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Does foraging efficiency vary with colony size in the fairy martin *Petrochelidon ariel*?

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Colonial breeding occurs in a wide range of taxa, however the advantages promoting its evolution and maintenance remain poorly understood. In many avian species, breeding colonies vary by several orders of magnitude and one approach to investigating the evolution of coloniality has been to examine how potential costs and benefits vary with colony size. Several hypotheses predict that foraging efficiency may improve with colony size, through benefits associated with social foraging and information exchange. However, it is argued that competition for limited food resources will also increase with colony size, potentially reducing foraging success. Here we use a number of measures (brood feeding rates, chick condition and survival, and adult condition) to estimate foraging efficiency in the fairy martin *Petrochelidon ariel*, across a range of colony sizes in a single season (17 colonies, size range 28–139 pairs). Brood provisioning rates were collected from multiple colonies simultaneously using an electronic monitoring system, controlling for temporal variation in environmental conditions. Provisioning rate was correlated with nestling condition, though we found no clear relationship between provisioning rate and colony size for either male or female parents. However, chicks were generally in worse condition and broods more likely to fail or experience partial loss in larger colonies. Moreover, the average condition of adults declined with colony size. Overall, these findings suggest that foraging efficiency declines with colony size in fairy martins, supporting the increased competition hypothesis. However, other factors, such as an increased ectoparasitism load in large colonies or change in the composition of phenotypes with colony size may have also contributed to these patterns.

Colonial breeding occurs across a broad range of taxa but is particularly common among the birds where it has evolved on numerous separate occasions, and occurs in at least 13% of species (Lack 1968, Wittenberger and Hunt 1985, Rolland et al. 1998, Brown and Brown 2001). Many potential benefits have been proposed to account for the evolution and maintenance for colonial breeding, although a general framework is lacking and evidence for most of these specific hypotheses is inconsistent or equivocal (reviewed in Wittenberger and Hunt 1985, Danchin and Wagner 1997, Brown and Brown 2001, but see Safran et al. 2007 for a new integrated approach). A common approach to exploring these putative benefits (and costs) of colonial breeding has been to examine how they change with natural variation in colony size (Wittenberger and Hunt 1985, Brown, Stutchbury and Walsh 1990, Brown and Brown 2001). Colony size varies by several orders of magnitude in most colonial birds, and there is often considerable size variation even within the same population (Brown et al. 1990, Danchin and Wagner 1997, Brown and Brown 2001).

Enhanced foraging efficiency is one of the principal benefits proposed for the evolution of colonial breeding,

and a range of hypotheses have been advanced that predict foraging success should increase with colony size (reviewed in Brown and Brown 1996, 2001). These include: (i) the information-center hypothesis that birds at the colony use information from successful foragers to locate food (Ward and Zahavi 1973, Brown 1988a), (ii) the recruitment-center hypothesis that birds forage more efficiently in groups and therefore recruit others to join them at food sources (Richner and Heeb 1996), and (iii) the spatial concentration and local enhancement hypothesis that when food sources are patchily distributed and short-lived, social foraging will be the most efficient way of locating and exploiting the resource (Krebs 1974, Brown 1988b, Buckley 1997).

Alternatively, it has been argued that colonial breeding may have a negative effect on foraging success because of the greater competition for limited food resources (Wittenberger and Hunt 1985, Brown and Brown 2001). Consequently, foraging efficiency has been predicted to decline with colony size because resources close to the colony become depleted, forcing colony members to fly increasingly further to locate food (Brown and Brown 2001). Both processes may also

operate concurrently, such that birds in larger colonies benefit from a greater capacity to locate food, but also suffer from increased competition. In this scenario, net foraging success may be unrelated to colony size or reach an optimum in colonies of intermediate size (Brown and Brown 2001).

While numerous empirical studies have explored the relationship between colony size and reproductive success (reviewed in Brown et al. 1990, Brown and Brown 2001), few have examined direct measures of foraging efficiency, such as the amount of food delivered to broods. In the most comprehensive study, the amount of food received by broods of cliff swallows *Petrochelidon pyrrhonota*, tended to increase with colony size (Brown 1988a, Brown and Brown 1996), but in the congeneric barn swallow *Hirundo rustica*, solitary pairs fed at higher rates than those in colonies in one population (Møller 1987) while no relationship was detected with colony size in another population (Snapp 1976). More commonly, foraging efficiency has been estimated using indirect measures, such as the condition and survival of both chicks and adults. Some of these studies have identified positive correlations, others negative correlations, while many have revealed no variation with colony size (reviewed in Brown and Brown 2001).

The most obvious conclusion from these empirical studies is that there is little consistency, even within populations or among closely related species, as to how foraging success changes with colony size (Brown and Brown 1996, 2001). Some of these studies, however, were based on a limited sample of colonies, and/or report findings from different years, which may be confounded by year effects (Brown and Brown 1996, Weaver and Brown 2005). Moreover, physical variation between colony sites (i.e. area of suitable nesting substrate) may often inhibit the distribution of birds in relation to local food abundance, obscuring associations between foraging success and colony size. Consequently, it remains unclear if the inconsistent findings, both within and between studies, reflect genuine differences in the effect of colony size on foraging efficiency, variation in the importance of confounding variable, or errors introduced by sampling bias or limited sample size.

