COSTS OF COLONIALITY AND THE EFFECT OF COLONY SIZE ON REPRODUCTIVE SUCCESS IN PURPLE MARTINS[1]

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Abstract. We measured how fighting, mate-guarding, ectoparasitism, and annual reproductive success varied with colony size in Purple Martins (*Progne subis*) in Tulsa County, Oklahoma, in 1997. Fights bird^{-1} hr^{-1} changed significantly with colony size, peaking in intermediate-sized colonies. Intensity of mate-guarding by males increased significantly with colony size. Ectoparasitism of nestlings by the martin mite (*Dermanyssus prognephilus*) increased significantly with colony size, but nestling body mass declined with mite load only for broods of six nestlings. Reproductive success did not vary significantly with colony size. Purple Martin colonies probably do not routinely reach large enough sizes for the costs of fighting or ectoparasitism to be important. These birds apparently do not experience direct benefits of coloniality, and groups likely form in response to limited nesting sites. The pattern in reproductive success suggests that Purple Martin colonies represent ideal free distributions of birds with respect to resource availability in each habitat patch, and mean fitness of birds in different patches is similar.

Key words: aggression, ectoparasitism, ideal free distribution, mate-guarding, Progne subis, *Purple Martin, social behavior.*

INTRODUCTION

Animals that nest colonially face inevitable costs of grouping. The two most important are increased competition for resources and a greater incidence of ectoparasitism and disease transmission in groups (Alexander 1974, Hoogland and Sherman 1976). Fighting, regarded as a manifestation of resource competition, and ectoparasitism increase with colony size in various species (Brown and Brown 1996), but relatively little is known in general about how these costs affect reproductive success in colonial birds. Because these and other costs and benefits of coloniality often affect different components of fitness in different ways, measuring their effects directly or in the same currency is difficult. One way around this problem is to focus on reproductive success in relation to colony size, which represents the net effect of all positive and negative group-size effects (Brown and Brown 1996, Danchin and Wagner 1997). Relatively few studies, however, have sought to measure reproductive success in a range of colonies of different sizes; most of the available information comes from studies done with other objectives

and containing data for six or fewer colony sizes (reviewed in Brown and Brown 1996).

The costs of coloniality should be especially important among birds that receive no direct benefits from grouping. This is the case among species that are forced into colonies as a result of limited nesting habitat. Whenever nesting sites are scarce, individuals may have no choice but to aggregate in the few suitable sites (Lack 1968, Wittenberger 1981, Schmutz et al. 1983). Often these species may not receive any of the benefits of coloniality, such as better predator avoidance or increased food-finding. In such cases, the inevitable costs of grouping should still persist and may lower fitness among individuals in the larger groups (Shields and Crook 1987). An inverse relationship between annual reproductive success and colony size is good evidence that coloniality represents a net cost and that animals aggregate simply because of limited breeding sites (Brown and Brown 1996).

The Purple Martin (*Progne subis*) is a semi-colonial swallow that often nests in small groups or solitarily (Brown 1997). In eastern North America, martins nest almost exclusively in multicompartment martin houses in backyards; in western North America the birds still use mostly natural cavities, rock crevices, and abandoned woodpecker holes in dead trees and giant cacti. Although solitary nesting is common (Stutchbury 1991a), colonies as large as 300

pairs have been reported (Brown 1997). The evolutionary history of coloniality in Purple Martins is unclear and subject to debate. Morton (1988), Morton et al. (1990), and Wagner et al. (1996) argued that martins have always had opportunities for colonial nesting, with dead snags containing many potential nesting cavities common before Europeans cut the eastern forest, and that opportunities for males and females to increase their reproductive success by seeking extrapair copulation caused the birds to form colonies. However, Johnston and Hardy (1962), Rohwer and Niles (1979), and Brown (1997) believed that the birds originally were primarily solitary and that the coloniality of eastern populations today reflects a shortage of nesting sites and the high density in which nesting compartments are now presented to the birds in the form of martin houses.

