years t and $t + 1$ was 18.9% ($n = 22027$ individuals),

Table 1. Measure of annual capture effort (total birds caught in nets during the second year) throughout the study area; number of settlement groups, origin colony sites, and destination colony sites in the network of sites used for the simulation study; and results of simulations to determine whether cliff swallows settled among colony sites randomly between each pair of successive years.

Years	Total net captures	Number settlement groups	Number origin sites	Number destination sites	Observed CV	Expected minimum CV	Expected maximum CV	<i>P</i>
1984–1985	1402	3	3	2	109.54	63.25	109.55	0.004
1985–1986	3007	4	2	4	121.65	62.35	148.07	0.014
1986–1987	4055	16	4	8	149.26	125.32	200.19	0.232
1987–1988	6058	38	8	9	147.31	67.35	128.60	0.000
1988–1989	9518	50	9	9	165.13	79.23	141.90	0.000
1989–1990	11,720	44	9	9	184.62	74.75	123.38	0.000
1990–1991	17,901	67	9	13	167.00	89.52	144.30	0.000
1991–1992	21,272	98	12	14	140.84	57.06	82.18	0.000
1992–1993	19,831	102	13	14	157.72	63.83	118.28	0.000
1993–1994	16,702	109	13	12	135.90	47.85	86.41	0.000
1994–1995	17,553	116	12	17	167.62	78.42	131.98	0.000
1995–1996	11,739	99	17	11	174.19	86.04	136.05	0.000
1996–1997	12,793	71	10	12	152.73	57.41	116.68	0.000
1997–1998	13,291	107	12	18	196.31	100.84	152.36	0.000
1998–1999	17,006	139	18	15	168.50	84.94	131.30	0.000
1999–2000	18,717	153	15	19	180.88	61.31	90.30	0.000
2000–2001	16,401	163	19	19	186.66	78.96	113.68	0.000
2001–2002	19,087	159	18	20	195.56	90.18	133.13	0.000
2002–2003	20,309	176	20	20	246.30	180.25	192.71	0.000
2003–2004	19,815	207	20	21	204.48	119.98	139.63	0.000
2004–2005	16,308	203	21	18	186.32	68.44	106.37	0.000
2005–2006	14,002	153	18	17	184.08	99.20	142.72	0.000
2006–2007	12,862	153	17	20	226.37	145.74	180.32	0.000
2007–2008	13,358	126	17	15	204.45	116.99	148.42	0.000
2008–2009	16,457	123	15	16	189.00	73.86	114.74	0.000
2009–2010	18,828	126	15	18	212.18	127.79	164.80	0.000
2010–2011	16,487	176	18	19	165.68	95.00	147.58	0.000
2011–2012	12,474	140	17	14	171.88	56.84	96.63	0.000
2012–2013	6361	70	13	10	146.51	57.23	96.53	0.000

compared to 13.2% for birds not known to have settled with a bird from their previous colony in years t and $t + 1$ ($n = 1579$ individuals). The difference in recapture percentages was significant ($\chi^2_1 = 32.0$, $P < 0.0001$).

DISCUSSION

The analyses reported here indicate that cliff swallows settle among colony sites between years in a more aggregated fashion than would be expected by purely random settlement at sites. The extent to which colony residents settle together the next year varies widely among colony sites, with some serving as major attractants within the network of colony sites. Group

integrity in general was higher for birds settling at parasite-free sites, at sites relatively close in proximity to the birds' previous colony site, and at colonies that were relatively similar in size to the previous year's colony. Some birds remained together for at least three successive years despite changing colony sites each year, and group integrity conferred apparent survival advantages and may have facilitated choice of colony sites where reproduction was more likely to be successful.

Do groups of cliff swallows from a previous year's site move together and choose a site collectively, or do members of a settlement group independently drift into a site and settle in staggered fashion? In the absence of radio-tracking birds

Table 2. Mixed-model regression analysis of group integrity in cliff swallows (proportion birds from an origin colony site in year t that settled at a destination colony site in year $t + 1$; GRPINTEG) in relation to potential predictor variables†.