In this study we investigated how estimates of foraging efficiency varied with colony size in the fairy martin *Petrochelidon ariel*, in terms of brood provisioning rate, nestling condition, proportion of pairs experiencing complete or partial brood loss, and parental condition. Within-pair variation in provisioning rate was also quantified because low variation may suggest that parents can locate food more reliably, potentially enabling them to withstand greater weather-induced fluctuations in food abundance. An electronic monitoring system was used to simultaneously record feeding rates at colonies of different size, allowing us to control for variation in weather conditions, known to strongly affect feeding rates in fairy martins (Magrath 1999, Magrath et al. 2007), and other Hirundines (Turner 1983, Brown and Brown 1996). Furthermore, each pair was monitored for an average of three complete days in an attempt to gain robust estimates of feeding rate.

The study population was ideal to assess relationships with colony size because: (i) all colonies were located under bridges of very similar construction, largely eliminating site differences that could contribute to variation in colony size

and foraging success (ii) the habitat surrounding these sites was relatively uniform, limiting variation in foraging success associated with local geographical features and food availability (iii) there was a relatively large number of variable sized colonies available for comparison in the one season ($n=17$), providing the opportunity to avoid potentially confounding annual effects, and (iv) all old nests were removed from colony sites prior to the breeding season so that they did not influence settlement patterns or subsequent breeding success (Brown and Brown 1996, Safran 2004). Hence much of the variation in the physical environment that may typically influence settlement decisions and reproductive success in colonial species was limited or absent.

Should foraging efficiency increase with colony size, such that parents can locate and capture prey more effectively, we predicted that provisioning rate would be greater and/or show less variation in larger colonies. Consequently, all else being equal, the condition of both nestlings and parents should improve with colony size. Alternatively, if foraging efficiency is inhibited by greater competition, we predicted that feeding rates, chick condition and survival, and adult condition will decline with colony size. If both processes operate concurrently, these measures may be highest in colonies of intermediate size or show no relation with colony size if they negate each other.

Methods

Study species and population

The fairy martin is a small, insectivorous member of the *Hirundinidae*, endemic to Australia. Most populations that breed in southern Australia appear to be migratory, returning from more northerly locations in late winter or early spring (Barrett et al. 2003, Higgins et al. 2006). Breeding occurs in colonies where pairs construct bottle-shaped mud nests, often at very high densities. Traditionally, colonies establish under overhanging cliffs or river banks, in cave entrances and tree hollows, but they now commonly use artificial structures such as bridges, culverts, pipes and mine shafts (Turner and Rose 1989, Magrath 1999, Higgins et al. 2006). Both sexes participate extensively in nest building, incubation and brood care (Magrath 1999). Foraging occurs either individually or in loose groups, and they prey almost exclusively on aerial insects (Higgins et al. 2006).

The study was conducted between August and December 2005 along a 75 km section of the Coleambally outflow channel, near Booroorban ($34^{\circ} 56'S$, $144^{\circ} 52'E$), in southwestern New South Wales, Australia. Along this stretch of the channel, there were 23 low concrete bridges that had all supported colonies in the past, as revealed by the presence of old nests that were in various states of decay. All bridges were approximately 18 m in length and 5 m in width. In early August prior to the arrival of birds, all old nests were removed to prevent birds from re-using nests. By late Sept., colonies had established under 21 of these 23 bridges. The distance between adjacent colonies ranged from 0.6–9.3 km (mean = 3.9 ± 2.2 SD). Birds from neighbouring colonies appeared not to forage together

(pers. obs.), although this possibility could not be excluded, especially for the few colonies that were less than one kilometer apart.

Colony size was estimated for 17 of these colonies using two methods. First, as the maximum number of concurrently active nests over the course of the breeding season (maximum colony size), which provides a single value for each colony. Nests were considered active from the time the first egg was laid until the brood fledged or the nest failed. By this estimate, colony size varied from 28 to 139 pairs (mean = 77.4 ± 29.9 SD). This maximum estimate, however, fails to account for changes in colony size over the course of the season, so a second measure of colony size was derived (current colony size) based on the number of concurrently active nests in a colony on each day of the season. For this estimate, a nest was considered active until 10 days after the brood first left the nest because fledglings typically remain around the colony for several weeks after fledging, often roosting in their natal nest (Magrath 1999). For analyses of feeding rates, we used the actual number of concurrently active nests on the day of monitoring. For analyses of chick condition and survival and adult condition, current colony size was calculated, for each nest, as the average number of concurrently active nests over the period for which the nest was active. This second method provides a nest-specific value that may better reflect the influence of conspecific number on foraging efficiency.

Monitoring nest contents

Once under construction, each nest was numbered and then checked every second or third day. Nest contents were inspected by way of an artificial entrance, constructed prior to egg laying by drilling a hole through the side wall, plastering in a 10 mm section of plastic tubing (50 mm diameter), and filling the hole with a removable polystyrene plug. These inspections allowed us to estimate the date of first egg laying (one egg laid per day), clutch size (maximum number of eggs in the nest), and the date of hatching (estimated age of oldest chick, day of hatching = 1), and fledging success (at least one chick present after d 15) for all nests in the population.