In this paper we examine to what degree competition for resources—in this case nest sites and potential mates—and ectoparasitism vary with colony size in Purple Martins. We assess how costly these may be to the birds, and examine the net effect on fitness for martins breeding in different sized groups. We test whether the costs of coloniality are sufficiently severe to cause annual reproductive success to decline with colony size. If so, this would support the hypothesis that the birds receive no direct benefits of grouping and that they are forced into colonies by a shortage of nesting sites. On the other hand, if Purple Martins experience net benefits of coloniality, annual reproductive success should increase with colony size.

METHODS

Our study was conducted at Purple Martin colonies in residential backyards in and around Tulsa, Tulsa County, Oklahoma, from early March to late July 1997. Fifteen different colonies were studied intensively, although we used data from as many as 24 for some analyses. Martins nested in aluminum martin houses that were mounted on top of retractable steel poles about 5 m above the ground, facilitating lowering for nest checks. At most of our colony sites, introduced House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*) that compete with Purple Martins for nesting sites (Jackson and Tate 1974, Brown 1977b) were controlled by the proprietors of the colonies, usually by removing their nests, and thus these species generally had

little influence on martin behavior or reproductive success in our study.

Prior to egg laying, we scored all fights between birds at different colonies during 1-hr observation periods. Watches were done between 06:30 and 11:00. Fights were defined as any aggressive interaction between two birds, including lunges by one bird at another, physical contact including grappling, and chases without physical contact. Participants were identified according to age and sex, but no birds were color-marked. In order to standardize for nesting stage among colonies, data on fighting were collected only prior to the laying of the first egg in a colony. This is the time of maximum interaction among birds as they form pairs and contest territories (Brown 1979, Stutchbury 1991b, C. Brown, pers. observ.).

From mid March to late May, we collected data on the intensity of mate-guarding among males. Focal pairs were observed for 1-hr periods, and each time that the female departed from a nesting house, her mate's behavior was recorded. The male's waiting time was the duration from when his mate flew from the house until he also flew from the house to follow her. Waiting times were recorded when females left to gather nesting material and to forage. Occasionally a male would leave the colony singly and thus leave his mate unattended. In these cases, we recorded the duration of time the male was absent (while his mate was unattended at the colony). Although none of these birds was color-marked, the martins had already formed pair bonds and claimed territories (nesting sites), so we assumed that when a pair left a given nest and returned to that nest, it was the same pair. Data on mate-guarding were collected on each pair until egg-laying began in their nest. To avoid pseudoreplication in the data on fighting and mate-guarding, multiple observations on the same putative bird (or pair) were averaged, and average values used in statistical analyses.

Colony size during the observations on fighting and mate-guarding was the total number of apparent residents defending cavities on a given day; colony size during the prelaying period changed frequently as more birds arrived at a site. For other analyses based on final colony size, we used the total number of active nests—those containing at least one egg—as our measure of colony size. A Purple Martin colony was defined as any group of birds occupying a clus-

ter of martin houses that interacted at least occasionally (Brown and Brown 1996). The best criterion for defining a colony was whether all birds at a site typically departed from the nesting houses together in response to a passing predator (cat or hawk). In practice, usually a colony was simply all birds occupying the nesting houses in a single backyard.

In late April, we began nest checks to determine date of first egg laying. Once egg laying began, nests were checked every other day, allowing us to determine final clutch size and date of hatching. Once hatching began in a nest, we discontinued checks at that nest until the nestlings were 12 days old. At that time we weighed the nestlings and counted the number of martin mites (*Dermanyssus prognephilus*) visible on each nestling; feather growth at day 12 was still limited enough to enable us to see mites present on the birds' bodies. When nestlings were 15 days old, we counted the number of nestlings alive in each nest as a relative measure of reproductive success. We did not check a nest again after day 15 to prevent premature fledging.

