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Nest spacing in relation to settlement time in colonial cliff swallows

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How colonial animals space their nests in relation to conspecifics may provide clues as to whether coloniality provides net benefits or occurs only because breeding sites are limited. We examined how nearest-neighbour distance varied in relation to settlement time in the highly colonial cliff swallow, *Petrochelidon pyrrhonota*, comparing observed nearest-neighbour distances to those expected if birds spread out to maximize nest spacing. Cliff swallows generally settled closer to each other than required by the available substrate, and clustered their nests closer in large colonies than in small ones. The first settlers at a colony site spaced themselves further apart than later arrivals but did not maximize nearest-neighbour distances. The first arrivals maintained greater nest spacing throughout the season than did birds that arrived later. Colony size and amount of nesting substrate had no effect on initial settlement distances of the first arrivals, but eventual nearest-neighbour distances declined with colony size. First arrivals may gain less from nesting with conspecifics and thus are less likely to cluster their nests than later arrivals, which may often be young or naïve birds that gain more from the social benefits of colonial nesting. The results are consistent with the presumed social advantages cliff swallows receive from coloniality and do not support the hypothesis that colonies result from nesting site limitation.

Why animals form breeding colonies is a major unresolved question in evolutionary ecology. The topic continues to stir lively debate (Danchin & Wagner 1997; Tella et al. 1998) and has been the focus of long-term studies (Hoogland 1995; Brown & Brown 1996; Danchin et al. 1998). One of the principal issues has been whether colonies form due to limited breeding habitat, with animals forced into nesting aggregations at a net cost, or result from social benefits of clustering (food finding, reduced predation; Lack 1968; Alexander 1974; Hoogland & Sherman 1976; Wittenberger 1981). The prevailing view has been that seabird colonies in particular are caused by a shortage of suitable nesting sites (islands, coastlines) inherent in marine environments, but a recent phylogenetic analysis of coloniality across birds suggests that colonial nesting evolved prior to occupancy of marine habitats (Rolland et al. 1998). Thus, whether seabirds truly form colonies due to a shortage of nesting sites is unclear, with new life given to the old controversy over the relative importance of habitat constraints versus social benefits in the evolution of avian coloniality.

Perhaps the best way to determine whether suitable nesting sites are limited in colonial birds is to increase nesting habitat experimentally and examine whether colonies dwindle as birds spread out. This was done in tree swallows, *Tachycineta bicolor*, in which an increase in the number of nestboxes led to birds settling in lower density (Muldal et al. 1985). However, in most colonial species, manipulating the amount or quality of nesting habitat is not practical. An alternative is to observe the spatial distribution of individuals at a given site. If nesting colonially affords only costs and no benefits of nesting with conspecifics, individuals should settle in places that tend to maximize their nearest-neighbour distances within a colony site. Maximizing nest spacing reduces the costs of grouping, which can be substantial in many species (reviewed in Brown & Brown 1996).

Among colonial species in which nest spacing has been studied, nests usually seem to be closer together than required by the amount of nesting substrate (Waltz 1981; Schmutz et al. 1983; Wittenberger & Hunt 1985; Szep 1991; Burger & Gochfeld 1993). This seems to suggest that these species receive active benefits from colonial nesting, yet in most cases the alternative that close nest spacing results from suitable nesting substrate within colony sites becoming saturated with settlers has not been tested. As colony size grows, later arrivals may be forced to cluster their nests near conspecifics simply because of space limitations dictated by the distribution

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of established settlers. However, if animals actively benefit from the presence of conspecifics, to maximize their benefits the first settlers should establish nest sites at closer distances than required by the substrate. The key is the behaviour of the initial settlers to arrive at a site, because they can choose how they settle relative to conspecifics.

Although nearest-neighbour distance per se has been studied among a few colonial species (e.g. Siegel-Causey & Hunt 1986; Emms & Verbeek 1989; Møller 1989; Burger & Gochfeld 1990; Brown & Brown 1996), usually the nearest-neighbour distances used were final ones calculated after all individuals had settled. An exception was a study of settlement patterns in cliff swallows, *Petrochelidon pyrrhonota*, by Meek & Barclay (1996), who found that birds in two small colonies tended to settle in old nests in proximity to each other. In this paper we report how nearest-neighbour distance varies with settlement time in cliff swallows, using a more extensive data set and different population from that of Meek & Barclay (1996). We ask if these birds settle in ways that maximize nearest-neighbour distances and how colony size and amount of nesting substrate affect settlement distances. Our intent is to evaluate whether cliff swallows actively cluster their nests at different times during the settlement process. We argue that this approach may be used with other species to determine the nature of the costs and benefits associated with coloniality.