In each of the 17 colonies, a sample of nests with hatchlings was selected for the capture of parents (mean number of nests/colony where at least one parent was caught = 33.2 ± 12.7 SD, range 6–51). These nests were subsequently checked again when the brood was (or would have been) between 12–16 d of age (mean nestling age = 13.6 ± 1.9 SD d) to determine the number and condition of chicks still present in the nest (mean number of broods measured/colony = 26.5 ± 10.1 SD, range 6–40). These nests were selected to represent the range in laying dates within each colony. For nest monitoring, colonies were visited between 09:00–18:00 h for periods of no longer than 60 min to minimize disturbance.

Measuring adult and nestling characteristics

Most adults were caught in the nest when their brood was 5–10 d old. Typically, both parents reside in the nest overnight during incubation and most of the nestling phase

(Magrath 1999), and were trapped by placing cotton-wool in the tunnel entrance before dawn. After sunrise, trapped birds were released into a clear plastic bag. Some other birds were caught using a customised nest trap that permitted birds to enter but not leave the nest.

All adults were fitted with a numbered aluminium leg band for identification. Body mass was measured to the nearest 0.1 g, tarsus length to the nearest 0.1 mm, and wing length to nearest 0.5 mm. Adult condition was calculated as the residual from the regression of body mass over tarsus length for all adults. Sex was determined by the presence (female) or absence (male) of a brood patch (Magrath 1999). Parents that were selected for the monitoring of brood feeding rates were fitted with a transponder, glued to the leg band (Magrath and Elgar 1997). For chicks from sampled broods (see above) we recorded mass, wing length and condition (estimated as the residual from the regression of mass over wing length plus wing length squared for all chicks). Wing length was strongly correlated with age ($r^2 = 0.67$, $n = 1,442$ chicks), and was a better predictor of mass ($r^2 = 0.28$, $n = 1,439$ chicks) than our estimate of age ($r^2 = 0.18$, $n = 1,452$ chicks) which was up to two days out for some chicks because of hatching asynchrony.

Monitoring brood provisioning rates

Nest visit rates were recorded using a transponder monitoring system that allowed us to collect data at multiple colonies simultaneously. Individuals were identified from their transponders as they arrived at, and departed from, their nests. Each transponder emits a unique identification code when in the close proximity of a powered antenna. To detect a bird arriving or departing, the natural tube-shaped nest entrance was replaced with an artificial nest entrance of similar dimensions and external appearance, into which an antenna coil was incorporated. The artificial tube entrance was installed at least two days before monitoring of feeding rates commenced. Each arrival registered for an individual was considered to be a feeding visit. In a previous study on the same population, the accuracy of the system was evaluated by concurrent videotaping of six monitored nests, each for a 3 h period. Ninety-two percent of 163 arrivals were assigned correctly and the probability of an error was independent of parents sex (Magrath et al. 2007).

Visit rates were recorded at a total of 44 nests from 10 colonies in three batches (22 nests from seven colonies between Nov. 10–14, 18 nests from eight colonies between Nov. 19–23, 4 nests from four colonies between Nov. 26–29). The nests in each batch were matched for estimated age (mean age on first complete day of monitoring = 8.0 ± 1.7 SD). The small number of nests in the final batch ($n = 4$) reflects the declining number of nests that remained active at this late stage of the season. Nests in each batch were recorded continuously for between one and four complete days (mean = 3.1 ± 1.2 SD days). For each complete day of monitoring we calculated: (i) the mean hourly visit rate and (ii) the between hour variation in visit rate (expressed as the coefficient of variation) for both male and female parent.

Statistical analyses

To account for the hierarchical structure of our data, analyses were performed using multilevel mixed modelling procedures in MLwiN 2.02 (Rasbash et al. 2004). To examine how feeding rates varied with colony size, a three level, normal response model was constructed with colony (level three), nest identity (level two), and each day of monitoring for each nest as replicate measurements (level one), constituting the random component of the model. This allows all variation in feeding rates to be partitioned across these three levels (or variance components). Potential explanatory variables (fixed component of the model) included colony size, brood size, brood age, parent sex, and day of monitoring (entered as a categorical variable to correct for seasonal effects and daily variation in weather conditions). Possible non-linear effects were explored by including the squared terms of colony size, brood size and brood age. To determine if the relationship with colony size differed between the sexes, we included the interaction between colony size and sex. The two estimates of colony size were strongly correlated ($r^2=0.67$) so were added to the model separately for derivation of their significance. A similar model was constructed to explore the hourly variation in individual feeding rate using the coefficient of variation as the response variable.

To examine how chick mass and our estimate of condition related to colony size, we used a two level model with colony (level two) and brood (level one) as the random component, and mean chick mass and condition for each brood as response variables. Colony size, brood size, brood age, hatching date, and their squared terms were entered as potential explanatory variables. In a similar model, brood variances for mass and condition were estimated (for broods with more than one chick) as the coefficient of variation of the chicks within each brood. Because the results for chick mass and our estimate of chick condition were qualitatively and statistically very similar we only report the analyses for condition.