Surveys in June, after all birds had arrived and established residency, were used to census the number of adult and subadult (yearling) males resident at each colony. Adult males are completely blue-black in plumage; yearling males resemble females (Rohwer and Niles 1979). However, only nests of adult breeders were used in these analyses. Our sample of subadult breeders was insufficient for separate statistical analysis. Because adult and subadult Purple Martins differ in arrival date, clutch size, fledging success, and other reproductive parameters (Finlay 1971, Brown 1978a, 1997, Morton and Derrickson 1990), parental age is a potentially confounding factor if data from all age classes are pooled.

RESULTS

COMPETITION FOR NEST SITES: FIGHTING

Most aggressive interactions were between males as they contested territories consisting of one or more nesting compartments within martin houses; occasionally females fought with other females over nesting sites. Fights were seen in most colonies, and fights per bird per hour increased significantly with colony size (Fig. 1). Incidence of fighting seemed to peak in intermediate sized colonies of 20–30 nests. We ob
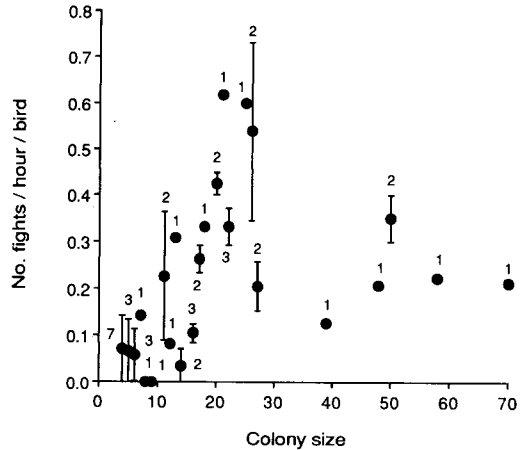

FIGURE 1.   Mean ($\pm$ SE) number of fights per hour per bird in relation to Purple Martin colony size (number of resident birds). Numbers by dots indicate total hours of observation per colony. Fights increased significantly with colony size ($r_s = 0.57$, $P = 0.004$, $n = 24$ colonies).

served no injuries or other deleterious consequences of fighting among martins in our study, although there are records of serious injuries during fighting and of birds being preyed upon by predators such as house cats during intense combat in which participants fall to the ground (Brown 1977a, 1997). Purple Martins gain nesting cavities by repeatedly challenging resident territory holders, usually winning a site through persistence (see Stutchbury 1991b).

Increased fighting in larger colonies could reflect different colony composition in relation to colony size. One way that colony composition potentially varies is in age structure (see Brown and Brown 1996). Subadult (yearling) male Purple Martins preferentially settled in larger colonies; the percentage of males in a colony that were adult decreased significantly with colony size ($r_s = -0.54$, $P = 0.006$, $n = 24$ colonies).

COMPETITION FOR MATES: MATE-GUARDING

Male Purple Martins routinely guarded their mates, following them when they left the nesting houses either to forage or gather nesting material. Among all colonies combined, males followed their mate when she left the colony on 362 (93%) of the total 390 departures observed. Mean ($\pm$ SE) male waiting time averaged 4.2 $\pm$ 5.2 sec ($n = 362$ total departures). Male waiting time decreased significantly with colony size
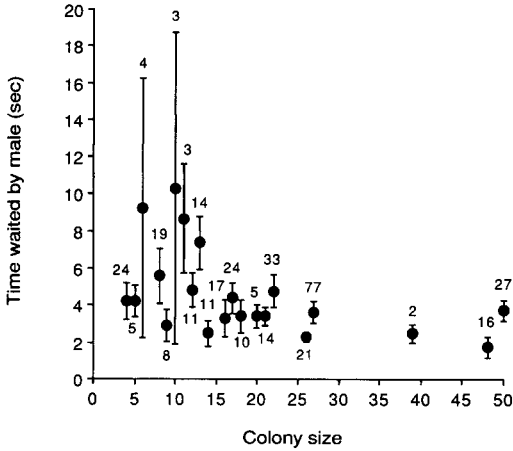
FIGURE 2.   Mean (± SE) time (sec) waited by a male before following his mate from the colony in relation to Purple Martin colony size (number of resident birds). Numbers above bars indicate sample size (number of observations) per colony. Time waited declined significantly with colony size ($r_s = -0.55$, $P < 0.001$, $n = 21$ colonies).

