

Seasonal decline in reproductive performance varies with colony size in the fairy martin, *Petrochelidon ariel*

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Abstract Reproductive success within populations often varies with the timing of breeding, typically declining over the season. This variation is usually attributed to seasonal changes in resource availability and/or differences in the quality or experience of breeders. In colonial species, the timing of breeding may be of particular importance because the costs and benefits of colonial breeding are likely to vary over the season and also with colony size. In this study, we examine the relationship between timing of breeding and reproductive performance (clutch size and nest success) both within and between variable sized colonies ($n=18$) of fairy martins, *Petrochelidon ariel*. In four of these colonies, we also experimentally delayed laying in selected nests to disentangle the effects of laying date and individual quality/experience on reproductive success. Within colonies, later laying birds produced smaller clutches, but only in larger colonies. The general seasonal decline in nest success was also more pronounced in larger colonies. Late laying birds were generally smaller than earlier laying birds, but morphological differences were also related to colony size, suggesting optimal colony size also varies with phenotype.

Experimentally delayed clutches were larger than concurrently produced non-delayed clutches, but only in larger colonies. Similarly, delayed clutches were more likely to produce fledglings, particularly later in the season and in larger colonies. We suggest that the reduced performance of late breeding pairs in larger colonies resulted primarily from inexperienced/low quality birds preferring to settle in larger colonies, possibly exacerbated by an increase in the costs of coloniality (e.g., resource depletion and ectoparasite infestations) with date and colony size. These findings highlight the importance of phenotype-related differences in settlement decisions and reproductive performance to an improved understanding of colonial breeding and variation in colony size.

Keywords Timing of reproduction · Date of season · Reproductive success · Colonial breeding · Colony size · Settlement decisions · *Petrochelidon ariel* · Fairy martin

Introduction

In most populations living in seasonal environments, reproductive activities are confined to a distinct period of the annual cycle. Furthermore, over the course of this “breeding season” predictable variation in reproductive success has been documented for a wide range of taxa including, most particularly, birds (Lack 1968; Perrins 1970; Verhulst and Nilsson 2008). Among birds, individuals that reproduce earlier in the season typically enjoy greater success than those breeding later, especially among populations that generally fledge only one brood annually (e.g., Daan et al. 1990; Brown and Brown 1996; Winkler and Allen 1996; Verhulst and Nilsson 2008). Such seasonal patterns may result from changes in food availability (e.g.,

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Verboven et al. 2001) or predation pressure (Götmark 2002). However, correlations between the timing of breeding and success are usually confounded by variation in individual “quality”. For example, individuals that breed earlier in the season may occupy superior territories (Daan et al. 1990), be in better physiological condition (Moreno et al. 1998; Bearhop et al. 1999), or have greater previous breeding experience (Moreno et al. 1998) than later breeders. Consequently, it is often difficult to assess the extent to which seasonal variation in reproductive success is attributable to the effects of timing per se (the date hypothesis), as opposed to differences in phenotypic quality (the quality hypothesis; Brinkhof et al. 1993; Verhulst and Nilsson 2008).

Experimental manipulation of the time at which individuals reproduce has provided the most fruitful approach to this problem. In birds, most of these manipulations have involved either cross-fostering clutches, so that some pairs rear young later and/or earlier than would have occurred naturally (e.g., Wardrop and Ydenberg 2003), or inducing females to lay replacement clutches by removing their original clutch (e.g., Arnold et al. 2004). Both manipulations are imperfect because the overall level of parental investment in incubation (cross-fostering) or egg production (clutch replacement) will also be systematically altered. Nevertheless, these experiments have been informative and suggest that both date and quality are often important, though evidence in support of the date hypothesis has been reported more frequently (Verhulst and Nilsson 2008).

In colonial breeding species, the situation may be further complicated by changes related to the social environment. Some degree of breeding asynchrony may mean that later breeders interact with more colony-mates than earlier birds as the colony increases in size. The opportunity to interact with more conspecifics may provide benefits to later breeding individuals, such as enhanced foraging efficiency through social mechanisms or the reduced risk of adult and nest predation. On the other hand, later breeders may have less choice of nest site, encounter greater competition for food, suffer from greater infestations of parasites, or in the case of males, experience a greater risk of cuckoldry. Such costs and benefits have all been predicted to influence reproductive success in colonial birds (Alexander 1974; Hoogland and Sherman 1976; Wittenberger and Hunt 1985; Brown and Brown 2001) and are likely to vary with the timing of breeding relative to others in the colony. Moreover, the consequences of breeding time may depend on the size of the colony, as most of these social effects are also expected to increase with colony size, at least to a point (Brown and Brown 1996, 2001).

