Colony size, reproductive success, and colony choice in Cave Swallows *Petrochelidon fulva*

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We investigated how annual reproductive success, as measured by the number of nestlings surviving to day 10 and the percentage of nests that were successful, varied with colony size of the Cave Swallow *Petrochelidon fulva* in south central Texas. We also studied whether Cave Swallows chose colonies, in part, on the basis of reproductive success at a site the previous year. Neither measure of reproductive success varied significantly with colony size for either first-wave or second-wave nestings. Mean clutch size per colony did not vary significantly with colony size. Mean nestling body mass, an index of parental foraging efficiency, was unrelated to colony size, except for broods of five, in which nestling mass declined significantly with colony size. Colony size was not significantly affected by reproductive success at the site the previous year, although sites with more successful nests during the first wave declined less in size during the second wave within the same season than did sites that had fewer successful first-wave nests. Unlike the closely related Cliff Swallow *Petrochelidon pyrrhonota*, Cave Swallows did not use breeding performance of conspecifics in choosing nest-sites, because they did not preferentially aggregate at sites that were the most successful the previous year. Coloniality in Cave Swallows did not appear to have a net negative effect on annual fitness, suggesting that colonial nesting was not solely a response to nest-site limitation, but the benefits of breeding colonially (if any) were unclear.

The selective factors that cause animals to form breeding colonies are still poorly understood. Empirical work over the last few decades has revealed several potential benefits of nesting together (e.g. better avoidance of predators, increased efficiency at finding food), but the relative importance of these effects is unclear in many species (Brown & Brown 2001). Because colonial nesting affords both benefits and costs, many of which are necessarily measured in different currencies (e.g. energy intake from foraging vs. the risk of predation), some researchers have suggested that focus should be given to reproductive success as an integrative (net) measure of the positive and negative effects of coloniality (Brown & Brown 1996, 2001, Danchin & Wagner 1997). Knowing how reproductive success varies with group size can yield clues as to whether colonies result from positive social interactions or reflect the animals simply being

forced into colonies by a scarcity of resources. For example, when reproductive success declines as colonies become larger, it is likely that colonial nesting is on average costly and that individuals have aggregated only because nesting sites are limited (Shields & Crook 1987, Brown & Brown 1996).

Reproductive success may also be important to the animals themselves in making settlement decisions. It has been suggested that breeding colonies often form in areas of habitat that are particularly favourable for nesting or that contain the best resources, and that individuals assess habitat patches in part by observing the reproductive success of conspecifics (Forbes & Kaiser 1994, Danchin & Wagner 1997, Doligez *et al.* 2002). First-time breeders, and birds that were unsuccessful elsewhere, are thought to settle in areas where other birds had high reproductive success the year before; coupled with philopatry of the successful residents, colonies thus form in some habitat patches. The areas most successful will tend to attract more and more animals, and colonies there should grow. Data for some species support this sort of habitat

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selection (Boulinier 1996, Danchin *et al.* 1998, Brown *et al.* 2000, Schjørring *et al.* 2000, Doligez *et al.* 2002), whereas those for others do not (Burger 1984, Erwin *et al.* 1998, Oro & Pradel 2000, Serrano *et al.* 2001, Safran 2004).

Studies on both the adaptive significance of coloniality and habitat selection based on conspecific assessment require empirical measures of reproductive success. Although a variety of studies have reported information on annual reproductive success of colonial birds, most of these have been limited by either a relatively small sample of colonies where nesting success was measured (often fewer than ten) and/or by the pooling of data across years (leading to potentially confounding year effects; Brown & Brown 2001). Thus, how reproductive success varies with colony size and how (if) it is used in settlement decisions is unknown for most species.

In this study, we measured annual reproductive success in relation to colony size for the Cave Swallow *Petrochelidon fulva*. We recorded data for both first and second nestings of birds in 17 colonies of different sizes within a single year. This yielded one of the larger samples available for analysis of how colony size affects reproductive success in birds, and our data were not confounded by year effects. By recording how colony size changed at these sites the following year, we also investigated whether these birds were sensitive to conspecific reproductive success in making between-year settlement decisions.

METHODS

Study animal

The Cave Swallow is a moderately colonial passerine that occupies a disjunct range in parts of northern South America, Central America, the West Indies, Mexico and the southwestern United States (American Ornithologists' Union 1998; West 1995). It is morphologically, behaviourally and ecologically similar to the well-studied and more widely distributed Cliff Swallow *Petrochelidon pyrrhonota*. Cave Swallows are colonial breeders, occupying colonies that can range from fewer than five to 1500 or more nests (Selander & Baker 1957, West 1995). They are highly social, feeding, nest-building and mobbing predators in large groups; they also spend the winter in large roosts (Komar 1997). Cave Swallows feed on flying insects caught at relatively high altitudes over open areas (West 1995, H. Weaver & C. Brown pers. obs.). They build mud nests that they attach to a wall or ceiling of a nesting site, although nest architecture varies between populations (Kirchman *et al.* 2000). Some nests resemble those of Barn Swallows *Hirundo rustica* in shape, whereas others look more like incomplete Cliff Swallow nests with the makings of an enclosed entrance tube. In our Texas study area, the birds generally build half-cup nests with flared rims, but variation exists even within the same colony. The Cave Swallow breeding season at our study site extends from at least late March to late August, during which time two broods are apparently attempted by many individuals. Our population is mostly migratory, with most birds probably wintering in Mexico or Central America, although in the mid 1980s some individuals began wintering in Texas (Lasley & Sexton 1987, McNair & Post 2001).