FIGURE 3.   Mean (± SE) time (sec) that a female was unattended by her mate in relation to Purple Martin colony size (number of resident birds). Numbers above bars indicate sample size (number of observations) per colony. Time unattended did not vary significantly with colony size ($r_s = -0.28$, $P = 0.25$, $n = 19$ colonies).

(Fig. 2), meaning males were quicker to follow their mate in larger colonies. This implies greater attentiveness by males and higher levels of mate-guarding in larger colonies.

The average time that females were left unattended by their mates tended to be longer in colonies of 10 nests or less, again suggesting lower levels of mate-guarding in smaller colonies, but average time females were unattended did not vary significantly with colony size when all colonies were considered (Fig. 3). No extrapair copulation attempts were observed in this study, and no intrapair copulations were seen.

ECTOPARASITISM

The mean number of martin mites per nestling increased significantly with colony size (Fig. 4), ranging from 2.1 mites per nestling in the smallest colony to 20.7 mites per nestling in the largest colony. Mites usually clustered at the base of the wing and tail feathers of the nestlings. Nestling body mass declined significantly with extent of ectoparasitism only for brood sizes of six (Fig. 5). Thus, martin mites may have depressed nestling weight and condition only for the largest broods.

REPRODUCTIVE SUCCESS

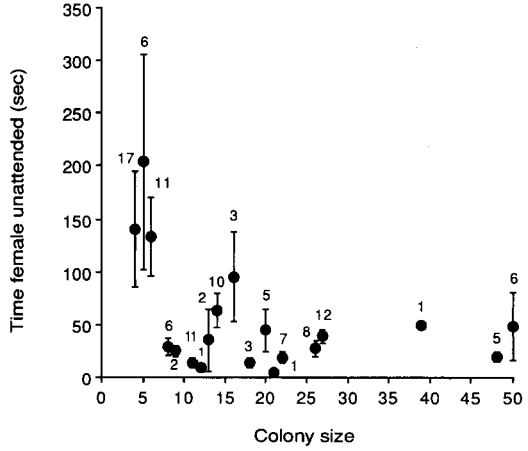Because differences among colonies in reproductive success could reflect initial differences

among colonies in clutch size (Brown and Brown 1996), we first examined whether clutch size varied with colony size in Purple Martins (Fig. 6). There was no significant correlation between clutch size and colony size for the sites in our study (Fig. 6). Annual reproductive success, measured as the number of nestlings sur-
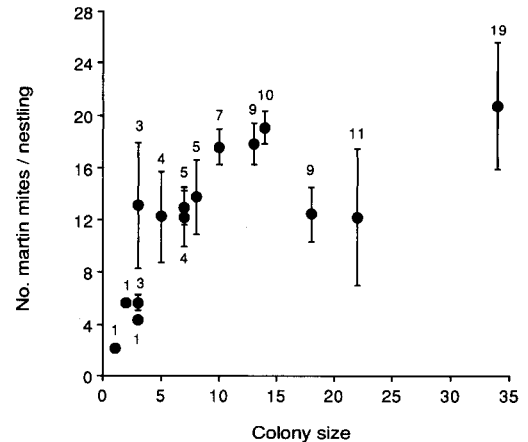