Variable	β (\pm SE)	P
Fumigation status of origin site‡	-0.365 (\pm 0.182)	0.045
Fumigation status of destination site‡	-1.112 (\pm 0.0671)	<0.0001
Year	0.0197 (\pm 0.0240)	0.41
Year (squared)	0.207 (\pm 0.0217)	<0.0001
Destination colony size	0.00637 (\pm 0.0504)	0.90
Proportion of immigrants from origin site among all immigrants at destination site	0.108 (\pm 0.0249)	<0.0001
Distance between origin and destination sites	-0.606 (\pm 0.0238)	<0.0001
Difference in colony size (destination minus origin)	0.448 (\pm 0.0549)	<0.0001
Difference in colony size (squared)	-0.101 (\pm 0.0164)	<0.0001
Whether origin colony was successful in year t §	0.372 (\pm 0.0991)	0.0002
Whether origin site was used in year $t + 1$ ¶	-0.146 (\pm 0.0653)	0.025

† Origin colony site was modeled as a random effect, $n = 4057$ settlement groups.

‡ In relation to fumigated as baseline.

§ In relation to origin colony being successful as baseline.

¶ In relation to origin site being used as baseline.

with known histories at the time of settlement (which is not practical), we do not know the answer to this question. However, we do know that cliff swallows initially arrive at sites as a group (Brown and Brown 1996) and that investigation of sites is a social activity engaged in by multiple birds at once. Because most of the residents of a colony tend to settle rather synchronously (Brown and Brown 1996), there is clearly the potential for familiar individuals to travel together and make collective assessments and settlement decisions. In addition, some birds that settle together may have collectively prospected at colony sites the previous year (Brown 1998, Brown et al. 2000) and could rely on that information in deciding where to settle and with whom.

Dynamics of group integrity

With dispersing cliff swallows tending to settle at sites closer to their former sites than at more distant locations (Brown et al. 2017a), group

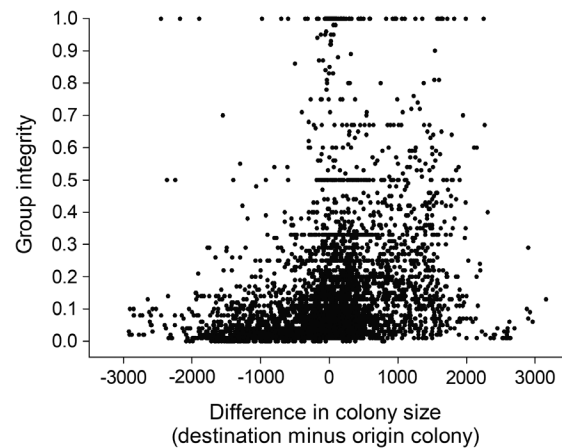


Fig. 4. Group integrity (proportion of all dispersing cliff swallows from an origin colony site settling at a given destination colony site; GRPINTEG) in relation to the difference in size (no. nests) between the destination and origin colonies (destination size minus origin size) for 4372 settlement groups. Points overlap extensively.

integrity should decay with distance from the colony site occupied the previous year. We found this generally to be the case, with distance having an effect independent of other variables. However, we also found that certain sites attracted a large number of settlement groups with relatively high group integrity, while other sites attracted relatively few such groups. This led to a network of colony sites in which group integrity did not depend strongly on linear distance between any two sites (Fig. 3). The implication is that some colonies are inherently more attractive to groups of collective settlers, while at the same time also more likely to provide such groups to other sites. Our challenge, thus, is to identify why colonies at these sites serve as both a destination and a source for collections of birds with higher group integrity.

Parasite-free (i.e., fumigated) colony sites are well known to be attractive to cliff swallows in our population (Brown et al. 2017a), probably because of enhanced reproductive success there (Brown and Brown 1986, 1996). If fumigated sites in general attract more settlers from other colonies, higher group integrity could reflect, in part, simply more birds moving to such sites. Fumigation status, however, could not explain all variation in group integrity, as other variables had

Table 3. Mixed-model regression analysis of extended group integrity in cliff swallows (proportion of birds settling together at a destination colony site in year $t + 2$ that had also settled together at an origin site in year t and at another site in $t + 1$; T2INTEG) in relation to potential predictor variables†.

Variable	β (\pm SE)	P
Fumigation status of origin site‡	-1.442 (\pm 0.592)	0.016
Fumigation status of destination site‡	1.463 (\pm 0.341)	<0.0001
Whether destination site was same as origin site§	-0.178 (\pm 0.269)	0.51
Difference in colony size (destination minus origin)	0.344 (\pm 0.121)	0.005
Difference in colony size (squared)	-0.0620 (\pm 0.0508)	0.22
Fumigation status of destination site* whether destination site was same as origin site	-1.107 (\pm 0.398)	0.0059

† Origin colony site in year t was modeled as a random effect, $n = 286$ settlement groups.

‡ In relation to non-fumigated as baseline.

§ In relation to destination colony site being the same as origin site as baseline.

significant effects independent of parasite load (Table 2).