The probability of complete brood loss between hatching and day 15 was examined using a binomial response model with colony (level two) and nest (level one) as the random component, and broods classified as either successful or not as a binary response variable. Colony size, date and their squared terms were entered as potential explanatory variables. However, complete brood failure before day 15 may have occurred for reasons unrelated to food supply, such as nest desertion, predation or parasitism/disease. Therefore, among the sample of nests where brood size was determined on the day of measurement (see above), we also assessed the probability of partial brood loss (at least one chick missing) using a similar model with broods classified as either complete (no chicks lost) or with partial loss.

To examine how adult condition related to colony size, we used a two level model with colony (level two) and nest (level one) as the random component, and adult mass and condition at the time of capture as response variables. Colony size, date, adult sex, brood age at the time of capture, the squared terms of these variables, and the interaction between colony size and sex were included as potential explanatory variables. Only adults caught during

their nestling period were used for these analyses. Regression analysis was used to determine if within-colony coefficient of variation in adult mass or condition varied with colony size. Because the results for adult mass and our estimate of condition were qualitatively and statistically very similar we only report the analyses for condition.

All multilevel models were derived using backward elimination of the possible explanatory variables (eliminated when $P > 0.05$), with the significance of each term determined using the Wald statistic, which approximates the χ^2 distribution. Model summary tables show all significant ($P < 0.05$) explanatory variables and non-significant variables of interest, along with the variance estimates and sample size for each random parameter (level) of the model. Non-significant interaction and squared terms were not included unless of particular interest.

Results

Provisioning rate and colony size

Feeding rate increased with brood size and varied between days of monitoring (Table 1, model 1a). However, feeding rate was not related to either maximum colony size (Table 1, Fig. 1) or current colony size (Table 1). Males visited the nest more frequently than females, but this difference did not vary with either measure of colony size (Table 1, model 1a). Adding our estimate of chick condition to model 1a (i.e. correcting for day, broods size and brood age) revealed that brood feeding rate was positively correlated to mean chick condition ($\chi^2 = 5.87$, $P = 0.02$).

Variation in feeding rate between hours of the day differed between monitoring days but was unrelated to sex, brood size, brood age, or either estimate of colony size (Table 1, model 1b). Adding our measure of chick condition to model 1b revealed that variation in feeding rate was negatively correlated to mean chick condition ($\chi^2 = 7.57$, $P = 0.006$). This suggests that more variable feeding rates were associated with lower quality chicks, supporting our assumption that higher variability may impede growth.

Nestling survival and condition

Across the population, 7% of 1,273 broods failed between hatching and fledging, while 44% of the 441 sampled broods experienced partial loss before the day of measurement (day 12–16). The probability of complete failure increased strongly with current colony size but also with maximum colony size (Table 2, model 2a, Fig. 2a). Similarly, the probability of partial loss increased with both maximum and current colony size (Table 2, model 2b, Fig. 2b). Partial loss was also more likely to occur in broods that were larger at hatching (Table 2, model 2b), as would be anticipated if partial loss is a consequence of insufficient food.

After correcting for the significant effects of brood age and date, chick condition was related to current (but not maximum) colony size, increasing then declining (Table 2, model 2c, Fig. 3). Adding our measure of parental condition to model 2c revealed that mean chick condition

Table 1. Model summaries examining the effects of colony size, parent sex, and brood characteristics on: (a) nest visit frequency and (b) hourly variation in nest visit frequency. Summaries were derived from normal response, hierarchical, mixed models (see Methods for details). All significant ($P < 0.05$) variables were included in the final model. The two estimates of colony size and their interaction with sex were added to the models separately for derivation of their significance.

	Explanatory variable	Co-efficient	χ^2	df	P
Model 1a.	Monitoring Day		43.38	9	<0.001
<i>Response variable:</i>	Brood size	1.73(0.29)	36.23	1	<0.001
Visit rate (visits/h)	Parent sex	1.39(0.31)	20.41	1	<0.001
	Brood age + brood age ²		9.36	2	0.009
	Maximum colony size	-0.008(0.008)	1.01	1	0.31
<i>Random term variance estimates:</i>	Maximum colony size ²		0.14	1	0.71
Colony - 0.33, $P = 0.25$, $n = 10$	Maximum colony size \times sex	0.016(0.011)	2.13	1	0.14
Pair - 1.04, $P = 0.03$, $n = 42$	Current colony size	-0.0051(0.01)	0.28	1	0.60
Bird-days - 5.7, $P < 0.001$, $n = 234$	Current colony size ²		0.0003	1	0.99
	Current colony size \times sex		0.81	1	0.37
Model 1b.	Monitoring Day		42.90	9	<0.001
<i>Response variable:</i>	Brood size	-0.006(0.015)	0.18	1	0.67
Hourly variation in visit rate	Parent sex	-0.02(0.02)	1.92	1	0.17
	Brood age + brood age ²		4.68	2	0.10
	Maximum colony size	0.001(<0.001)	0.64	1	0.42
<i>Random term variance estimates:</i>	Maximum colony size ²		0.55	1	0.46
Colony - 0.001, $P = 0.38$, $n = 10$	Maximum colony size \times sex	0.001(<0.001)	1.06	1	0.30
Pair - 0.003, $P = 0.08$, $n = 42$	Current colony size		0.01	1	0.92
Bird-days - 0.02, $P < 0.001$, $n = 234$	Current colony size ²		0.64	1	0.42
	Current colony size \times sex	0.001(<0.001)	3.72	1	0.05

was positively related to maternal condition ($\chi^2 = 8.10$, $P = 0.004$), and to a lesser extent paternal condition ($\chi^2 = 5.59$, $P = 0.02$).