Cliff swallows are particularly appropriate for this study because they nest on artificial structures that permit objective measurement of nesting habitat. To examine whether birds settle in ways that maximize nearest-neighbour distance, one must know the extent of available nesting substrate at a site. For many species this requires subjective assessment of habitat suitability, often in the absence of knowing what exactly the animals look for in a nesting site. In cliff swallows, however, nesting substrate is uniform within a colony site. Cliff swallows often breed on concrete highway bridges and culverts, and nesting substrate is simply the extent of concrete wall at the site. Our approach is to use the known quantity of nesting habitat at a colony site to calculate the expected nearest-neighbour distance that would maximize the spacing between active nests for each successive arrival at the site. We then compare the expected distances to the actual nearest-neighbour distance for each pair at the time of settlement.

METHODS

Study Animal and Study Site

The cliff swallow is a 20–28-g Neotropical migrant that breeds throughout most of western North America and winters in southern South America. It builds gourd-shaped mud nests and places them beneath overhanging rock ledges on the sides of steep cliffs or underneath the protected eaves of artificial structures such as bridges or highway culverts. Cliff swallows often breed in dense colonies, although colony size within a single population varies widely. At our study site, mean colony size ± SE is 393.0 ± 24.3 nests, range 1–3700 (Brown & Brown 1996). Cliff swallows typically have a short breeding season, 10 weeks or less in our study area, and raise only one brood (Brown & Brown 1995). Most birds arrive in the study area in May, and breeding is largely completed by the end of July.

We studied cliff swallows along the North and South Platte rivers near Ogallala, in primarily Keith and Garden counties, southwestern Nebraska, 1982–1998. Our study area is approximately 150 × 50 km and contains about 160 separate colony sites, about 100 of which are active in any given year. These colony sites consist of both natural cliffs along the south shore of Lake McConaughy and artificial sites such as bridges, buildings and highway culverts. The colonies included in this study were situated in culverts, permitting objective measurement of the extent of nesting substrate. Our study site is described in detail by Brown & Brown (1996).

Field Methods

Because cliff swallows do not defend nesting territories, they were not considered as having settled at a site until they began nest building, which fixed their spatial position within the colony relative to conspecifics (Brown & Brown 1996). We determined settlement dates of cliff swallows by checking nests within colonies every other day. Whenever a nest was begun anew, known by the birds' placing dabs of mud on the wall, or whenever an old existing nest was first occupied, known by the appearance of fresh mud on its entrance, we recorded the date and began checking its status and contents. We continued to check nests regularly until eggs hatched. However, for some sites we did not have exact dates of first nest building, because the colony was not discovered to be active until after nest building had begun. For these sites we used first-egg date to infer relative settlement time. This was justified based on a sample of 603 nests where we knew the exact date of nest initiation (when mud was first placed), for which date of the first egg correlated strongly with the date the nest was started (r=0.96, N=603, P<0.0001). Nests were ranked on the basis of their start date, with the earliest (first) one(s) at a site given rank 1. Nests begun on successive days were ranked sequentially, with adjacent ranks always separated by at least 1 day. Any nests starting on the same day were given equal rank, meaning some colonies may have had multiple simultaneous arrivals designated as the first, second, or third arrivals at the site. We did not have information on the specific identities of the different settlers and thus did not know the past histories of birds arriving at different times. Cliff swallows usually form pairs at about the time nest construction begins (personal observations); a male and female at a given nest site develop a 'mutual tolerance' for each other (Emlen 1954). This made it impractical to try to designate arrival times separately by sex. Colony size refers to the maximum number of active nests (those with at least one egg laid), and substrate size is the total vertical concrete expanse on which nests could be built at a site; methods for determining each are given in Brown & Brown (1996).

For the analyses in this paper, the birds in each highway culvert were considered a single, separate colony (see Brown & Brown 1996). Residents from throughout each culvert interacted with each other (for example, during foraging or when responding to a predator) but did not interact with birds in other culverts or bridges. In practice, each colony was always a highly discrete group of nests separated from the next nearest colony by more than 3 km of habitat unsuitable for nesting. 'Colony' refers explicitly to a collection of birds nesting at a given site. Linear distances between adjacent nests (from the centres of nest entrances) were measured at the end of the nesting season. We used these distances to calculate nearest-neighbour distance for each nest at the time of settlement, defined as the distance along the same wall to the nearest nest that was active on the settlement date. The first nest to become established at a colony site had no nearest-neighbour distance (unless two or more nests began simultaneously on that date), because it had no neighbours. We refer to the 'first' arrival(s) at a site as the first one(s) that established a nearest-neighbour distance, either when two or more nests were started on the first day, or when only one was started on the first day and another the next day, allowing a calculation of the first nearest-neighbour distance at the site. If two simultaneous arrivals were closest to each other, we included the nearest-neighbour distance between them only once in our analyses. We also calculated the final nearest-neighbour distance for all nests after all birds in the colony had settled.