Components of reproductive success have been shown to vary (usually decline) over the course of the breeding season in a range of colonial birds (Brown and Brown

2001). However, few studies have experimentally manipulated the timing of breeding in colonial species (Verhulst and Nilsson 2008), while none appear to have examined if seasonal changes in reproductive performance relate to colony size. Colony-size-related differences in seasonal patterns of reproductive performance may be critical to the processes promoting and maintaining coloniality. Assuming all else is equal, steeper seasonal declines in reproductive performance in small colonies would suggest that the social benefits of coloniality outweigh the costs, at least in terms of reproductive output. Furthermore, this would indicate that these benefits very much depend on the timing of breeding relative to others in the colony. Indeed, important social benefits (and costs) of coloniality may have largely been obscured in many previous studies that have reported on the relationship between mean reproductive performance and colony size (Brown and Brown 2001).

Colony-size-related seasonal variation in the social benefits and costs of coloniality may also contribute to explaining intra-specific variation in colony size. A steeper seasonal decline in reproductive performance in small colonies should promote greater variation in colony size than would be expected from resource distribution alone, because late arriving birds should prefer to settle in larger colonies. Conversely, less variance may be expected if the seasonal decline in performance increases with colony size. In most colonial birds, colony size may vary by several orders of magnitude, even within the same population, but our understanding of this variation remains limited (Brown et al. 1990; Danchin and Wagner 1997; Brown and Brown 2001).

In this study, we aim to examine how timing of laying relates to reproductive performance (clutch size and nest success) within colonies of varying size in the fairy martin, *Petrochelidon ariel*. This population was ideal to assess this question because (a) colony sites were all of similar physical construction, mostly eliminating site differences that could contribute to variation in performance; (b) the habitat surrounding these colony sites was similar, limiting variation in success associated with local food availability; (c) the number of colonies was relatively large ($n=18$), and these were compared in the same season, avoiding potentially confounding annual effects; (d) laying both within and between colonies was asynchronous, allowing us to statistically distinguish between date of season effects as opposed to relative laying date within the colony; and (e) old nests from previous years were removed from all colony sites prior to the arrival of birds, avoiding variation in the timing of laying and reproductive success that may be attributable to the use by some pairs of existing nests.

We examined the reproductive performance of individuals in relation to both natural and experimentally induced variation in timing of laying. Laying was manipulated in a subset of colonies by delaying the construction of system-

atically selected nests. This allowed us to compare the performance of delayed versus non-delayed birds throughout the season and in colonies of different sizes. Additionally, we compared the morphology of birds both across and within colonies to determine if particular phenotypes were associated with timing of laying, colony size, or reproductive performance. These data allow us to determine whether seasonal changes in reproductive performance are a function of colony size, and whether these changes are best explained by individual quality differences or date-related changes in social or other ecological factors.

Materials and methods

Study species and population

The fairy martin is a small, sexually monomorphic, 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 birds 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°56' S, 144°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 so that they could not influence settlement patterns (e.g., Safran 2004). By late September, colonies had established under 21 of these 23 bridges. The distance between adjacent colonies ranged from 0.6 to 9.3 km (mean=3.9±2.2 SD). Birds from neighboring colonies appeared not to forage together (pers. obs.), although this possibility could not be excluded, especially for the few colonies that were less than 1 km apart. Colony size was estimated for 18 of these colonies as the maximum number of concurrently active nests over the course of the breeding season. 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).

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 (assuming one egg laid per day), clutch size (maximum number of eggs in the nest), date of hatching (estimated age of oldest chick; day of hatching = 1), and nest success (at least one chick present after day 15) for all nests in the population. Colonies were visited between 0900 and 1800 h for periods of no longer than 60 min to minimize disturbance.

Manipulation of laying date

The bottle-shaped mud nests of fairy martins are usually constructed over a period of several weeks and weigh about 500 g, or 50 times the adult mass. Once complete, the nest is lined with grass and usually feathers before the clutch is laid (Magrath 1999; this study). We delayed laying by removing about two thirds of the mud structure just prior to its completion, and before lining commenced. Typically, pairs continued construction of the nest following this disruption, as they also do under natural circumstances when part of the structure collapses during construction. Manipulations were performed in a subset of four colonies that had maximum sizes of 28, 42, 94, and 113 pairs. Over a 3-week period from when the first egg was laid at the colony, about one third of nests were delayed. The interval from the delay procedure to laying of the first egg was 16.4±4.8 SD days ($n=107$) compared with 7.6±4.0 days ($n=167$) for nests at the same stage of construction that were not delayed ($F_{1,272}=223$; $p<0.001$, $n=275$ nest), indicating that the manipulation delayed laying for an average of almost 9 days. This interval of 9 days equated to approximately one standard deviation of the variation in laying dates in each of the four experimental colonies (8.88, 11.92, 9.39, and 11.06 days, respectively).