There was no clear association between within-brood variation in chick condition and either estimate of colony size (Table 2, model d).

Adult condition

After correcting for seasonal variation and the negative effects of brood size, our estimate of adult body condition declined with current colony size but not maximum colony size (Table 3, Fig. 4). This relationship was similar for both sexes (Table 3). Within-colony variation in adult condition was unrelated to maximum colony size (linear regression models, $n = 17$ colonies, $P = 0.27$).

Discussion

Provisioning rate and colony size

The potential advantages of social foraging are expected to be most significant when food resources are distributed unpredictably in time and space (Buckley 1997, Rolland et al. 1998, Brown and Brown 2001). In the study population, we regularly observed fairy martins foraging in loose groups that sometimes involved the majority of birds in the colony (pers. obs.). These groups suggest that birds were often foraging on aggregations of aerial insects, and we frequently observed ephemeral insect swarms in the vicinity of the colonies. Consequently, we may have expected foraging efficiency to increase with colony size if the probability of swarm detection increased with colony size and swarms were sufficiently large that little depletion occurred, regardless of the number of foraging birds (Brown and Brown 1996). However, we found no indication that parents in larger colonies were more successful in terms of feeding rates. After controlling for the effects of brood size and brood age, provisioning rate was unrelated to colony size for either sex, nor was there any evidence that hourly variation in feeding rate was affected by colony size. These results suggest either that colony size had little influence on foraging efficiency or that the increased likelihood of

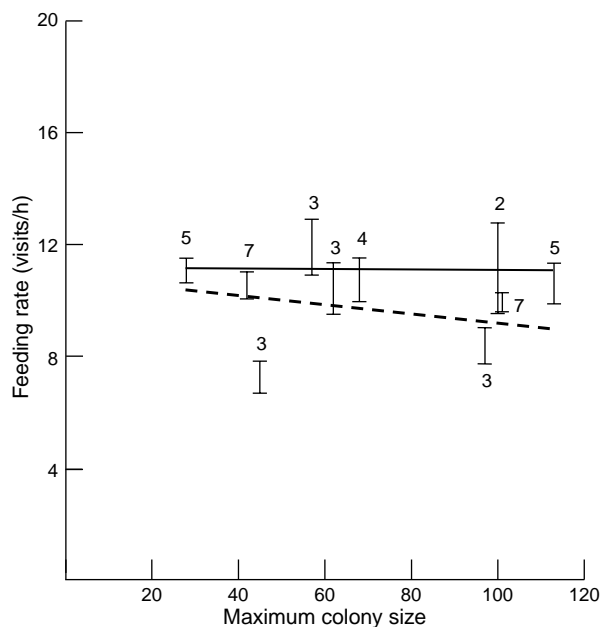


Figure 1. Brood provisioning rates by fairy martin parents in relation to colony size (defined as the maximum number of concurrently active nests). The solid and broken lines show the model predicted relationship for males and females respectively (see Table 1). Vertical bars represent standard errors about the mean feeding rate of sampled parents for each colony. Numbers adjacent to the bars indicate the sample of broods.

Table 2. Model summaries examining the effect of colony size, brood characteristics and seasonal effects on: (a) complete brood loss, (b) partial brood loss, (c) chick condition, and (d) variation in chick condition. Summaries were derived from binomial (models a and b) or normal (models c and d) response, hierarchical, mixed models (see Methods for details). All significant ($P < 0.05$) variables were included in the final model. The two estimates of colony size were added to the models separately for derivation of their significance.

	Explanatory variable	Coefficient	χ^2	df	P
Model 2a: Complete brood loss	Hatch date + Hatch date ²		85.81	2	<0.001
	Maximum colony size	0.027(0.011)	5.63	1	0.02
	<i>Random term variance estimates:</i>				
	Maximum colony size ²		2.08	1	0.15
	Clutch size		0.40	1	0.53
Colony 0.003, $P = 0.03$, $n = 17$	Current colony size	0.092(0.013)	47.84	1	<0.001
	Pair - 0.063, $P < 0.001$, $n = 1273$		0.80	1	0.37
	Current colony size ²				
Model 2b: Partial Brood loss	Clutch size	0.459(0.154)	8.86	1	0.003
	Maximum colony size	0.009(0.004)	5.37	1	0.02
	Maximum colony size ²		0.48	1	0.49
	Brood age		0.94	1	0.33
	Hatch date		0.56	1	0.45
Colony - 0.02, $P = 0.69$, $n = 17$	Current colony size	0.011(0.004)	5.95	1	0.01
	Pair - 0.24, $P < 0.001$, $n = 441$		0.06	1	0.81
	Current colony size ²				
Model 2c: Chick condition	Brood age	-0.09(0.03)	13.43	1	<0.001
	Hatch date	-0.023(0.005)	17.17	1	<0.001
	Current col size + Current col size ²		8.70	2	0.003
	Brood size		0.40	1	0.53
	Maximum colony size		0.66	1	0.42
Colony - 0.045, $P = 0.15$, $n = 17$	Maximum colony size ²		0.02	1	0.89
	Pair - 1.16, $P < 0.001$, $n = 451$				
	Maximum colony size ²				
Model 2d: Variance in condition	Hatch date	0.005(0.002)	5.48	1	0.02
	Brood age		0.67	1	0.41
	Brood size		0.01	1	0.92
	Maximum colony size		0.19	1	0.66
	Maximum colony size ²		0.01	1	0.92
Colony - 0.0001, $P = 0.22$, $n = 17$	Maximum colony size		0.05	1	0.82
	Pair - 0.002, $P < 0.001$, $n = 425$		0.59	1	0.44
	Current colony size ²				

finding food in large colonies was negated by the greater competition for these prey.