We analysed each colony separately because each culvert differed in physical size, thus requiring different expected nearest-neighbour distances for each settlement time. In these analyses and in our past work (Brown & Brown 1996), we consider colonies active at the same site in different years to be independent. The rationale for this included the fact that colony size and environmental conditions (e.g. extent of ectoparasitism) usually changed between years, and there was often turnover among the individuals in the colonies (Brown & Brown 1996). We indicate in some analyses, however, cases in which different colonies were situated at the same site in different years. We had appropriate data for 15 colonies, which were selected from among the total set of colonies in the study area based on their accessibility for nest checks and for measurement of nearest-neighbour distances and (except for one on a natural cliff) their being situated on uniform substrates. Colonies larger than 375 nests were not studied simply because of the difficulty in getting both settlement times and actual nearest-neighbour distances for that many birds.

Calculating Expected Nearest-neighbour Distances

We calculated the expected distance between active nests on each settlement date assuming each successive arrival maximized its distance from its nearest neighbour along the same culvert wall. This required knowing the total length of nesting substrate and the number of birds already residing in the colony on each settlement date. We assumed the entire length of a highway culvert's concrete wall was suitable nesting substrate. This assumption seemed justified because the wall was uniform in composition and cliff swallows nested throughout all parts of most culverts in our study area. We did not include in this study a few culverts consisting of long tunnels because of apparent avoidance of the darkest interior areas by cliff swallows. In contrast to Meek & Barclay (1996), who sought to determine whether cliff swallows occupied nests randomly, we focused on determining specifically whether the birds settled in a way that maximized nearest-neighbour distance. An emphasis on distance between settlers made it possible to consider both colony sites where the birds primarily occupied existing nests and those where nests were built anew, and further allowed us to incorporate in the analysis physical space where the birds could have theoretically built nests (cf. Meek & Barclay 1996). For one colony situated on a natural cliff, we did not attempt to calculate expected settlement distances because of possible heterogeneities in substrate quality within the site.

RESULTS

Do Birds Maximize Nearest-neighbour Distances?

We had data on actual nearest-neighbour distance, and the distance expected assuming maximal spacing among residents, in relation to settlement time for cliff swallow colonies ranging in size from 13 to 375 nests (Fig. 1). There was variability between colonies, with a few showing nearest-neighbour distances similar to those expected from maximal spacing and birds in others clearly settling closer together than predicted (Fig. 1). Colonies with close settlement distances tended to be ones where nests were clustered together in bunches, whereas those with greater nearest-neighbour distances were ones with nests spread out in long lines throughout the culvert. Colony b was situated on a natural cliff site and thus had no expected distances, but the pattern of observed nearest-neighbour distances was similar to that of colonies on highway culverts (Fig. 1).

Overall observed and expected nearest-neighbour distances differed significantly in seven of 14 colonies (Fig. 1). However, only the first birds to arrive at a site have much choice in nest position. Later birds are constrained by those already settled and do not have the option at many sites of widely spacing themselves. In most colonies, the first cliff swallows to settle at a site clustered their nests more closely than expected, in some cases markedly so (colonies e1, e3; Fig. 1). Across all colonies (N=14), observed nearest-neighbour distances at the time of settlement differed significantly from expected distances for first ($t_{13} = -2.489$, P=0.027) and second arrivals ($t_{13} = -2.196$, P=0.047), and almost for third arrivals ($t_{13} = -1.881$, P=0.083), but not for any other rank-ordered arrival classes (P>0.05). The first arrivals settled at an average of 44.8% of the maximum distance and second arrivals 31.9% of the maximum distance. After about the first 5 days of site occupancy, enough birds had usually arrived so that any nest clustering was indistinguishable from maximum nest spacing, especially in the