FIGURE 4.   Mean (± SE) number of martin mites per nestling per nest in relation to Purple Martin colony size (number of active nests). Numbers above bars indicate sample size (number of nests) per colony. Mites increased significantly with colony size ($r_s = 0.72$, $P = 0.002$, $n = 15$ colonies).
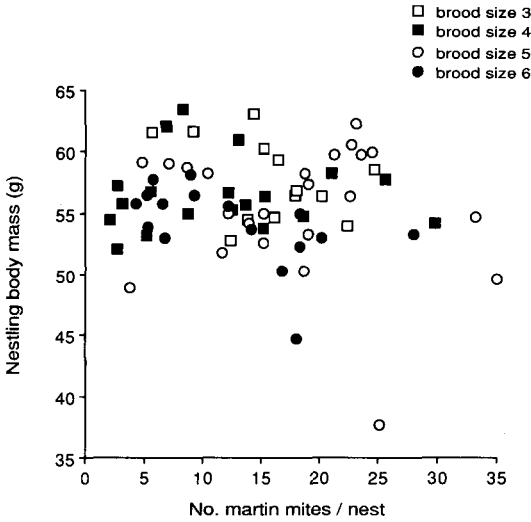
FIGURE 5. Mean (± SE) nestling body mass (g) at 15 days of age per nest in relation to number of martin mites per nestling per nest for different Purple Martin brood sizes. Each dot represents a single nest. For all brood sizes combined, mass did not vary significantly with mite load ($r_s = -0.06$, $P = 0.64$, $n = 72$ nests). For brood size 6, mass declined significantly with mite load ($r_s = -0.58$, $P < 0.02$, $n = 17$ nests) but did not vary significantly with mite load for brood size 3 ($r_s = -0.30$, $P = 0.32$, $n = 13$), 4 ($r_s = 0.11$, $P = 0.66$, $n = 19$), or 5 ($r_s = 0.08$, $P = 0.70$, $n = 13$).

FIGURE 6. Mean (± SE) clutch size per nest in relation to Purple Martin colony size (number of active nests). Numbers by bars indicate sample size (number of nests) per colony. Clutch size did not vary significantly with colony size ($r_s = 0.09$, $P = 0.73$, $n = 12$ colonies).

viving to day 15, did not vary with colony size over the range of colony sizes (1–54 nests) we studied (Fig. 7).

DISCUSSION

The inevitable costs of group-living—increased competition for resources and increased transmission of ectoparasites (Alexander 1971, 1974)—both apply to Purple Martins. Birds in larger colonies fought more over nesting sites and males showed more intense mate-guarding, presumably in response to a greater likelihood of their mate being subject to extrapair copulation. Martins in larger colonies experienced more per-capita parasitism by hematophagous mites. Yet paradoxically, these apparent costs resulted in no net reduction in reproductive success for birds in the larger colonies, at least as measured by annual fledging success.

COSTS OF RESOURCE COMPETITION

Competition for nesting sites should be intense in Purple Martins, given the existence of a large population of nonbreeding floaters (Brown
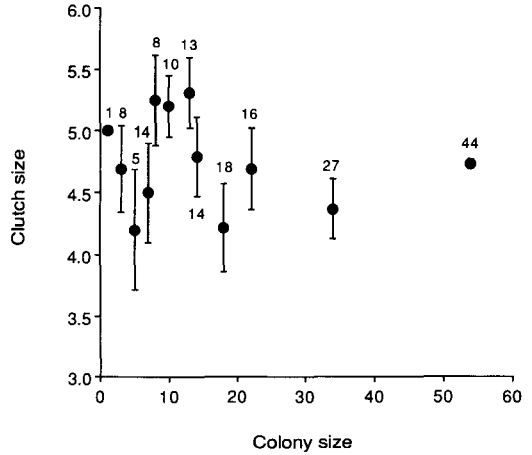
1978b, Rohwer and Niles 1979, Stutchbury 1991b). Floaters contest nesting sites by repeated challenges to residents who often control access to multiple cavities within a martin house. Virtually all fights in Purple Martins are between territory holders and birds seeking nesting sites; established neighbors rarely confront each other
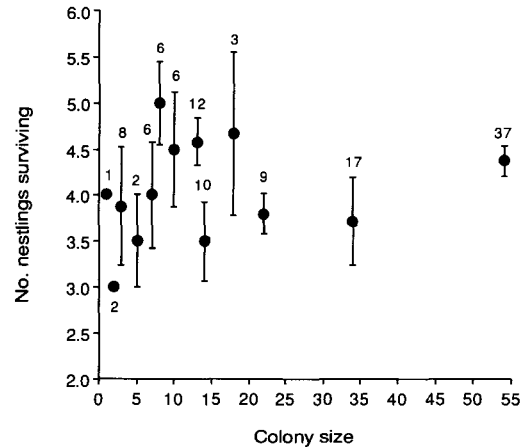