When controlling for distance between the sites, fumigation status, and other variables, cliff swallows exhibited a greater degree of group integrity at colonies that were relatively similar in size to the one they used the previous year. If residents of a given colony are ones with a heritable preference for colonies of that size (Brown and Brown 2000), by virtue of their settling there in the current year, more of those birds should remain together the next year when settling at another colony of that size than at colonies of vastly different sizes. This analysis adds to the evidence that cliff swallows have phenotypic specializations for particular colony sizes (Brown and Brown 1996, Brown et al. 2005, Brown 2016).

Our analyses thus suggest that the preferred sites in the colony network are the fumigated sites that are attractive for these reasons and draw groups of collective settlers. They are also likely attractive because they are perennially used, vary less in size from year to year, and thus provide a temporally stable colony location with

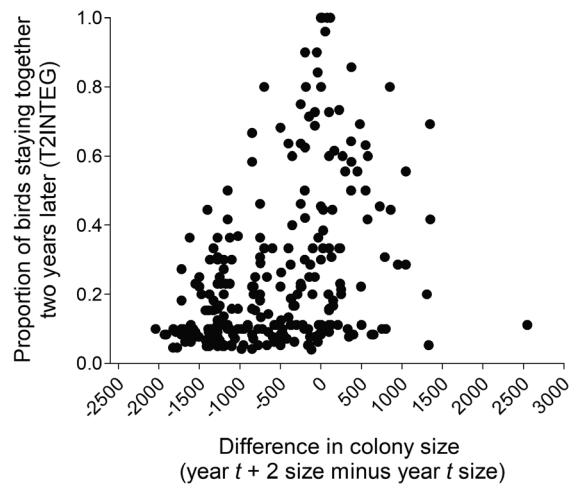


Fig. 5. The proportion of cliff swallows settling at a destination site in year $t + 2$ that had previously settled together at different sites in years $t + 1$ and t (T2INTEG), in relation to the difference in colony sizes (no. nests) of those sites (year $t + 2$ size minus year t size) for 286 settlement groups in which extended group integrity was known.

Table 4. Mixed-model regression analysis of whether a cliff swallow destination colony was successful (at least some nests fledged young; yes/no) in relation to potential predictor variables, including the average group integrity for birds settling at the destination colony from different origin colonies (average GRPINTEG)†.

Variable	β (\pm SE)	P
Fumigation status of destination site‡	-0.166 (\pm 0.052)	0.0015
Year	-0.020 (\pm 0.011)	0.058
Year (squared)	-0.039 (\pm 0.011)	0.0004
Destination colony size	0.017 (\pm 0.014)	0.223
Total number of settlement groups at site	-0.0094 (\pm 0.014)	0.494
Average GRPINTEG	0.035 (\pm 0.013)	0.0054

† Destination colony site was modeled as a random effect, $n = 572$ destination colonies.

‡ In relation to fumigated as baseline.

which many birds in the population are likely familiar (Brown et al. 2017a). However, they do not function solely as sinks, attracting dispersers and retaining them over time, because these colonies also provide settlement groups that show

high levels of group integrity when settling elsewhere. The reasons for this are unclear.

Advantages of group integrity

While benefits of associating with familiar conspecifics have been identified in some species (Conradt and Roper 2000, Griffiths et al. 2003, Aplin et al. 2012, Grabowska-Zhang et al. 2012, Farine et al. 2015), we know little about potential advantages of familiarity among colony residents in highly social species such as cliff swallows (or colonial species in general). Our analyses suggest that group integrity may improve annual survival, assuming that recapture likelihood approximates relative survival. Recapture probability for birds known to have settled with familiar conspecifics the previous year was 43% higher than that of birds not known to have resided with familiar conspecifics. This difference was probably a conservative estimate, because some of the individuals not known to have collectively settled may have in fact had birds from their previous colony present that we failed to detect. That much change in annual survival can be enough to drive natural selection, given that minor differences in lifespan can translate into relatively large gains in lifetime reproductive success in both the closely related house martin (*Delichon urbica*; Bryant 1989) and other small passerine birds (Clutton-Brock 1988). In addition, cliff swallow settlement groups with higher group integrity tended to settle in colonies that were ultimately more likely to be successful in producing at least some offspring. Both results suggest that selection favors birds' retaining of associations with familiar conspecifics between years.