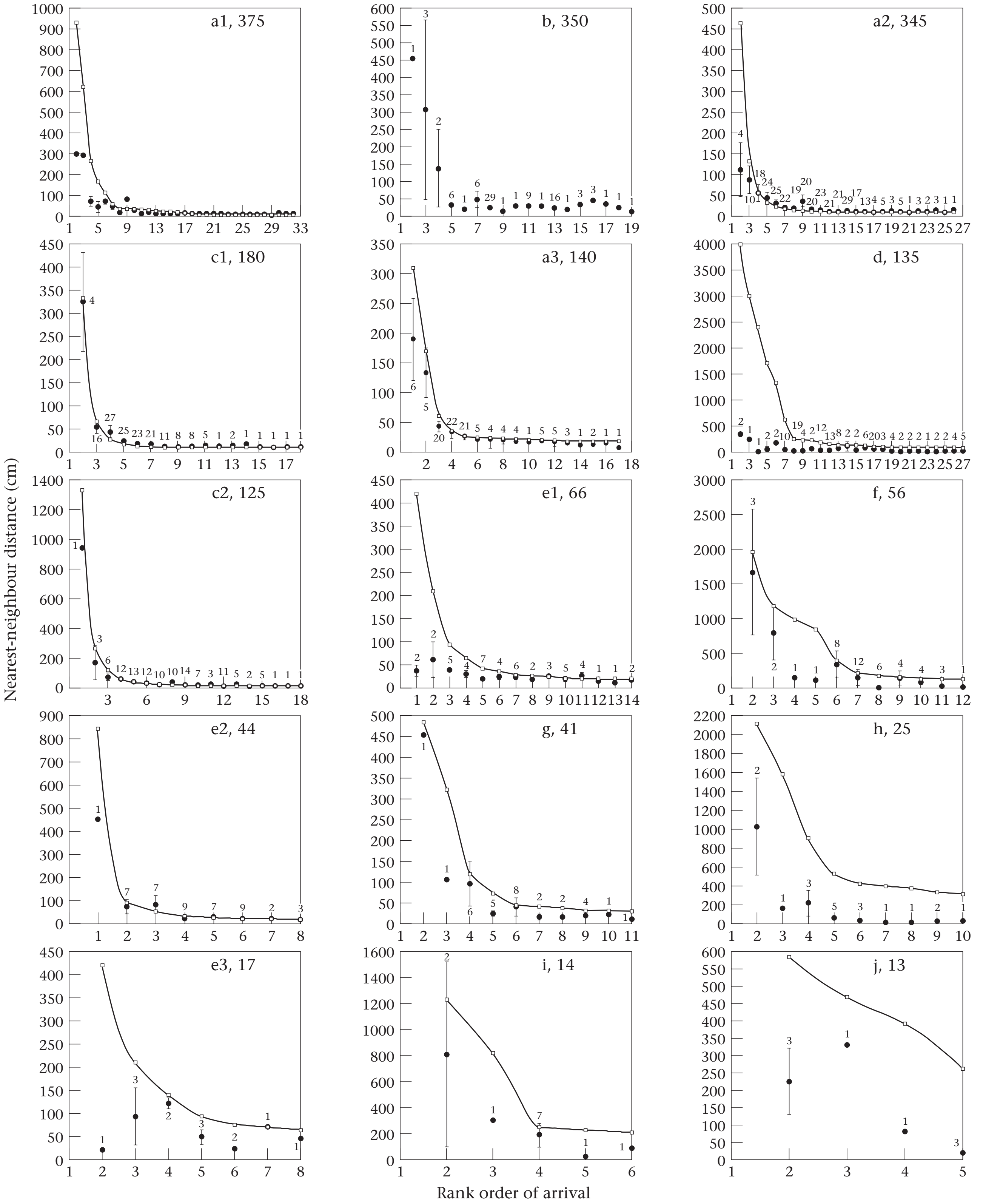

Figure 1. Observed (●) and expected (–□–) nearest-neighbour distance (mean±SE) assuming maximal spacing among all current colony residents in relation to rank order of settlement time in 15 cliff swallow colonies (a1–j). Colony size is also shown; colonies beginning with the same letter (e.g. a1, a2, a3) were situated at the same site in different years. Colony b was on a natural cliff that precluded calculation of expected distances. Sample sizes (number of birds) shown above means. Overall observed distances differed significantly from expected distances (paired *t* tests, $P<0.05$) in seven colonies (a1, c1, d, e3, h, i, j); in the remaining seven (a2, a3, c2, e1, f, e2, g), distances did not differ significantly (NS).

larger colonies. Cliff swallows had a largely irreduceable minimum nearest-neighbour distance (8–15 cm), reached whenever adjacent nests touched each other and shared walls (Brown & Brown 1996). In most colonies, there was a substantial difference in nearest-neighbour distance between the very first birds to settle at a site (rank 1 and 2) and all others, with the first birds more widely spaced than those settling even a day or two later.