Few previous studies have examined brood feeding rate in relation to colony size and those findings were somewhat equivocal. In cliff swallows, prey delivery rate tended to increase with colony size, although not significantly, and there was some indication of a decline in the largest colonies. However, feeding rates were collected over three years, potentially obscuring or confounding the relationship (Brown and Brown 1996). In the barn swallow, solitary pairs feed their brood at a higher rate than those in colonies in one population, although there was no relationship between feeding rate and the number of pairs in the colony that were engaged in nestling feeding (Møller 1987). In another population of barn swallows, feeding rates were unrelated to colony size, but these data were not collected concurrently, contributing to the high variation in feeding rate observed within colonies (Snapp 1976).

The amount of food delivered to broods is not only determined by the provisioning rate. Load size per visit and prey quality will also influence the net value of the food received (Hoogland and Sherman 1976, Wright et al. 1998) and we did not quantify either of these parameters. However, we have at least some evidence that our measure of feeding rate reflected the amount of food delivered as feeding rate was positively correlated with both chick mass and condition, a relationship rarely demonstrated. Other studies have also found good correspondence between feeding rates and the total amount of food delivered (Nolan et al. 2001). Nevertheless, the relationship between feeding rate and amount of food may have varied with colony size (Hoogland and Sherman 1976). Indeed, in the cliff

swallow, the amount of food delivered per visit increased appreciably with colony size, although annual effects may have contributed to this relationship (Brown 1988a, Brown and Brown 1996).

Nestling survival and condition

While we were unable to quantify the amount of food delivered to broods, our measures of complete and partial brood loss and nestling condition may provide useful indirect estimates of foraging success. We found that the probability of both complete and partial brood loss increased with colony size, while chick condition was lowest in the largest colonies. Similar findings have been reported for other hirundinids, as chick mass declined with colony size in bank swallows *Riparia riparia* (Hoogland and Sherman 1976), barn swallows (Snapp 1976), and the largest broods of cave swallows *Petrochelidon fulva* (Weaver and Brown 2005), while partial brood loss increased with colony size in the cliff swallow (Brown and Brown 1996). Our results suggest that broods in smaller colonies were provisioned with more food, indirectly supporting the hypothesis that competition for food and local food depletion increased with colony size. Greater food provisioning may have resulted from larger load sizes and/or greater provisioning rates, that we failed to detect because our analyses of provisioning rates, based on 44 broods from 10 colonies, had lower statistical power than our analyses of condition and survival, based on at least 420 broods. Moreover, variation in partial brood loss and chicks condition stem from cumulative differences accrued

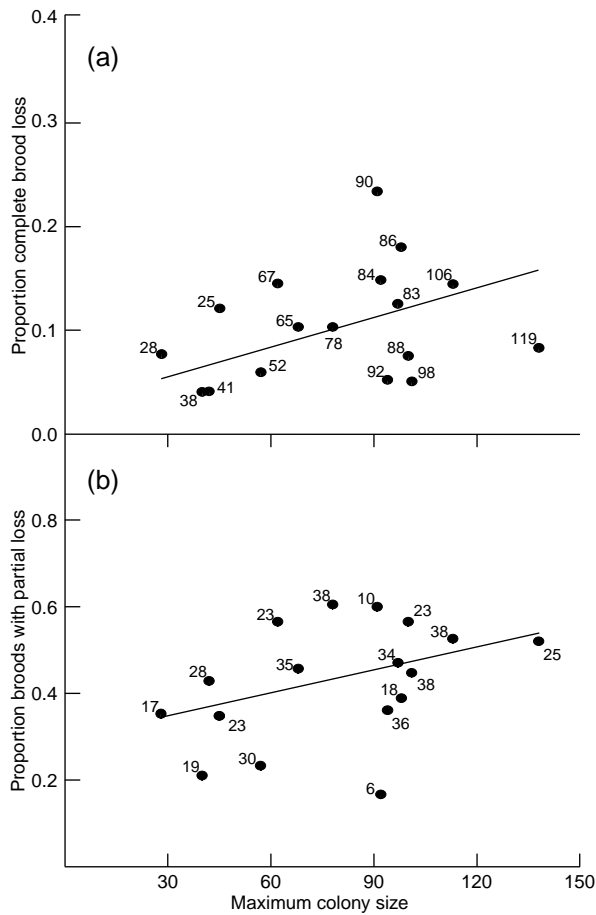


Figure 2. Proportion of fairy martin broods experiencing: (a) complete loss and (b) partial loss in relation to colony size (defined as the maximum number of concurrently active nests). The solid lines show the model predicted relationship (see Table 2). The points represent the proportion of sampled broods incurring: (a) complete loss and (b) partial loss for each colony. Numbers adjacent to the points indicate sample of broods.

throughout the nestling period that are more likely to be detected than differences in feeding rates obtained from only a few days of this period.