Parental characteristics

In 17 of the 18 colonies, a sample of nests was selected for the capture of parents (mean number of nests/colony where at least one parent was caught was 33.2±12.7 SD; range 6–51). These nests were systematically selected to represent

the full range of laying dates within each colony. Most adults were caught in the nest when their brood was 7–12 days 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 customized nest trap that permitted birds to enter but not leave the nest. Early in the season, some adults were also trapped using mist nets positioned parallel to the bridge. All adults were fitted with a numbered aluminum leg band (supplied by the Australian Bird and Bat Banding Scheme) for identification. Body mass was measured to the nearest 0.1 g, tarsus length to the nearest 0.1 mm, and wing length to the nearest 0.5 mm. Sex was determined by the presence (female) or absence (male) of a brood patch (Magrath 1999). We also derived a measure of body condition by calculating the residuals from the regression of body mass over tarsus length for all adults. The relationship between tarsus length and body mass was very weak ($r^2=0.04$, $n=826$), so this measure of condition was strongly correlated with mass ($r^2=0.96$).

Data analysis

To account for the hierarchical structure of the data, most analyses were performed using the multilevel mixed modeling procedures in MLwiN 2.02 (Rasbash et al. 2004). To examine natural variation in clutch size a two level, normal response model was constructed with colony (level two) and nest identity (level one) constituting the random component of the model. Potential explanatory variables included colony size, laying date of the season, and the relative laying date within the colony (expressed as the deviation of the laying date from the median laying date for each particular colony, such that early clutches within a colony had negative values and late clutches had positive values). Possible non-linear effects were explored by including the squared terms for each of these explanatory terms. The model was first examined with main effects only so that the overall effect of each variable could be estimated to allow comparison with previous studies. Subsequently, all interaction terms were introduced into the model and non-significant ($p>0.05$) terms then dropped until a final model was derived that included only significant terms or terms included in significant interactions. Experimentally delayed nests were excluded from this analysis of the natural patterns. Furthermore, only first or replacement clutches were used for analysis. A similar procedure was used to examine natural variation in nest success, except that we used a binomial response model, with clutches classified as either successful (producing at least one fledgling) or not, as a binary response variable.

Similar models were constructed to assess the effects of the delay treatment on clutch size and nest success in the four experimental colonies. In these models, delay treatment (delayed or not) was entered as an additional explanatory term, along with the interactions between the delay treatment and other explanatory variables.

We examined the relationship between reproductive performance (clutch size and nest success) and parental phenotype (tarsus length, wing length, body mass, condition, and their interactions with sex) using a three-level model with colony (level three), nest (level two), and individual (level one) as random parameters. Experimentally delayed pairs were excluded from these analyses. Using the same dataset and model structure, we also constructed a series of models to examine associations between the same parental phenotypic traits (now used as dependent variables) and laying date, relative laying date, and colony size. For the analyses of body mass, we only used measurements collected when adults were feeding nestlings, because most birds were caught during this period and the mass of fairy martins, unlike wing and tarsus length, is known to vary between different stages of the nesting cycle (Magrath 1999).

In all models, the significance of explanatory terms was determined using the Wald statistic, which approximates the χ^2 distribution. Final models are presented in summary tables that include all significant terms ($p<0.05$), non-significant main effects, and non-significant interaction terms of particular interest.

Results

Temporal distribution of laying

Across the entire population, first and replacement clutches were laid between September 4th and November 18th (median lay date was October 15th; $n=18$ colonies, 1,474 clutches). Comparing between colonies, first clutch date varied from September 4th to October 15th, while the period over which first and replacement clutches were laid ranged from 29 to 70 days (mean= 46.2 ± 9.5 (SD) days; $n=18$ colonies). Colonies in which laying commenced earlier generally became larger in size ($F_{1,16}=7.77$, $p=0.013$), but there was no relationship between colony size and the date of last clutches ($F_{1,16}=0.26$, $p=0.62$, $n=18$). Only 29 second clutches were produced in the population, laid across eight colonies between November 3rd and December 2nd.

Natural variation in reproductive performance

Across the population, clutch size ranged from two to five eggs (mean= 3.7 ± 0.7 SD; $n=1,474$ clutches). Mean clutch

size varied between colonies from 3.5 to 4.1 ($n=18$ colonies). In a model excluding delayed nests, we found that clutch size declined with relative laying date ($\chi^2=16.4$; $df=1$, $p<0.001$; $n=1,237$ clutches), increased with laying date ($\chi^2=12.0$; $df=1$, $p<0.001$) but was unrelated to colony size ($\chi^2=0.003$; $df=1$, $p=0.96$). However, examination of interaction terms between these main effects revealed that the decline in clutch size with relative laying date was only evident in larger colonies (relative laying date \times colony size; Table 1, Fig. 1a).