The Cave Swallow has undergone a dramatic range expansion and nest-site shift in Texas within the last 30 years. Before 1970, Cave Swallows were limited to nesting in natural caverns and sinkholes, where they attached their nests to cavern walls or ceilings in the twilight zones (Selander & Baker 1957). The birds are still restricted to such nest-sites in southeastern New Mexico (West 1988, 1995). Before 1970, only about 30 active cavern nesting sites in Texas were known, all restricted to the limestone cave topography of the Edwards Plateau (Selander & Baker 1957, Baker 1962, Reddell 1967). In the early 1970s, however, Cave Swallows began using highway culverts and bridges as nesting sites (Martin 1974, Palmer 1988), and in so doing expanded their range outside of the Edwards Plateau. The species has occupied areas well to the north, east and south of its historical range in Texas (including our study area), with breeding populations now as far east and south as the Gulf Coast and almost as far north as the Red River. In these recently occupied areas, Cave Swallows nest exclusively in culverts and bridges, where their nests are attached to vertical walls near horizontal ceilings. Cave Swallows have come into relatively recent contact with Barn and Cliff Swallows that also nest in culverts.

Study site

Our study site was centred at the Rob and Bessie Welder Wildlife Foundation, near Sinton, Texas (28°06′N, 97°22′W), and included portions of San Patricio, Refugio, Bee and Live Oak counties. In this area, Cave Swallows nested exclusively in highway culverts and on bridges. We selected colonies for study largely on the basis of their proximity to the Welder Wildlife Foundation and the ease of access to the

nests. The topography was mostly flat, coastal plain with some rolling hills near Beeville. Most culverts contained dry streambeds, although a few would retain standing water for up to 1 week after rainfall. At many colonies, trees such as live oak *Quercus* sp., elm *Ulmus* sp., and mesquite *Prosopis* sp. grew on both sides of the culvert. Most colonies were at least 3 km from the next nearest colony.

Nest checks

We began observations on 8 April 2001 and conducted nest checks at each colony every other day for the entire 2001 nesting season (until early August). Nests were numbered by chalk marks on the concrete substrate and nest contents observed with a flashlight and dental mirror. Nests were not checked during rainy weather, and we did not spend longer than 1.5 h per visit at any colony (Brown & Brown 1996). Once the hatching date for a nest was determined, we did not check that nest again until the nestlings were 10 days old, at which time they were weighed with a 50-g spring balance and examined visually for ectoparasites. Body mass was averaged for all nestlings in a nest, and the mean mass per nest was used in all analyses. The number of nestlings alive at day 10 was used as one measure of reproductive success, as in other studies of swallows (Brown & Brown 1996); if a nest failed during the egg stage or before the nestlings were 10 days old, it was given a '0' in calculating the mean number of surviving nestlings. We also calculated the percentage of all nests to have had at least one egg laid that eventually produced at least one nestling surviving to day 10. Clutch size was the maximum number of eggs recorded in a nest, which, in some cases, contained parasitic eggs laid by a conspecific (Weaver & Brown 2004).