The increased nest spacing established by the earliest arrivals at a site was maintained throughout the season. Mean ± SE final nearest-neighbour distance (i.e. that determined at the end of the nesting season after all birds had settled) was 108.6 ± 63.3 cm across colonies (N=15) for the first arrivals at a site, 72.6 ± 30.2 cm for second arrivals, and 34.6 ± 10.3 cm for third arrivals. For all nests averaged across all colonies (N=4853), final nearest-neighbour distance was 38.6 ± 2.4 cm, with 74.8% of all birds maintaining a final nearest-neighbour distance of less than 20 cm.

Effects of Colony Size, Amount of Substrate and Nest Age on Settlement Patterns

Because in most colonies active clustering of later arrivals could not be distinguished from the maximizing of settlement distance (Fig. 1), we used the first three or four arrivals at each colony site to investigate the effects of colony size and amount of substrate. We calculated the average nearest-neighbour distance for the first, second and third sets of arriving birds at the time of settlement and compared these to the final colony sizes (number of nests) at each site (Fig. 2). There was no significant correlation between initial nearest-neighbour distance and colony size for the first and second arrivals at a site, but initial nearest-neighbour distance declined significantly with colony size for the third arrivals (Fig. 2). This may reflect the fact that at most sites multiple birds arrived simultaneously by the third day (up to 20 nests initiated that day at some large colonies), which reduced the birds' ability to spread out. Final nearest-neighbour distances (at the end of the season) declined significantly with colony size (Fig. 2), reflecting the increased density of larger colonies (see Brown & Brown 1996).

The amount of available substrate (total area of concrete wall) had no significant effect on nearest-neighbour distance (Fig. 3). Although there was a trend for initial settlement distances to increase at colony sites with larger substrates, the correlations were not significant, and there was no obvious influence of substrate size on nearest-neighbour distances at the end of the season after all birds had settled (Fig. 3). The analyses of colony size and substrate size (Figs 2, 3) use 13 colonies for which we had both initial and final nearest-neighbour distances; in two other colonies nests had failed (fallen) before the end of the season and precluded getting final nearest-neighbour distances. Inclusion of these two sites in the correlation analyses had no effect on the conclusions about initial nearest-neighbour distance (above).

We detected a possible difference in settlement patterns among colonies depending on whether old existing nests were reoccupied or whether nests were built anew that season. In colonies a1, a3, c1 and c2 (Fig. 1), in which birds primarily reoccupied existing nests, settlement distances among the first arrivals seemed to match more closely that expected from maximal nest spacing. At the other sites birds built new nests, and the first arrivals tended to space themselves more closely.

DISCUSSION

Our analyses revealed that cliff swallows often settled closer together than necessary based on the available nesting substrate. Often this could not have been discerned by looking at the final distribution of nearest-neighbour distances in a colony. Only the initial settlers at a colony site had much choice in where to settle relative to conspecifics, and the first arrivals positioned themselves consistent with the benefits they presumably gain from colonial nesting.

Cliff swallows experience many advantages associated with coloniality, most related to enhanced food finding and better avoidance of predators (Brown & Brown 1996). Given these benefits, it is perhaps not surprising that the birds cluster their nests closely. Having close neighbours allows nest owners to monitor other birds' foraging success more easily (Brown 1986), assess opportunities for extrapair mating better (Wagner 1993) and reduce the time and energy of nest building through sharing of nest walls (Gauthier & Thomas 1993; Brown & Brown 1996). The latter advantage of grouping possibly explains the closer spacing at sites where new nests had to be built. Nest clustering was easiest to detect in small colonies (see also Meek & Barclay 1996) and among the first settlers at larger sites; later arrivals at large colonies also may have preferred to nest closely, but we could not distinguish active clustering from that forced by the size of the nesting substrate relative to colony size.

However, when given a choice in nest spacing, cliff swallows generally did not nest at the minimum nearest-neighbour distances seen in the larger colonies. Birds in small colonies and the first settlers in larger colonies spread their nests at intermediate distances, suggesting that when possible the birds avoid the close spacing of the larger colonies. Cliff swallows also experience multiple costs of colonial nesting, including increased ectoparasitism and competition for resources including mates (Brown & Brown 1996). The birds may attempt to avoid or minimize these costs by some degree of nest separation. Ectoparasitism in particular can be ameliorated in part by wide nest spacing, which potentially reduces within-colony transmission of swallow bugs that crawl on the substrate (Brown & Brown 1996). Meek & Barclay (1996) reported that male cliff swallows tended to cluster their nests but that females settle randomly. In their case, how exact settlement times of individual birds could be determined before they were colour-marked or why optimal nest spacing should differ among the sexes was unclear.