Population-wide, 82% of 1,443 clutches produced at least one 15-day-old chick (our definition of nest success). Across colonies, the proportion of successful nests ranged from 0.63 to 0.96 (mean= 0.83 ± 0.11 SD; $n=18$ colonies, 1,443 clutches). In a model excluding delayed nests, the proportion of successful nests declined with relative laying date ($\chi^2=9.61$, $df=1$, $p=0.002$, $n=1,196$ clutches) and was strongly related to laying date (combined linear and squared terms of laying date; $\chi^2=39.45$, $df=2$, $p<0.001$), with the greatest likelihood of nest success in mid-season and the lowest in the late season. Again, there was an interaction between relative laying date and colony size, with the decline in nest success most evident in larger colonies (Table 1; Fig. 1b).

Effects of delayed laying on reproductive performance

Among the four experimental colonies, the nest delay had no overall effect on clutch size, regardless of relative laying date (Table 2; Fig. 2a). However, there was a significant interaction between the delay treatment and colony size (Table 2), with delayed pairs producing larger clutches than non-delayed pairs only in the larger colonies (Fig. 2b).

Delayed clutches were generally more likely to be successful than concurrently produced non-delayed clutches ($\chi^2=6.64$, $df=1$, $p=0.01$, $n=296$ clutches). However, the disparity was dependent on relative laying date (delay treatment \times relative laying date; Table 2), as delayed

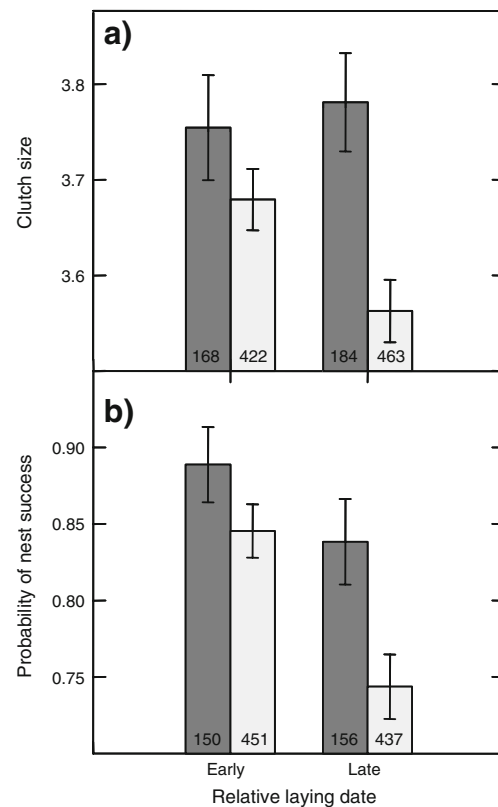


Fig. 1 Clutch size (a) and probability of nest success (b) in relation to relative laying date within colonies and colony size. Values indicated by the bars represent predicted estimates derived from the modeling procedure (see “Materials and methods” and “Results”). The error bars show standard error about the raw data. Numbers inside the bars indicate the sample size of clutches. The mean size of small (gray bars) and large (light gray bars) colonies was 49 ± 13 SD ($n=8$ colonies) and 100 ± 16 SD ($n=10$ colonies) pairs, respectively

clutches were more likely to be successful than non-delayed clutches only when produced relatively late within the colony (Fig. 2c). Furthermore, delayed clutches were more successful than non-delayed clutches only when produced in the larger colonies (delay treatment \times colony size; Table 2, Fig. 2d). Again, in this subset of experimental

Table 1 Model summaries examining the effects of laying date, relative laying date and colony size on (a) clutch size and (b) nest success