Designating first- and second-wave nestings

Cave Swallows in our study area nested essentially throughout the summer, often with the same individuals presumably nesting at least twice. At most colonies, this resulted in two temporally distinct 'waves' of reproductive activity. In most cases these consisted of a first clutch laid in a nest, followed by a second clutch (and rarely a third) in the same nest. The temporal separation of these two waves of nesting is shown for two representative colonies of small and large size (Fig. 1). However, because birds were not marked, we could not be certain that the same
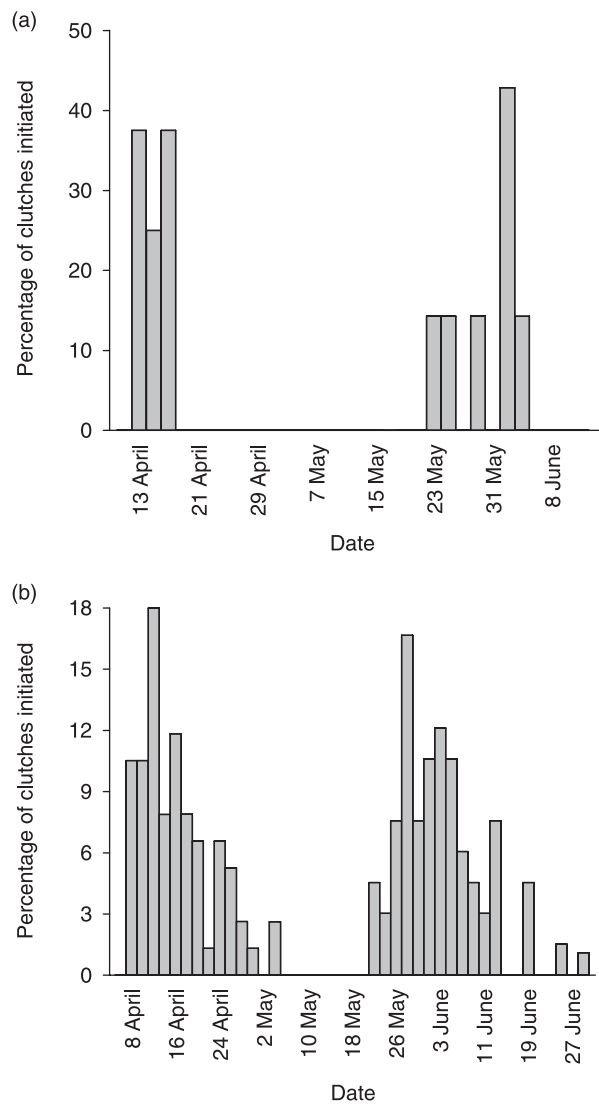

Figure 1. Percentage distribution of clutch initiation dates in two representative Cave Swallow colonies of small (a) and large size (b). The two separate groups in each represent the first and second waves of nesting. No Cliff Swallow nests were included. In (a), *n* = 8 nests in the first wave and *n* = 9 nests in the second wave; in (b), *n* = 77 nests in the first wave and *n* = 73 nests in the second wave.

individuals that had nested earlier were in fact attempting second broods, and thus we refer to these as only the first and second waves. Usually, the first breeding attempt in a given nest was designated as part of the first wave for that colony and the second nesting attempt in that nest as part of the second wave. In a few cases, however, the first egg laid in a nest coincided with the second wave of egg-laying.

Because these clutches were probably laid by late-arriving, perhaps younger birds laying for the first time, or by birds laying for the second time in a new nest, they were functionally distinct from the first clutches laid at the beginning of the breeding season. These late clutches were assigned to the second wave if they met the criteria of being a statistical outlier in the first wave. We used the quartiles method to detect outliers (Zar 1999) and designated dates as outliers through the analysis of boxplots (Schlotzhauer & Littell 1997), with the method repeated until no outliers remained in the first-wave category. Because of the difference in clutch initiation dates between the waves (Fig. 1), the fact that some of the same individuals may have been represented in both waves, and the possibility that the second wave consisted of some birds that differed qualitatively (younger, less experienced) from those in the first wave, we performed all analyses separately for each wave.

Designating colony size

Colony size was defined as the maximum number of nests at a site to have contained one egg (Brown & Brown 1996). We checked all nests at all colonies, so we had an exact colony size for each site. Colony size was designated separately for each wave of nesting. Colony size tended to be smaller during the second wave at most sites, owing in part to nests falling from the substrate, but also because some nests did not receive a second clutch. Consequently, colony sizes for first- and second-wave nestings at the same site usually differ in our analyses.

Most Cave Swallow colonies in our study area also contained active Cliff Swallow nests. Cliff Swallows typically arrived later and sometimes interspersed their nests among the Cave Swallow nests (in many instances touching). In other cases, Cliff Swallows occupied separate sections of a culvert or placed their nests in a linear row adjacent to or abutting a row or cluster of Cave Swallow nests. In all cases, however, regardless of nest placement, the Cave and Cliff Swallows at a site interacted and behaved as a single colony. During alarm responses, both species flew together, circling and calling near the entrance to a colony. After a disturbance, both would return to a colony site at the same time. One definition of a colony is that individuals interact in the mobbing of predators or in foraging (Brown & Brown 1996, 2001). For these reasons, the colony sizes used in most analyses in this paper combined counts of active Cave and Cliff Swallow nests. Other studies have also combined two or more ecologically related species in designating functional colony sizes (Burger 1981). All Cliff Swallow nests at our sites were checked for occupancy, allowing us to know whether one or more eggs were laid in them, but data on Cliff Swallow reproductive success were not recorded. For the 17 colonies during the first wave, the mean ($\pm$ se) percentage of the colony size at a site consisting of Cliff Swallow nests was 11.5 ($\pm$ 3.4) and ranged from 0 to 37.9%. For the same 17 colonies during the second wave, the mean percentage was 11.1 ($\pm$ 3.2) and ranged from 0 to 40.4%. We excluded Cliff Swallow nests from our measure of colony size only for the analyses involving the effect of reproductive success on colony-size change (below).