Although settlement distances have been studied for a number of territorial animals (e.g. Stamps 1988; Stamps & Krishnan 1990; Muller et al. 1997), ours is among the first studies of a colonial species with quantitative information on nest spacing in relation to settlement time. In some gulls, colony formation has been described to occur in a centripetal fashion, with the first birds spacing themselves relatively widely through defence of territories and then later moving closer together as more birds settle (Kharitonov & Siegel-Causey 1988). This leads to a pattern similar to the one we observed in cliff swallows, in which the first arrivals settle further apart than later ones. However, swallows differ substantially from gulls in that they do not defend territories (only their nest), and thus once a cliff swallow's spatial position is fixed by building its nest, it cannot move closer to or further from conspecifics. Later in the nesting season, the first arrivals in cliff swallow colonies are nesting closer to others than at the time of settlement, but this occurs because later arrivals choose to settle near the first residents.

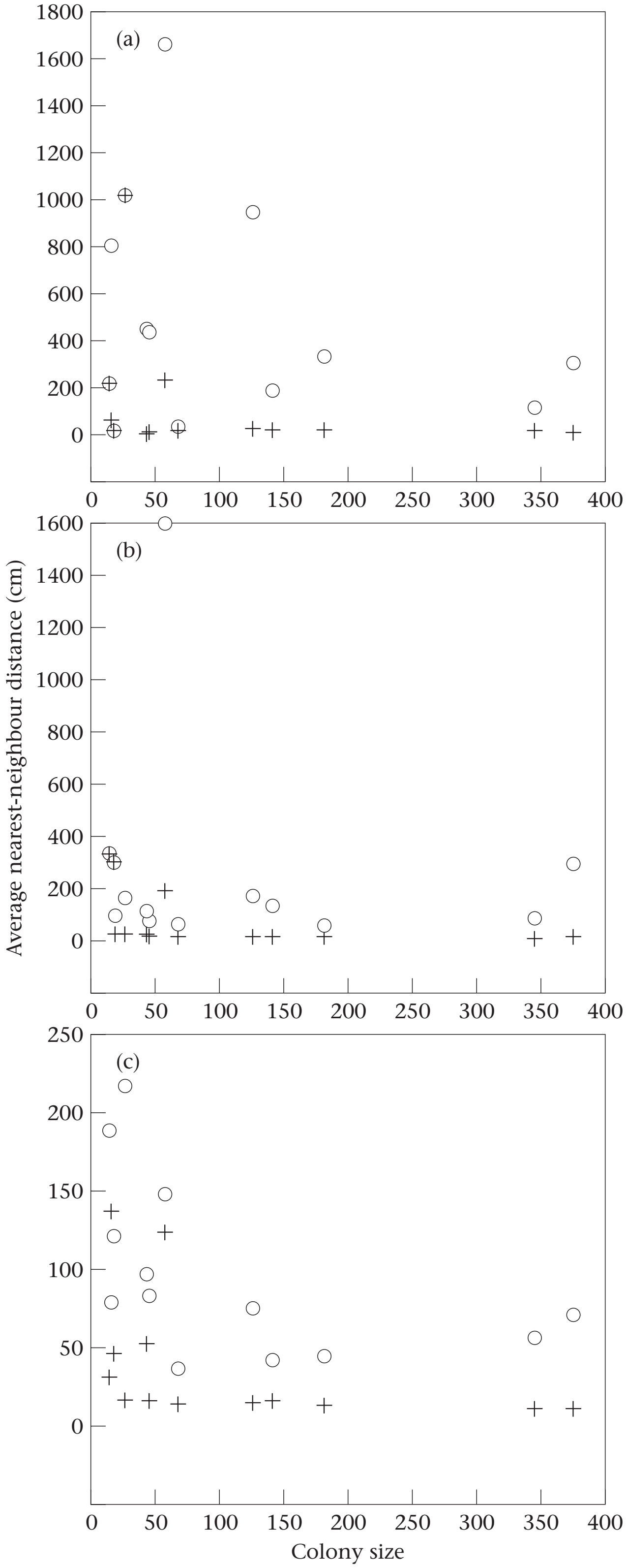

Figure 2. Average initial (○: at time of settlement) and final (+: at end of nesting season) nearest-neighbour distances in relation to cliff swallow colony size (total number of active nests) for (a) first, (b) second and (c) third settlers at the site. For initial distances (N=13 colonies), there was no significant correlation between distance and colony size for first (r_S=−0.170, P=0.58) or second (r_S=−0.335, P=0.26) settlers, but distance declined significantly with colony size for third settlers (r_S=−0.69, P=0.009). For final distances (N=13 colonies), distance declined significantly with colony size for first (r_S=−0.66, P=0.014), second (r_S=−0.87, P<0.001), and third settlers (r_S=−0.83, P<0.001). Note that the scale of the Y axis differs in (c).