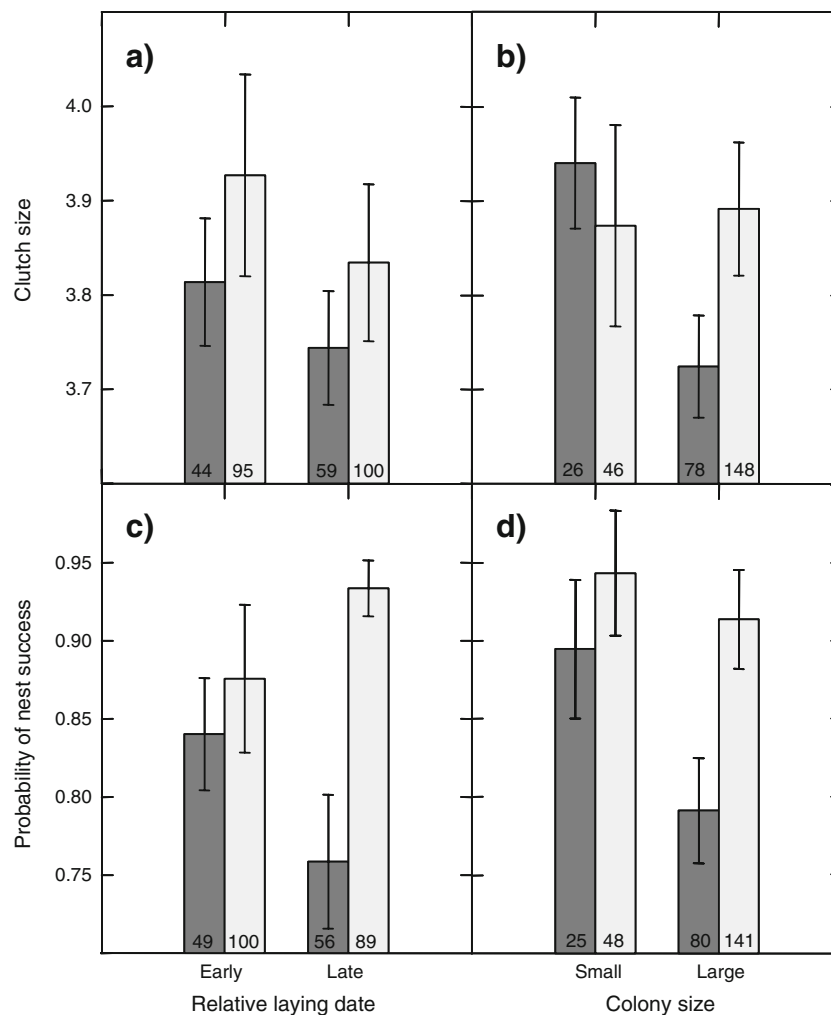
Response variable	Explanatory variable	Co-efficient (\pm SE)	χ^2	df	p
(a) Clutch size $n=18$ colonies, 1237 clutches	Laying date	0.017 (0.007)	6.54	1	0.01
	Relative laying date	-0.008 (0.009)	0.83	1	0.36
	Colony size	-0.00007 (0.002)	0.002	1	0.96
	Relative laying date \times colony size	-0.00015 (0.00006)	5.38	1	0.02
(b) Nest Success $n=18$ colonies, 1196 broods	Laying date	0.80 (0.23)	11.81	1	0.001
	Laying date ²	0.023 (0.005)	17.14	1	<0.001
	Relative laying date	-0.015 (0.039)	0.14	1	0.70
	Colony size	-0.002 (0.007)	0.08	1	0.78
	Relative laying date \times colony size	-0.0008 (0.0003)	6.59	1	0.01

Summaries were derived from normal response, hierarchical, mixed models (see “Materials and methods” for details). All listed variables were included in the final models

Table 2 Model summaries examining the effects of experimentally delayed laying on (a) clutch size and (b) nest success

Response variable	Explanatory variable	Co-efficient (\pm SE)	χ^2	df	p
(a) Clutch size <i>n</i> =4 colonies, 298 clutches	Relative laying date	0.07 (0.07)	1.00	1	0.32
	Colony size	-0.005 (0.002)	6.81	1	0.009
	Delay	-0.35 (0.23)	2.22	1	0.14
	Laying date	-0.07 (0.07)	1.13	1	0.29
	Delay \times colony size	0.0051 (0.0025)	4.10	1	0.04
	Delay \times relative laying date	-0.007 (0.010)	0.48	1	0.48
(b) Nest success <i>n</i> =4 colonies, 294 clutches	Relative laying date \times colony size	-0.0001 (0.0001)	0.91	1	0.34
	Relative laying date	0.19 (0.08)	6.47	1	0.01
	Colony size	-0.021 (0.010)	4.77	1	0.03
	Delay	1.13 (0.44)	5.00	1	0.03
	Laying date	0.43 (0.38)	1.28	1	0.26
	Delay \times colony size	-0.11 (0.05)	4.42	1	0.04
	Delay \times relative laying date	0.34 (0.12)	7.52	1	0.006
	Relative laying date \times colony size	-0.002 (0.0007)	8.63	1	0.003

The summary for model (a) was derived from a normal response model and for (b) using a binomial response model (see “Materials and methods” for details). All variables shown in bold were included in the final models



colonies, the decline in nest success with relative laying date was most evident in the larger colonies (Table 2).