Alternatively, our results may be explained by some other factor that inhibits nestling growth and also increases with colony size. In the cliff swallow, for example, the

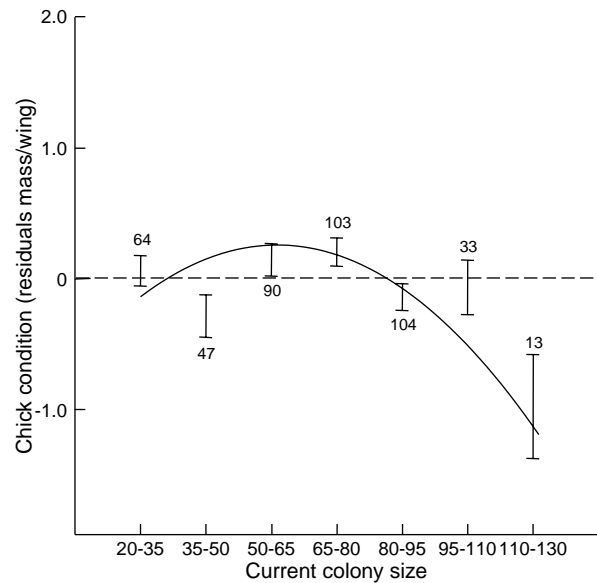


Figure 3. Estimate of chick condition in relation colony size (defined as the current number of active nests). The solid line shows the model predicted relationship (see Table 2). Vertical bars represent standard errors about means of the average condition of the chicks in each brood sampled from within seven categories of colony size. Numbers adjacent to the bars indicate the sample of broods.

absence of a relationship between chick mass and colony size and the greater incidence of partial brood loss in larger colonies, even though the amount of food delivery appeared to increase with colony size, was attributed to an increase in the cost of ectoparasitism (Brown and Brown 1996). Ectoparasite infestations are known to increase with colony size and adversely affect nestling growth and survival in cliff swallows (Brown and Brown 1996) and other Hirundines (Hoogland and Sherman 1976, Shields and Crook 1987, Davis and Brown 1999). While we did not quantify ectoparasite abundance in this study, infestations of a blood-feeding hemipteran were commonly observed on nestlings, and may have contributed to the lower condition and survival prospects of chicks in the largest colonies.

Another possible explanation for the observed decline in chick condition and survival in larger colonies is that the average quality and/or experience of parents was lower in

Table 3. Model summary examining the relationships between date, colony size and sex on parental condition. Summary was derived from a normal response, hierarchical mixed model (see Methods for details). All significant ($P < 0.05$) variables were included in the final model. The two estimates of colony size and their interaction with sex were added to the models separately for derivation of their significance.

	Explanatory variable	Coefficient	χ^2	df	P
<i>Response variable: Body condition</i>	Date + Date ²		6.62	2	0.01
	Brood size	-0.060(0.023)	6.69	1	0.01
	Current colony size	-0.004(0.001)	8.73	1	0.003
<i>Random term variance estimates:</i> Colony - 0.01, $P = 0.10$, $n = 17$ Pair - 0.38, $P < 0.001$, $n = 828$	Current colony size ²	-0.00005(0.00003)	2.12	1	0.15
	Brood age	-0.006(0.005)	1.58	1	0.21
	Parent sex	-0.017(0.041)	0.17	1	0.68
	Maximum colony size	-0.00094(0.0011)	0.69	1	0.41
	Maximum colony size ²	0.00002(0.00003)	0.23	1	0.63
	Current colony size \times sex	-0.002(0.0015)	1.92	1	0.17
	Maximum colony size \times sex	-0.0017(0.0014)	1.27	1	0.26

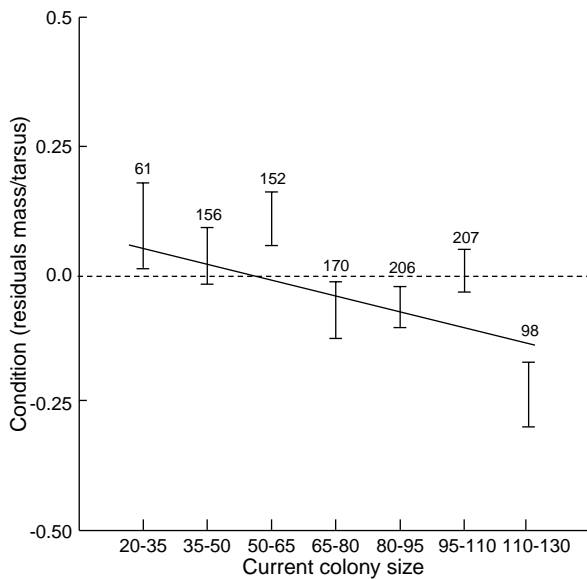


Figure 4. Estimate of adult condition in relation to colony size (defined as the current number of active nests). The solid line shows the model predicted relationship (see Table 3). Vertical bars represent standard errors about the mean condition of adults sampled from seven categories of colony size. Numbers adjacent to the bars indicate the sample of adults.

larger colonies. For example, the proportion of younger birds may have increased with colony size, which could account for the apparent decline in reproductive performance. While we had no information on the age of parents in this study, the proportion of younger birds has been shown to increase with colony size in a range of species including cliff swallows (Brown and Brown 1996) and barn swallows (Shields and Crook 1987).