Measuring colony-size change

To determine how Cave Swallow colony size changed at a site between years, in 2002 we surveyed colony sizes at the same colony sites studied in 2001. Active nests were counted during three principal periods in May, mid June and late July, and the 2002 colony size at a site consisted of the maximum number of active Cave Swallow nests found at any time. This corresponded in most cases to the first period of nesting at a colony, and thus the 2002 colony sizes were first-wave figures. Following Brown *et al.* (2000), we used the annual nest counts (N) to infer the relative annual increase in the number of breeders at a given colony site. The rate of increase was computed as the ratio of the nest counts at each site in the two successive years (2001 and 2002), N_{t+1}/N_t, using first-wave colony sizes in both years. This parameter reflects the demographic balance between the negative effects of adult mortality and emigration, and the positive effects of recruitment of philopatric yearlings and immigration (Brown *et al.* 2000). The ratios for the colony sites were ranked, with 1 being the site with the greatest proportional increase from 2001 to 2002 (highest ratio). Measures of reproductive success at each site were ranked similarly (1 being the highest). Ties were assigned the same rank. In the same manner, for a within-year analysis, we computed the ratio between the number of Cave Swallow nests in the first wave (N_t) and those in the second wave (N_{t+1}).

Statistical analyses were performed with SAS (SAS Institute 1990). Because data were not normally distributed or (in some instances) consisted of ranked categories, we used non-parametric Spearman rank correlations in all analyses.
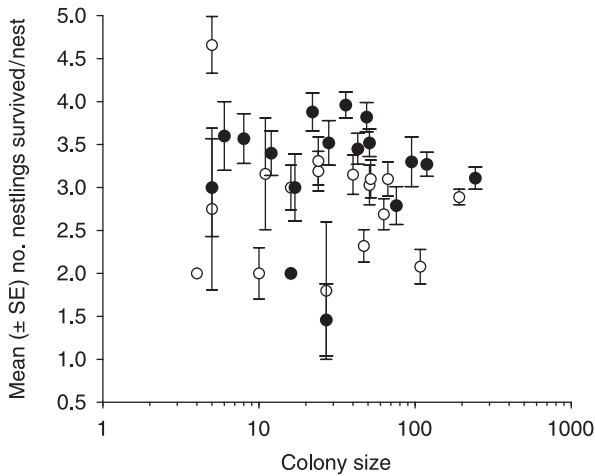
Figure 2. Mean (± se) number of nestling Cave Swallows surviving to day 10 per nest in relation to colony size (number of nests) for first-wave (●) and second-wave nestings (○). Nestling survival did not vary significantly with colony size for either first-wave ($r_s = -0.06$, $P = 0.83$, $n = 17$ colonies) or second-wave nestings ($r_s = -0.07$, $P = 0.79$, $n = 17$ colonies). Sample sizes (number of nests) for each colony, in order of ascending colony size, were (first wave) 4, 5, 7, 10, 1, 13, 18, 15, 23, 26, 37, 28, 40, 39, 30, 48 and 79, and (second wave) 1, 3, 4, 7, 6, 11, 19, 21, 5, 20, 37, 29, 20, 39, 28, 56 and 101.

RESULTS

Reproductive success

The range of colony sizes in our study was 5–243 nests. For the 17 colonies within this range, the mean number of nestlings surviving to day 10 per nest per colony did not vary significantly with colony size for either first- or second-wave nestings (Fig. 2). However, the percentage of successful nests, another index of reproductive success, tended to decline in larger colonies for first-wave nestings (Fig. 3). Most of the smaller Cave Swallow colonies had 100% nest success. The mean Cave Swallow clutch size per nest per colony did not vary significantly with colony size for either first- or second-wave nestings (Fig. 4).

Nestling body mass

As a measure of parental foraging efficiency at different sites, we compared the mean nestling body mass per nest per colony for broods of different sizes across the colony-size range. There was no significant effect of colony size on nestling mass for broods of 1–4 nestlings during either the first or the second wave (Fig. 5). However, mean nestling mass declined sig-
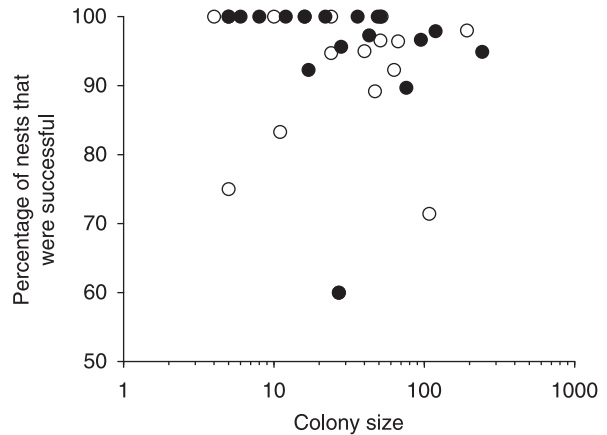