Adult phenotype, timing of laying, and reproductive performance

Within colonies, earlier laying birds generally had longer tarsi ($\chi^2=17.6$, $df=1$, $p<0.001$, $n=17$ colonies, 835 birds) compared to birds laying later. However, both this relationship and the relationship between wing length and relative laying date were dependent on colony size. The difference in tarsus length between earlier and later laying birds was only evident in larger colonies (relative laying date \times colony size; Table 3) such that early laying birds in large colonies had the longest tarsi in the population while late birds in large colonies had the shortest (Fig. 3a). In contrast, the difference in wing length between early and late birds was most pronounced in smaller colonies (relative laying date \times colony size; Table 3, Fig. 3b), despite a positive correlation between wing length and tarsus length ($r=0.29$, $n=1027$, $p<0.001$). As weighed when feeding nestlings, pairs that laid late relative to others in the colony were heaviest, while pairs that produced clutches mid-season were lightest (Table 3; Fig. 3c). A similar non-linear pattern was evident for our measure of body condition (Table 3; Fig. 3d). However, these within-colony patterns in mass and condition were unrelated to colony size (Table 3; Fig. 3).

Parents with longer tarsi produced larger clutches ($\chi^2=5.45$, $df=1$, $p=0.02$, $n=17$ colonies, 822 birds, effect estimate= 0.121 ± 0.052 SE), and while this relationship did not differ significantly between the sexes ($\chi^2=0.28$, $df=1$, $p=0.60$), it was most evident in females (effect estimate 0.147 versus 0.090). There was no relation between clutch size and parental wing length, body mass, or condition for either sex ($p>0.30$ for all). Similarly, nest success was unrelated to any of these morphological traits in either sex ($p>0.25$ for all).

Discussion

The observed decline in our measures of reproductive performance with relative laying time was evident primarily in larger colonies. As far as we are aware, this is the first

study to show that seasonal variation in reproductive performance is a function of colony size. However, similar patterns could be widespread among colonial species, as the data to assess this relationship have rarely been reported. In another study that reports on similar data, both the clutch size and brood size (at day 10) of cliff swallows, *Petrochelidon pyrrhonota*, were shown to decline within colonies over the season, but the magnitude of these declines was unrelated to colony size (Brown and Brown 1996). Below we assess whether our findings are best explained in terms of (a) a general seasonal decline in food availability (date hypothesis), (b) non-random distribution of phenotypes in relation to relative laying time and colony size (quality hypothesis), and/or (c) variation in social costs (or benefits) in relation to relative laying time and colony size (social costs hypothesis).

Seasonal decline in food resources

A decrease in the production of food resources (e.g., emergence of invertebrate prey) has been implicated in the seasonal decline of reproductive performance by a range of studies (Verhulst and Nilsson 2008), but does not appear to provide a sufficient explanation for our findings. First, after statistically correcting for within-colony effects (relative laying date), both clutch size and nest success actually increased with date of the season, suggesting the lack of a population-wide decline in production of food resources. Second, the absence of a seasonal decline in the success of experimentally delayed clutches, in contrast to the decline in success among clutches that were not delayed, suggests that differences in individual quality contributed to the natural variation within colonies. Finally, a general seasonal decrease in production of food resources cannot alone explain why declines in performance were primarily evident in large colonies.

Phenotypic variation with relative laying time and colony size

Later laying by younger individuals has been reported in many birds, including several members of the Hirundinidae (Møller 1994; Winkler and Allen 1996; Banbura and Zielinski 1998; Balbontin et al. 2007). Additionally, young birds often produce smaller clutches and experience lower breeding success than older conspecifics (Forslund and Pärt 1995; Brown and Brown 1996).

In our population, the lower quality and/or experience of later laying birds is implied by the findings from our experimental delay of laying. Delayed pairs tended to produce larger clutches than non-delayed pairs, while among late nesting pairs the likelihood of nest success was greater for delayed than non-delayed pairs. This suggests that naturally late laying birds had poorer parental

◀ **Fig. 2** Effect of the experimental delay on clutch size and nest success in relation to relative laying date (**a** and **c**, respectively) and colony size (**b** and **d**, respectively). Values indicated by the bars (gray bars = non-delayed; light gray bars = delayed) represent predicted estimates derived from the modeling procedure (see “Materials and methods” and “Results”). The error bars show standard error about the raw data. Numbers inside the bars indicate the sample size of clutches. The mean size of small and large colonies was 49 ± 10 SD ($n=2$) and 104 ± 13 SD ($n=2$) pairs, respectively