The first arrivals at a site, while not maximizing their distance from conspecifics in most cases, did maintain greater nest spacing across the season than later arrivals. The first birds at a colony had an average final nearest-neighbour distance of 109 m, and the second arrivals, 73 m, which was at least twice the average nearest-neighbour distance for the population. How the nest spacing of the early arrivals was maintained is unclear, because cliff swallows do not defend space around their nests and thus do not actively prevent other birds from settling near them. Models incorporating territory size and how some individuals settle such that others cannot squeeze in between them (Getty 1981; Stamps & Krishnan 1990) cannot apply to this species. Cliff swallows defend only their nest, and unless a later arrival tries to intrude into their nest, residents will allow others to build nests adjacent to, directly underneath, or on top of their nest without physical confrontation. Greater nest spacing could be achieved if the first arrivals settled closer to the eventual edges of the colony where overall nest densities are lower (Brown & Brown 1996). This would occur if later arrivals tended to cluster together (as they apparently do in cliff swallows; Fig. 1), creating an epicentre and leaving the first arrivals in lower-density areas, as described for some gulls (Kharitonov & Siegel-Causey 1988).

The difference in nest spacing between the first arrivals and later settlers may reflect to some degree the different preferences of these individuals. The close spacing adopted by cliff swallows that arrive later may not strictly reflect space constraints at the site, because many apparently unused but suitable colony sites exist in our study area (Brown & Brown 1996). Later arrivals could settle at these sites to achieve more dispersed nest spacing. That they choose instead to crowd into the larger colonies is consistent with the hypothesis that younger and more inferior individuals (which are apt to arrive later) gain proportionately more from larger colonies than the birds that arrive first and spread out (Fig. 1) or nest in smaller colonies (Brown & Brown 1996). Different rules of habitat selection may be used by experienced versus naïve settlers: in house wrens, *Troglodytes aedon*, for example, experienced males tend to settle far from conspecifics, whereas naïve males prefer to settle near other wrens (Muller et al. 1997). This pattern probably reflects the greater reliance by naïve settlers on the information provided by conspecifics in territorial species such as wrens (Stamps 1988) and in colonial species such as cliff swallows (Brown et al., in press), and also underscores the importance of social benefits of group size for certain individuals (Brown & Brown 1996). We did not have information on the identities of the birds that arrived at different times, although in bank swallows, *Riparia riparia*, older, more experienced birds arrive at colony sites first (Jones 1987). The variation in the degree of nest clustering among colonies (Fig. 1) could reflect differences in the proportions of experienced (perhaps philopatric) versus naïve cliff swallows occupying the sites. Philopatry per se is unlikely to affect nest selection in cliff swallows, however, because individuals seldom reoccupy the same nest in consecutive years (Brown & Brown 1996).

That nest spacing in cliff swallows is generally closer than predicted suggests that they actively benefit from the presence of conspecifics and that coloniality is not solely a response to a favorable habitat patch or lack of nesting sites. Nearest-neighbour distance, whether that of the first arrivals or of birds after all had settled, did not vary significantly with the amount of nesting substrate, indicating that cliff swallows maintained essentially the same nest spacing regardless of how much nesting habitat was available. If these birds are forced into colonies by limited nesting sites, nest spacing should be greater in physically large sites that allow the birds to spread out. That we did not find this to be the case (Fig. 3; also see Fig. 2), that colony size does not vary significantly with substrate size (Brown & Brown 1996) and that the birds clearly cluster their nests, seems to rule out nesting site limitation as an evolutionary reason for coloniality in this species.