FIGURE 7. Mean (± SE) number of nestlings surviving to 15 days per nest in relation to Purple Martin colony size (number of active nests). Numbers by bars indicate sample size (number of nests) per colony. Number of nestlings surviving did not vary significantly with colony size ($r_s = 0.17$, $P = 0.49$, $n = 13$ colonies).

over nest compartments (C. Brown, pers. observ.). The greater per-capita fight rate in larger colonies suggests that either floaters contest sites more persistently in large colonies or more floaters visit large colonies. We have no data to discriminate among these alternatives, although regardless of cause, residents of large colonies have to contend with more territorial challenges. Rohwer and Niles (1979) assumed that larger Purple Martin colonies were advantageous in some way and that subadult males mimic females in plumage in order to gain access to nesting cavities especially in large colonies. We found disproportionately more subadults settled in large colonies in accordance with Rohwer and Niles' prediction, but this could have reflected simply a lower resident-to-cavity ratio among the numerous martin houses in large colonies. This would improve a subadult floater's odds of wrestling a cavity from a resident's territory. The increased rate of fighting in larger colonies could reflect repeated challenges from subadults who are more persistent in their attempts to acquire nesting cavities in larger colonies.

Fighting per se is costly for Purple Martins and other swallows, because serious injury sometimes results (Kuerzi 1941, Brown 1977a). Our data do not allow us to quantify this cost in relation to colony size, but presumably the risk of falling victim to a house cat (*Felis domesticus*) or other predator during a fight also is greater in large colonies where fights are more frequent.

Purple Martins engage in extrapair copulation and the risk of cuckoldry apparently can be high. Although we observed no extrapair copulations in this study and less than five were seen in a 13-year study in Texas (C. Brown, unpubl. data), up to 43% of the nestlings in nests of subadult males in a Maryland colony were sired by extrapair males (Wagner et al. 1996). We do not know how the incidence of extrapair fertilization varies with colony size in martins, but the increased attentiveness of males and their closer following of females in larger colonies suggest that the birds are sensitive to the greater opportunities for extrapair mating. This presumably reduces the time males have for foraging or nest-building independent of the likelihood of extrapair fertilization. Purple Martins are among only a few species in which mate-guarding intensity is known to vary intraspecifically with social group size (Brown and Brown 1996).

COST OF ECTOPARASITISM

Although infestations of ectoparasitic martin mites clearly increased with Purple Martin colony size, they did not apparently represent a serious cost to these birds. Nestling body mass was significantly lower among highly infested nests only for broods of six nestlings, suggesting that mites may be costly only in large broods where less food is presumably available per nestling. Broods of six occur at a frequency of about 14% in the southern Great Plains region (Brown 1978a). Lowered nestling mass in the larger broods may impair post-fledging survival prospects for Purple Martins, as in other species (Brown and Brown 1996); mites may also affect body mass at fledging or length of the nestling period, which we did not study. Nevertheless, our results showed a relatively limited effect of mites and thus are in contrast to those of Moss and Camin (1970), who performed a mite removal experiment using fumigation and concluded that mites did represent a serious cost to Purple Martins. They found that clutch and brood sizes were larger and nestling mass was greater in the absence of mites. We used only untreated colonies exposed to natural levels of ectoparasitism, and our results may reflect a phenotypic correlation between ectoparasitism and parental ability (Linden and Møller 1989). Perhaps better quality parents produce better quality young who can sustain greater parasite infestations at less net cost, and thus we saw no strong relationship between mite burden and nestling condition. Moss and Camin's (1970) removal experiment still would suggest that exposure to the larger numbers of parasites in larger colonies should have some negative effect.