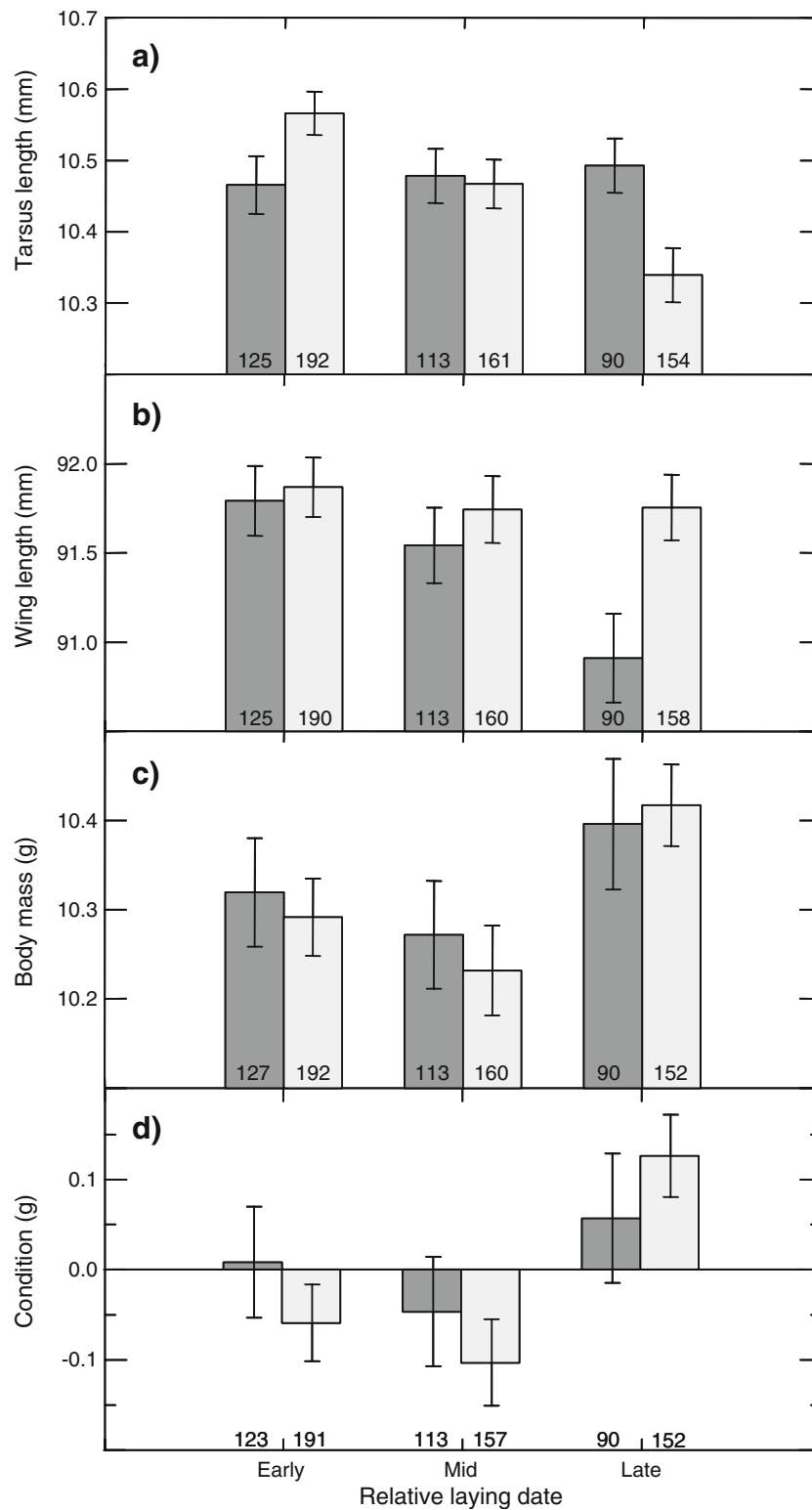


Fig. 3 Parental tarsus length (a), wing length (b), body mass (c) and body condition (d) in relation to relative laying date and colony size. Values indicated by the bars represent predicted estimates derived from the modeling procedure (see “Materials and methods” and “Results”). The error bars show standard error about the raw data.