Figure 3. Percentage of Cave Swallow nests that were successful (= 1 nestling surviving to day 10) in relation to colony size (number of nests) for first-wave (●) and second-wave nestings (○). Percentage of successful nests declined with colony size for first-wave nestings ($r_s = -0.46$, $P = 0.06$, $n = 17$ colonies) but did not vary significantly with colony size for second-wave nestings ($r_s = -0.26$, $P = 0.32$, $n = 17$ colonies). Sample size for each colony is given in Figure 2.
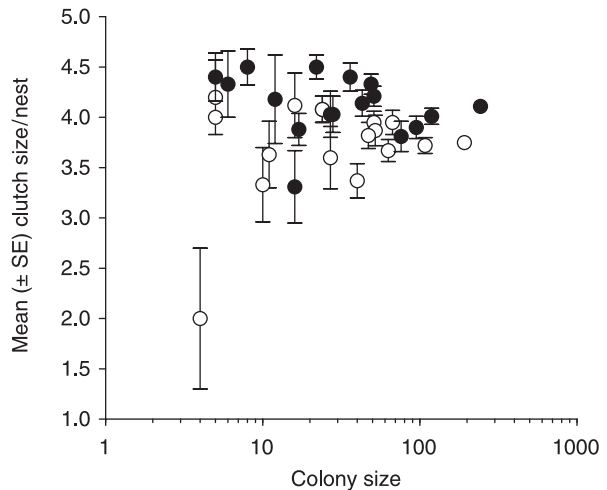

Figure 4. Mean (± se) Cave Swallow clutch size per nest in relation to colony size (number of nests) for first-wave (●) and second-wave nestings (○). Clutch size did not vary significantly with colony size for either first-wave ($r_s = -0.39$, $P = 0.12$, $n = 17$ colonies) or second-wave nestings ($r_s = -0.04$, $P = 0.87$, $n = 17$ colonies). Sample sizes for each colony (number of nests), in order of ascending colony size, were (first wave) 5, 6, 8, 11, 16, 17, 22, 26, 27, 32, 41, 33, 46, 64, 51, 77 and 161, and (second wave) 4, 5, 5, 9, 11, 16, 23, 24, 25, 37, 45, 46, 31, 52, 41, 73 and 145.

nificantly with colony size for broods of five nestlings during the first wave (Fig. 5; no data were available for broods of five during the second wave because few such broods occurred then). Although most
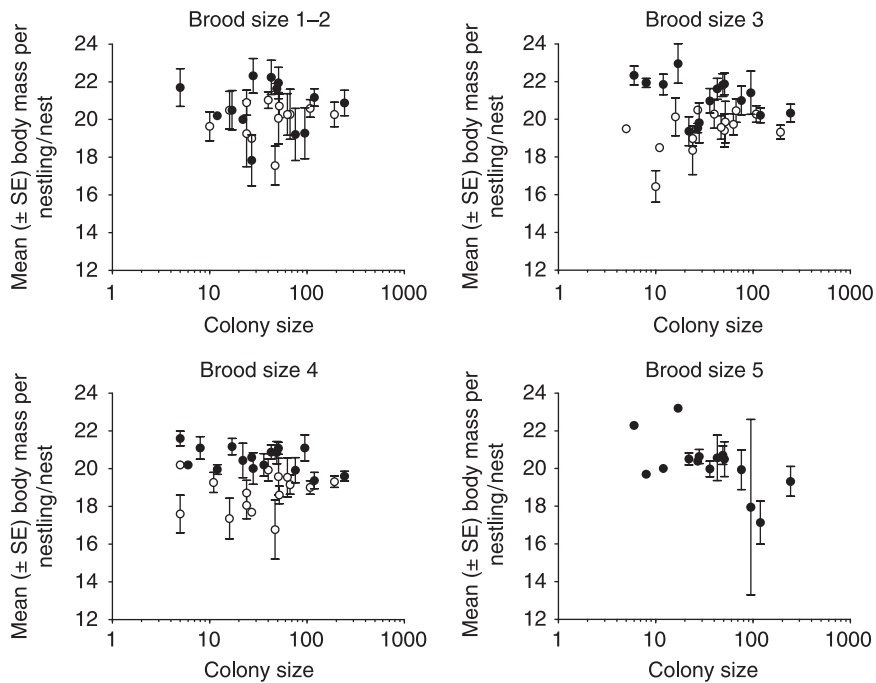
Figure 5. Mean (± se) Cave Swallow body mass (g) per nestling per nest in relation to colony size (number of nests) for broods of different sizes during first-wave (●) and second-wave nestings (○). Body mass did not vary significantly with colony size for broods of 1–2 nestlings during either first-wave ($r_s = -0.03$, $P = 0.93$, $n = 13$ colonies) or second-wave nestings ($r_s = 0.16$, $P = 0.60$, $n = 13$ colonies), nor for broods of three nestlings during either first-wave ($r_s = -0.39$, $P = 0.15$, $n = 15$ colonies) or second-wave nestings ($r_s = 0.44$, $P = 0.10$, $n = 15$ colonies), nor for broods of four nestlings during either first-wave ($r_s = -0.43$, $P = 0.09$, $n = 16$ colonies) or second-wave nestings ($r_s = 0.19$, $P = 0.49$, $n = 15$ colonies). Body mass declined with colony size for broods of five nestlings ($r_s = -0.55$, $P = 0.03$, $n = 15$ colonies).

correlation coefficients were non-significant, the four for first-wave brood sizes were all negative, and the three for second-wave brood sizes were all positive (Fig. 5).