The mechanism producing the increased ectoparasitism in larger colonies is unknown both for Purple Martins and social species in general (Brown and Brown 1996), but presumably consists in part of a greater likelihood of within-colony parasite transmission. In larger colonies, ectoparasites are more likely to encounter a suitable host through either their own dispersal or incidental or intentional physical contact (e.g., fighting) among hosts (Hoogland 1979). This promotes parasite survival and allows parasites to spread among hosts and potentially overcome density-dependent limitations on reproduction in a single host nest. The close spacing of nest compartments in Purple Martin nesting houses

facilitates movement of mites between nests. Possibly, infested hosts may also prefer to settle in larger colonies, thereby introducing more parasites to the site, as suggested for other swallows (Brown and Brown 1996).

REPRODUCTIVE SUCCESS AND THE EVOLUTION OF COLONIALITY

Reproductive success in Purple Martins did not vary significantly with colony size, suggesting that birds had similar fitness whether breeding in a large or small colony. This was contrary to our initial prediction that martins should suffer a net cost of coloniality and that reproductive success should decline with colony size. Several possibilities may explain the pattern we observed: (1) resource competition, ectoparasitism, and other group-size effects are not costly to martins, (2) these effects are costly, but we measured them over too small a range in colony sizes and too short a time period to detect the costs, (3) there are benefits of coloniality in Purple Martins that interact with the costs to produce no net change in fitness across group sizes, or (4) martin colonies represent ideal free distributions of birds among habitat patches such that fitness is equal among all.

It seems unlikely that fighting and ectoparasitism have no associated costs (see above). Even in well studied species such as Cliff Swallows (*Petrochelidon pyrrhonota*), the cost of fighting has been hard to quantify (Brown and Brown 1996). On occasion, Cliff Swallows become injured or drown during fights, and we have the same anecdotal evidence for Purple Martins. The risk of this during fighting may be small, but it exists and will increase whenever birds fight more. Ectoparasitism is costly at least to birds raising larger broods (this study) and probably represents a serious cost for Purple Martins in general (Moss and Camin 1970).

The absence of a relationship between reproductive success and colony size may more likely reflect the limited range of colony sizes in our study. Purple Martin colonies have been reported to reach 300 nests or more in size (Stutchbury 1991a, Brown 1997), but these colonies are exceptional, and most are less than 35 nests. We had one colony of 54 nests in this study, which was the largest we were aware of in northeastern Oklahoma. The costs of grouping may not express themselves unless colony size is greater than what we observed. In the well studied Cliff

Swallow, many of the group-size effects would not be detected over a colony-size range of only 1–54 nests (see Brown and Brown 1996). Colony size in Purple Martins is highly dependent on availability of nesting sites in a locale with most people installing only one nesting house, and perhaps for this reason colonies larger than 35–50 nests are rare. Unfortunately, there have been no systematic studies of Purple Martin reproductive success using very large colonies ($\geq$ 100 nests), so whether these large groups are beneficial or costly relative to small colonies is unknown.

That we found no net reproductive cost of coloniality in Purple Martins could also mean that these birds experience some benefits of nesting in large colonies. Evidence that large colonies may be advantageous in some way include the apparent preference of yearlings for larger colonies, a pattern also seen in highly colonial Cliff Swallows in which it is thought that yearlings have more to gain from the social benefits of large colonies than do older birds (Brown and Brown 1996); and our finding that sites that were to later contain large colonies were occupied earliest (Davis 1998). The two benefits of large groups most commonly proposed for colonial birds are reduced predation through enhanced detection or deterrence of predators and enhanced food-finding through transfer of information about food sources (Ward and Zahavi 1973, Hoogland and Sherman 1976, Brown and Brown 1996). Purple Martins do form small mobs in response to predators (Stutchbury 1991a), but if larger colonies are more effective in deterring predation, this should have been reflected in our data on annual reproductive success. We observed nothing to indicate that martins in residential backyards in any way avoided predators more effectively in larger colonies. We acknowledge, however, that suburban yards represent a largely predator-free environment unlike that in which the birds' social behavior evolved, and our results (Fig. 7) thus may be artifactual. Purple Martin colonies also did not appear to serve as information centers (Ward and Zahavi 1973). Using the same observational methods as Brown (1986) to show information sharing in Cliff Swallows, we found no evidence that martins routinely followed others from a colony site to food (Davis 1998). Because martins feed on large, single prey (Walsh 1978, C. Brown, pers. observ.) that tend not to occur in swarms, infor-