Cliff swallows are thought to phenotypically sort among colonies based on inherent characteristics such as propensity to be parasitized, reaction to stress, or personality (Brown and Brown 1996, Brown et al. 2005, Roche and Brown 2013). This leads to non-random distributions of individuals among, for example, different colony sizes. By maintaining associations with individuals of similar phenotype, a bird could better ensure that it resides in a colony with the right type of individual. For example, a bird prone to being infested by swallow bugs and that consequently exhibits behavior that minimizes parasitism risk (e.g., by not investigating as many old nests where bugs hide), should preferentially

associate with other such individuals and thereby reduce the chance that its colony will be heavily infested by ectoparasites. Or, birds with such parasite aversions could band together to assess sites and collectively choose ones where parasite risk is reduced. In these ways, they could improve both their own chances of survival and the likelihood that reproduction at the chosen colony site would be successful. While the exact mechanisms whereby familiarity confers advantages in cliff swallows are unknown, our results do suggest fitness-related benefits of maintaining some degree of group integrity from year to year.

That associations can remain intact for up to three years, with on average 17–50% of birds settling together the second year also settling together the third year, suggests that these perennial associations can be important, perhaps by helping members choose similar colony sizes across years. Birds that showed the highest levels of extended group integrity (from years t to $t + 2$) settled in colonies of relatively similar size in these years (Fig. 5), and this pattern matched that for birds that had been together for only one year (Fig. 4). Extended group integrity in cliff swallows was greater among birds that returned to the same colony site they had occupied two years earlier, perhaps reflecting sustained group-based familiarity with certain sites even when not using them in a particular year.

Other correlates of collective dispersal

In the only other similar study in a colonial bird, Francesiaz et al. (2017) found that slender-billed gulls maintained associations among colony residents across years. This species rarely uses the same colony site in successive years, with therefore many opportunities for individuals to settle together at another site. Colony residents from sites that produced successful nesting tended to remain together at the next year's site more so than did birds from unsuccessful colony sites (Francesiaz et al. 2017). This suggested that gulls were sensitive to success, and this influenced their tendency to stay with familiar conspecifics. However, we found the opposite in cliff swallows, with greater group integrity, on average, among dispersers from unsuccessful colony sites. This may be because cliff swallows, being more philopatric than slender-billed gulls, are

more likely to respond to past success at a site by re-occupying it (Brown et al. 2000, 2017a), and thus, fewer birds in general disperse from highly successful sites.

A similarity between slender-billed gulls and cliff swallows is that birds seemed to be more attracted to a colony when it contained a greater proportion of members of their colony from the previous year (Table 2; Francesiaz et al. 2017). Thus, in both species, colonies that were a hodge-podge of birds from many different sites the previous year had lower group integrity from any single site, suggesting that individuals may prefer colonies where a greater proportion of residents are potentially familiar to them.

We found evidence of a curvilinear effect of year on collective dispersal, with smaller group tenacity values in the middle years of our study (from about 1994 to 2000) than during earlier or later years. This coincided with a period of reduced philopatry occurring in the same years, for unknown reasons. However, one interpretation is that a severe weather event in 1996, which reduced the population by about 50% (Brown and Brown 1998), led to a reduction in the number of large colonies for several years afterward (Brown et al. 2013, 2017a). Without large colonies to attract groups of collective dispersers, overall levels of group tenacity may have remained low until the population had recovered enough to sustain the normal number of large colonies. This was apparent especially in the connectedness of the colony network in 1996–1998 (Fig. 3).

We do not know whether birds settling together at a colony site reside in spatial proximity within the colony. If they do so, this would suggest benefits of having close neighbors with whom an individual is familiar, such as those reported for territorial species that reduce aggression toward known neighbors (Temeles 1994). However, limited data on nest occupancy by known birds in consecutive years suggest no pattern with respect to either where an individual settled the previous year or the individuals settling near a focal bird (C. Brown, S. Hannebaum, *unpublished data*). Cliff swallows probably more likely gain from group integrity by better stacking a colony in general with phenotypically compatible individuals or ones of similar personality, irrespective of where familiar individuals actually nest within the colony.

The results reported here are consistent with an individual-based study of philopatry and dispersal in cliff swallows, in which extent of parasitism at a site had a strong effect on whether an individual was philopatric or not (Brown et al. 2017a). Here, we show that the extent of group integrity among individuals is also driven by parasite load. However, we found that similarity in a colony's size (not large size per se) is a major determinant of group integrity, a result that was not apparent in the individual-based analysis (Brown et al. 2017a). These results add to others suggesting that phenotypic sorting, especially in regard to colony size, is a major component of habitat choice in cliff swallows and other colonial animals (reviewed in Brown 2016). Colonial birds that form and re-form colonies each breeding season provide many opportunities for further study of the dynamics and adaptive advantages of group integrity.

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