Colony choice and reproductive success

All colony sites used by Cave Swallows in 2001 were used again in 2002 although not necessarily by the same number of birds. A colony site's change in size between 2001 and 2002 was unrelated to reproductive success of Cave Swallows in either the first or the second wave at the site in 2001. This was the case when we used the mean number of nestlings surviving to day 10 as an index of reproductive success (Fig. 6) and when we used the percentage of successful nests (first-wave nestings, $r_s = 0.10$, $P = 0.71$, $n = 17$; second-wave nestings, $r_s = 0.00$, $P = 0.99$, $n = 17$). However, there was a relationship between reproductive success and colony-size change within a year (Fig. 7). Sites that produced more offspring per nest during the first wave tended to decrease less in colony size during the second wave.

DISCUSSION

We found little evidence of an effect of colony size on reproductive success or annual colony choice in Cave Swallows. Studies on other swallows have also found no effect of colony size on reproductive success (Hoogland & Sherman 1976, Snapp 1976, Brown & Brown 1996, Davis & Brown 1999, Safran 2004; cf. Shields & Crook 1987, Huhta 1999). Our results, based on one of the larger single-year sample sizes (number of colonies) available, are consistent with the trend among studies for those with the larger sample sizes to find no significant effect of colony size on annual nesting success (Brown & Brown 2001). The only other studies of colony choice in relation to reproductive success in swallows found that more successful sites tended to increase in size the next year for Cliff Swallows (Brown *et al.* 2000) but not for Barn Swallows (Safran 2004).

Reproductive success and coloniality

The lack of any relationship between colony size and reproductive success in Cave Swallows may reflect
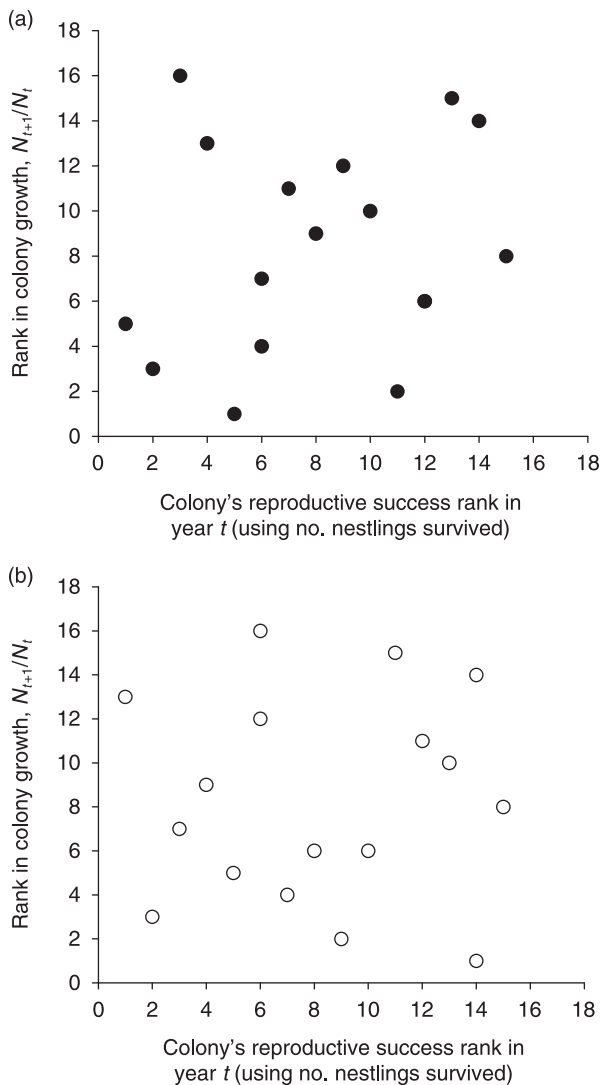
(a)

(b)

Figure 6. Between-year growth rank of a Cave Swallow colony site in 2002 (time $t + 1$) in relation to how the site ranked in reproductive success (measured by the number of nestlings surviving to day 10 per nest) in 2001 (time t). Highest values received rank 1. In (a), reproductive success was for first-wave nestings in year t, and in (b) for second-wave nestings in year t. There was no significant correlation between colony growth and reproductive success ranks in either (a) ($r_s = 0.23$, $P = 0.37$, $n = 17$) or (b) ($r_s = 0.03$, $P = 0.91$, $n = 17$).