We suggest that measurement of nearest-neighbour distance relative to settlement time may provide insight into the evolution of coloniality for other, less well-studied species. These sorts of data should be gathered as a first step towards determining whether a given colonial species is simply nesting site or habitat limited and

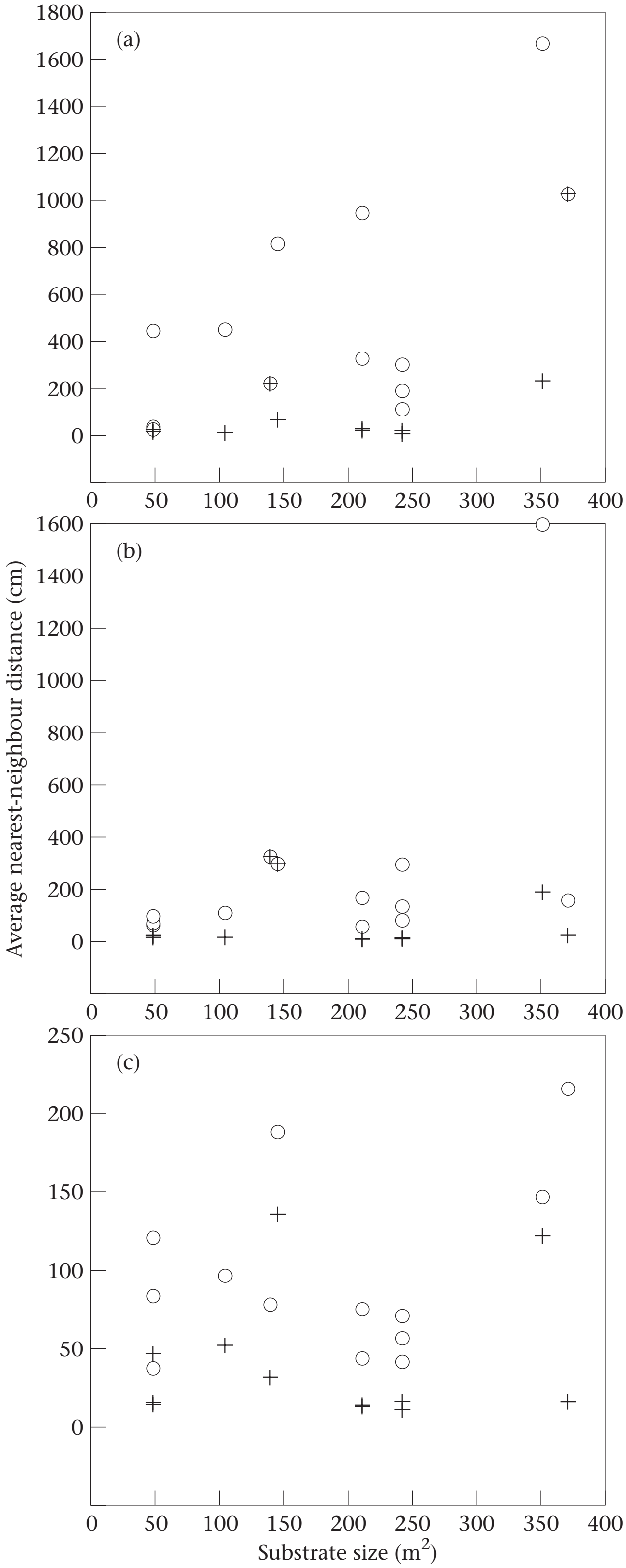

Figure 3. Average initial (○: at time of settlement) and final (+: at end of nesting season) nearest-neighbour distances in relation to size of nesting substrate of a cliff swallow colony site (m^2) for (a) first, (b) second and (c) third settlers at the site. For initial distances (*N*=13 colonies), there was no significant correlation between distance and substrate size for first (r_S=0.46, *P*=0.11), second (r_S=0.43, *P*=0.14), or third settlers (r_S=0.13, *P*=0.68). For final distances (*N*=13 colonies), there was no significant correlation between distance and substrate size for first (r_S=0.15, *P*=0.64), second (r_S=−0.03, *P*=0.92), or third settlers (r_S=−0.17, *P*=0.59). Note that the scale of the *Y* axis differs in (c).

forming colonies for that reason, or whether there are active advantages of coloniality and nest clustering. Emphasis should be on the spacing of the initial settlers at a site. If animals are cueing strictly on local resources that make some patches better than others, then we would predict that individuals should spread out as much as possible within a patch (colony site) to minimize the inevitable costs of grouping. Measuring nearest-neighbour distance in relation to settlement time will suggest whether the social benefits of coloniality are likely to be important. The primary limitation of the approach presented here is that it requires accurate assessment of what constitutes suitable nesting habitat in order to predict maximum nearest-neighbour distance. Although this could be problematic for some species, virtually all studies of coloniality have to characterize suitable nesting habitat in some way if only to address whether nesting sites are limited. We urge that analysis of nearest-neighbour distance in relation to settlement time become standard in studies of vertebrate coloniality.

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