Adult condition

Another indirect approach to assessing the relationship between foraging efficiency and colony size is to compare the condition of parents across colonies of different size. Body mass, particularly relative to body size (our measure of condition), provides an indication of an individual's energy reserves (Jones 1987), and subsequent survival prospects (Brown and Brown 1996). In our study, the assumption that greater mass indicated superior body condition was supported by the positive relationship between adult condition with both chick condition and chick survival. This suggests that adults prefer to retain at least some energy reserves during the nestling period, even though some weight loss is likely to be an adaptation to reduce the energetic cost of chick feeding activities (Norberg 1981, Witter and Cuthill 1993).

During nestling feeding, the condition of both male and female parents was negatively correlated with concurrent but not maximum colony size. This suggests that adult condition was related specifically to the number of conspecifics, again consistent with the hypothesis that increased competition resulted in food depletion and reduced foraging success in larger colonies. In cliff swallows, the relation between body mass in the latter stages of the breeding season and

colony size was inconsistent between years, although individuals in small colonies tended to lose more weight than those in large colonies (Brown and Brown 1996). This raises the possibility that the negative relationship between adult body condition and colony size, observed in our study, may already have existed at the time of settlement, and did not result from living in colonies of different size.

Conclusions

Overall, our findings suggest that foraging efficiency may have declined with colony size in this population of fairy martins. Feeding rates were similar across our sample of colony sizes, however, the more integrative measures of chick condition and survival declined, while adults in larger colonies were lighter. This suggests that increased competition, leading to local food depletion, may select against the formation of very large colonies.

The distribution of breeding birds across the available colony sites in the study area provides some support for this idea. Colonies established at 21 of the 23 possible sites, suggesting that birds preferred to disperse across most of the possible sites rather than aggregate in a few large colonies, even though suitable nest substrate was plentiful even in the largest colonies. Indeed, a limitation of colony sites may have forced some individuals to join colonies that were larger than optimal. Shortage of nesting habitat has long been considered a possible cause of coloniality and colony size variation (Lack 1968, Snapp 1976), although empirical support for this idea is limited (Brown and Brown 2001).

Alternatively, larger colonies may have been favoured, at least by some individuals, to minimise the risk of predation (Alexander 1974, Brown and Brown 2001). Generally, predation risk is anticipated to decline with colony size, through earlier predator detection, more intense communal defence, and dilutions effects (Brown and Brown 2001, but see Varela, Danchin and Wagner 2007). Consistent with this idea, both daily survival probability during the breeding season and first year survival probability has been shown to increase with colony size in cliff swallows (Brown and Brown 1996, 2004). We observed the predation of an adult and several fledglings by hobby falcons *Falco longipennis*, while sparrow hawks *Accipiter cirrhocephalus*, were suspected in several other cases of adult predation. Consequently, some individuals may have elected to trade-off foraging efficiency with predation risk.

Despite the lack of evidence, enhanced foraging efficiency may still play an important role in the evolution of coloniality in the fairy martin. For example, the benefits of social foraging may primarily accrue over the lower range in natural colony sizes. Our smallest colony was estimated to include at least 28 breeding pairs, larger than the average size of 17 pairs reported for fairy martins at natural sites (Magrath 1999). Most of the gains in foraging efficiency may already have accumulated in colonies of this size, suggesting that foraging efficiency may be optimal in intermediate colony sizes (Pulliam and Caraco 1984, Brown et al. 1990). This is consistent with our data on chick condition which was highest at intermediate sized colonies.

It is also possible that the benefits of larger colonies only become important during periods of adverse weather.

Indeed, in cliff swallows, individuals in small colonies were more severely affected by poor weather than those in large colonies (Brown and Brown 1996). In the season of this study, there were no prolonged periods of cold or rain which are known to reduce breeding success and even result in adult mortality in fairy martins (Magrath 1999) and other hirundines (Hoogland and Sherman 1976, Brown and Brown 1996). Had conditions been less favourable, the relationships between our measures of foraging efficiency and colony size may have been quite different.

Finally, it is clear that correlations between our estimates of foraging efficiency and colony size may have been confounded by the non-random distribution of phenotypes. Such a biased distribution may occur if the optimal colony size varies with phenotype (Shields and Crook 1987, Brown and Brown 1996, Hoi and Hoi-Leitner 1997, Davis and Brown 1999). For example, young birds may be less effective at avoiding predation and favour the security of larger colonies, despite greater costs of ectoparasitism or cuckoldry. Ideally, experimental manipulations of colony size should be employed to decouple such associations between phenotype, food availability and colony size. In practice, however, avoiding such biases may prove difficult because only reductions would be possible and post-manipulation, phenotype-related movement of birds may be inevitable, not to mention the ethical considerations of such an intervention. It is also clear that an understanding of individual-level settlement decisions, which (as implied above) are likely to vary with phenotype, will be necessary to develop a more comprehensive understanding of why colonies form and vary in size (Brown and Brown 2001, Safran et al. 2007).

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