Figure 7. Within-year growth rank of a Cave Swallow colony site during the second wave of nesting in 2001 (time $t + 1$) in relation to how that site ranked in reproductive success (measured by the number of nestlings surviving to day 10 per nest) during the first wave of nesting in 2001 (time t). There was a nearly significant correlation between colony growth rank and reproductive success rank ($r_s = 0.47$, $P = 0.06$, $n = 17$).

either that the colony-size range observed in our study was too small for an effect of colony size to be expressed, or that the costs and benefits of coloniality in Cave Swallows balance each other for each colony size. There is evidence for both possibilities in other species. In Purple Martins *Progne subis*, Davis and Brown (1999) concluded that the absence of an effect of colony size on reproductive success resulted
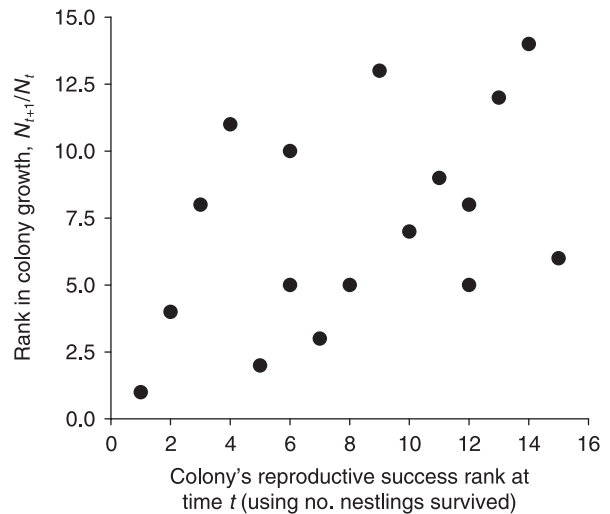
in part because colonies do not typically reach large enough sizes for either the costs or the benefits of group living to be expressed. In Cliff Swallows in some years, reproductive success does not vary with colony size even over a large range of colony size, despite obvious costs and benefits of coloniality that change markedly over that same size range (Brown & Brown 1996). In the case of Cliff Swallows, this seems to reflect a balance between the positive and negative consequences of nesting in a colony of a given size.

In Cave Swallows, colonies can reach up to 1500 nests in size (Selander & Baker 1957, West 1995). Although it appears that the largest colonies occur in natural caverns, we know little about the extent of natural variation in Cave Swallow colony size. Selander and Baker's survey of colonies in caves before the birds began using culverts revealed one with 1500 nests, two with at least 200 nests, eight with 50–200 nests and three with fewer than ten nests. A colony at Carlsbad Caverns in New Mexico apparently consisted of more than 1000 nests, yet other cave sites have contained fewer than 50 birds (Kincaid & Prasil 1956, Johnston 1960, Baker 1962, Wauer & Davis 1972). The colony sizes in our study encompassed part of the known colony-size range, but we had no colonies larger than about 200 nests. Thus, it is possible that a greater effect of colony size (either positive or negative) would be seen in the largest

colonies (1000 or more nests) that did not occur in our study area. On the other hand, our colony-size range of 5–243 nests was relatively large for songbird studies, and over the same range of colony sizes an effect on reproductive success has been detected in some years in the closely related and ecologically similar Cliff Swallow (Brown & Brown 1996). For this reason, our results probably reflect a real absence of colony-size effects in Cave Swallows and are not merely an artefact of not having studied the extremely large colonies.

We found that nestling mass was unaffected by colony size for all but the largest broods of five nestlings. Nestling mass at day 10 is an index of parental foraging efficiency (Hoogland & Sherman 1976, Snapp 1976, Brown 1988), and has been used to infer the extent of the benefits of information transfer during foraging for birds in colonies of particular sizes (Brown & Brown 1996). Cave Swallow foraging behaviour is qualitatively similar to that of Cliff Swallows (C. Brown, M. Brown & H. Weaver pers. obs.), in which colonies serve as information centres and foraging efficiency varies with colony size (Brown & Brown 1996). In our Texas study area, Cave Swallows and Cliff Swallows foraged together, and it is possible that they used each other to gain information on foraging sites. However, we found no evidence that information transfer (if it occurred) or other factors (such as composition of the foraging habitat; Brown *et al.* 2002) affected foraging success as measured by nestling mass. This could reflect either an absence of social foraging in Cave Swallows, in which case no effect of colony size would be expected, or that other factors also affect nestling mass, perhaps in opposing ways. In Cliff Swallows, for example, nestling mass reflects a tradeoff between the advantages of social foraging that increase with colony size and the disadvantages of ectoparasitism that also increase with colony size (Brown & Brown 1996). Interestingly, despite the co-occurrence of Cliff and Cave Swallows in many colonies, we found little evidence that ectoparasitism is important in Cave Swallows. Although we observed some swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*) on the outside of Cave Swallow nests, we found bugs present on only seven nestlings from seven nests in three colonies, and these were not the largest colonies. Thus, it seems unlikely that ectoparasitism influences either reproductive success or nestling mass in Cave Swallows over the range of colony sizes that we studied.