mation on where food was last found is unlikely to be important (Brown and Brown 1996).

One hypothesis to explain coloniality in Purple Martins is that these birds settle in colonies to gain advantages associated with extrapair mating (Morton et al. 1990, Wagner 1993, Wagner et al. 1996). Some males can benefit from larger colonies by the greater opportunities there to seek extrapair copulations, and females may gain by being able to mate with any genetically superior male in the group; colonies in this case may represent "hidden leks" (Danchin and Wagner 1997). There is some evidence that older males may recruit other yearling males to colony sites with predawn site-advertisement songs (Morton 1985, 1988), presumably with the objective of later cuckolding the subadults. However, extrapair mating tactics change only the variance in reproductive success among individuals within a colony (see Wagner et al. 1996) and have no obvious influence on the mean number of young raised per nest. Thus, advantages associated with extrapair mating could not have initially caused aggregation; birds that began nesting colonially would not have had higher average fitness than birds nesting solitarily. Purple Martin colonies might now serve as "hidden leks," and in this case—and in the absence of other group-size effects—we would not expect any detectable effect of colony size on average reproductive success per nest (Fig. 7). Because not all individuals benefit from them, extrapair mating tactics seem more likely a secondary adaptation arising after the birds initially aggregated.

Given the Purple Martin's reliance on nesting cavities it does not construct, we think the most likely cause of its coloniality is shortage of suitable nesting sites. The distribution of these sites has probably always been unpredictable and now is heavily influenced by artificial multicompartment martin houses that present nesting sites in high density (Johnston and Hardy 1962, Brown 1997). Coloniality may be an inevitable result of this patchy resource. Morton's (1988) historical analysis of Purple Martin nesting sites is consistent with coloniality resulting from limited nesting sites: in areas where dead snags with numerous woodpecker holes occurred in high abundance, martins historically formed large colonies. Nesting-site limitation does not preclude the formation of large colonies (e.g., as in some seabirds) but rather simply explains why

the birds aggregate. The large number of floaters in most Purple Martin populations (Brown 1978b, Rohwer and Niles 1979, Stutchbury 1991b) also is consistent with these birds being limited by availability of breeding sites.

The lack of a relationship between annual reproductive success and colony size is consistent with Purple Martins being distributed among breeding sites in an ideal free way (Fretwell and Lucas 1970, Tregenza 1995). Colony sites represent patches of breeding habitat containing variable amounts of resources (nesting cavities): more nesting cavities at a site lead to more birds occupying that patch. Colony size in Purple Martins appears to be largely determined by how many nesting houses are installed in a given backyard. If the birds are distributed such that each individual gets an equal fraction of the resource, fitness among patches should be equal (Brown and Rannala 1995, Tregenza 1995). At least as measured by mean annual fledging success, fitness seemed to be the same among Purple Martins in all colonies. An ideal free sorting of birds into different colony sizes that reflect local resource abundance is most likely when the social and ecological costs and benefits of group size are weak or nonexistent (Brown et al. 1990). This is exactly the situation in Purple Martins: our results suggest that colonies seldom apparently reach large enough sizes for the costs of grouping to be serious, and there are no obvious benefits to living in colonies. Therefore, the birds fill up the breeding sites roughly in proportion to local nesting site availability, and reproductive success remains the same among sites. Purple Martins may be the first species identified in which coloniality reflects an ideal free sorting of birds among resource patches with equal fitness expectations for all.

ACKNOWLEDGMENTS

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