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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.

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, & Piertney, 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, Donázar, & Tella, 2004; Serrano, Tella, Forero, & Donázar, 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, Donázar, & 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 colonially 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 ± 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, &