That nestling mass declined in larger colonies for broods of five in Cave Swallows is consistent with data on Cliff Swallows that show increased rates of nestling starvation in larger colonies for larger broods (Brown & Brown 1996). The results seem to suggest that *Petrochelidon* swallows have difficulty raising larger broods in the larger colonies. In Cliff Swallows this was thought to indicate food depletion around the larger colonies that greater foraging efficiency via information transfer could not overcome (Brown & Brown 1996). This is also a possible interpretation in Cave Swallows.

Our results allow us to rule out strong positive effects of coloniality in Cave Swallows. This suggests that these birds do not receive net advantages to group living and that we would not expect directional selection for larger colony sizes in this species. Our results also suggest that there are no strong net costs of coloniality. Whenever individuals suffer lower reproductive success in larger groups, it seems likely that coloniality (with its consequent costs) is forced upon them by a shortage of nesting sites; if more nesting sites were available, presumably they would spread out to reduce the costs (Muldal *et al.* 1985; Brown & Brown 1996, 2000a). Our data thus do not support the interpretation that Cave Swallows form colonies only because nesting sites are limited. However, we acknowledge that we could be misled by the birds' current use of highway culverts and bridges. These sorts of nesting sites are undoubtedly more common in the landscape than caverns and sinkholes, and the birds now may be spreading out and nesting in smaller average colony sizes than they did historically in caves. Data on reproductive success of birds in large cavern colonies would help to resolve whether Cave Swallows ever experience net costs of coloniality. It is also possible that we might have seen different patterns had our study extended across several years. Although we can conclusively dismiss strong group-size effects in the 2001 season, coloniality in Cave Swallows might afford stronger benefits (or costs) in years with unusual weather or decreased food availability, as seen in Cliff Swallows (Brown & Brown 1996, 2004).

If there are no net costs and no net benefits to Cave Swallow coloniality, why do these birds nest in colonies? Other studies finding no effect of group size on fitness have grappled with this question (reviewed in Brown & Brown 2001) with no satisfactory answers. One possibility is that colony size reflects phenotypic distributions of individuals who have different attributes (Brown & Brown 2001). Whenever individuals perform differently in social environments of different types, whether due to fixed inherent

qualities or to age, experience or condition, groups of different sizes may form and be maintained (Brown & Brown 2000b, 2001, Safran 2004). For example, individuals of some species have heritable preferences for particular social environments, reflecting physiological, morphological or behavioural differences among individuals (Brown & Brown 2000b, Møller 2002, Brown *et al.* 2003). In such cases, similarity in fitness among birds in differently sized colonies would be expected, and an effect of colony size might be demonstrated only if colony size was experimentally altered to force birds to breed in a colony to which they were not suited.

Reproductive success and colony choice

Evidence from both solitary and colonial birds indicates that individuals at times may assess the reproductive success of conspecifics at a site and on that basis decide whether to settle there the following year (Danchin *et al.* 1998, Brown *et al.* 2000, Doligez *et al.* 2002). This sort of 'public information' is likely to be of value whenever the quality of a breeding territory or colony site (and the resources associated with it) is autocorrelated between years; otherwise, one cannot predict success at a site next year from how conspecifics did there this year. Some have argued that habitat selection based on assessment of conspecifics can itself cause coloniality (Shields *et al.* 1988, Forbes & Kaiser 1994, Danchin & Wagner 1997).

We found no evidence that Cave Swallows based settlement decisions on past reproductive success at a site. If this occurred, the colonies with the highest reproductive success in 2001 should have increased the most in size in 2002, both through philopatry of past residents and especially through recruitment of other individuals that had assessed the nesting success there in 2001. Our results may reflect a lack of autocorrelation in colony-site quality between years, as found for Barn Swallows (Safran 2004), making this mechanism of habitat selection unreliable. That Cave Swallows did not settle in a way consistent with assessment of conspecifics' past breeding performance may mean that this species simply uses other cues in selecting colony sites. If, for example, individuals base their choice of colony site on their own inherent abilities (Brown & Brown 2000b), how other birds perform at a given site is irrelevant unless an individual can also assess the other birds' inherent abilities and relate them to its own.

We found some indication, however, that reproductive success might have influenced within-year settlement patterns. Although the tendency was for all colony sites to decline in size between the first and second waves, sites with the more successful nests during the first wave did not decline as much in the second wave. This may indicate that newcomers assessed the success of conspecifics and settled at the better sites, but it may also only reflect the fact that successful birds in the first wave were themselves less likely to leave the site and more likely to raise a second brood there. Without data on the identities of the birds present in the first and second waves, the within-year pattern is difficult to interpret.

In conclusion, Cave Swallow reproductive success did not vary with colony size, and these birds' annual settlement decisions were not based on how conspecifics performed at a site the previous year. Coloniality in Cave Swallows appears to confer neither positive nor negative effects on fitness, at least as measured by annual nesting success. Determining how the many potential costs and benefits of coloniality (e.g. Brown & Brown 1996) interact in Cave Swallows to produce the observed patterns, and whether colony size might affect annual survivorship and lifetime reproductive success, are priorities for future studies.

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