Numbers inside the bars indicate the sample size of clutches. The mean size of small (gray bars) and large (light gray bars) colonies was 49 ± 14 SD ($n=7$ colonies) and 100 ± 16 SD ($n=10$ colonies) pairs, respectively

Table 3 Model summaries examining relationship between laying date, relative laying date, and colony size, and the (a) tarsus length, (b) wing length, (c) body mass, and (d) body condition of breeding adults

Response variable	Explanatory variable	Co-efficient (\pm SE)	χ^2	df	p
(a) Tarsus <i>n</i> =17 colonies, 835 birds	Colony size	0.00001 (0.0005)	0.0001	1	0.99
	Relative laying date	0.013 (0.005)	7.20	1	0.007
	Laying date	-0.003 (0.003)	1.22	1	0.27
	Sex	0.03 (0.03)	1.00	1	0.32
	Colony size \times relative laying date	-0.00023 (0.00006)	17.10	1	<0.001
(b) Wing <i>n</i> =17 colonies, 839 birds	Colony size	-0.003 (0.005)	0.27	1	0.60
	Relative laying date	-0.07 (0.02)	7.73	1	0.005
	Sex	0.90 (0.15)	35.60	1	<0.001
	Laying date	-0.03 (0.03)	1.26	1	0.26
	Colony size \times timing of laying	0.0006 (0.0003)	5.65	1	0.02
(c) Mass <i>n</i> =17 colonies, 839 birds	Colony size	-0.003 (0.001)	9.90	1	0.002
	Relative laying date	0.017 (0.005)	12.23	1	<0.001
	Relative laying date²	0.0008 (0.0002)	22.06	1	<0.001
	Laying date	-0.014 (0.004)	9.99	1	0.002
	Sex	-0.018 (0.042)	0.18	1	0.67
	Colony size \times relative laying date	0.00004 (0.00008)	0.32	1	0.57
(d) Condition <i>n</i> =17 colonies, 825 birds	Colony size	-0.003 (0.001)	9.56	1	0.002
	Relative laying date	0.016 (0.005)	11.65	1	0.002
	Relative laying date²	0.0008 (0.0002)	25.56	1	0.001
	Laying date	-0.012 (0.005)	7.47	1	0.005
	Sex	0.027 (0.043)	0.41	1	0.52
	Colony size \times relative laying date	0.00003 (0.00008)	0.11	1	0.74

Summaries were derived from normal response hierarchical, mixed models (see “Materials and methods” for details). All variables shown in bold were included in the final models

abilities or invested relatively less in reproduction than those laying earlier. Similar findings have been reported in other experimental studies where delays were achieved by inducing pairs to lay replacement clutches. Compared to non-delayed pairs, delayed pairs produced larger clutches in the starling, *Sturnus vulgaris* (Christians et al. 2001), great tit, *Parus major* (Verhulst et al. 1995), and blue tit, *Cyanistes caeruleus* (Nilsson 2000), while greater fledging success was reported for delayed thick-billed murres, *Uria lomvia* (De Forest and Gaston 1996), magpies, *Pica pica* (De Neve et al. 2004), great tits (Verhulst et al. 1995), and common terns, *Sterna hirundo* (Arnold et al. 2004).

In this study, we also found that the superior performance of the delayed birds, in terms of both clutch size and nest success, was only evident in the larger colonies. In accord with this finding, the disparity in clutch size and nest success between naturally early and late laying birds was also greatest in larger colonies. Neither of these results can be explained by age or quality differences alone unless younger or lower quality birds also tended to settle in larger colonies. This is quite likely as the proportion of younger birds is known to increase with colony size in several other hirundinids, including the cliff swallow (Brown and Brown 1996) and barn swallow (Shields and Crooks 1987).

In this study, we had no information on the age of individuals, but we did find that structurally larger birds

generally laid earlier and (independent of relative laying date) produced larger clutches. Larger structural size may allow birds to store greater energy reserves enabling them to commence breeding earlier and produce larger clutches. Indeed, a study on the cliff swallow revealed that structurally larger birds were more likely to survive an extreme period of cold weather experienced during the breeding season than smaller birds (Brown and Brown 1998). Furthermore, larger size may also confer a mating advantage to males. In another population of fairy martins, males that gained extra-pair paternity were significantly larger than those that they cuckolded (Magrath 1998), a disparity revealed in a number of other species (Akçay and Roughgarden 2007).

Significantly, the decline in structural size with relative laying date was only evident in the larger colonies, indicating that among the late arrivals, the smaller birds appeared to prefer settling in larger colonies. Assuming that smaller birds were of lower quality (at least in terms of reproduction), this non-random pattern of settlement could explain why reproductive performance declined over the season more steeply in larger colonies.

In view of the positive correlation between tarsus length and wing length, it is perhaps surprising that the decline in wing length with relative laying date was only evident in smaller colonies. However, smaller wing length may be

advantageous in terms of foraging efficiency, and there is evidence in the cliff swallow that structural size and wing length can experience simultaneous selection in opposite directions (Brown and Brown 1998). Consequently, birds with relatively long wings for their size may have the least successful phenotype in terms of breeding performance, though selection may favor this profile in other contexts such as migration or predator avoidance.

Adult body mass (and our estimate of condition) was also related to relative laying date, but in this case the pattern was unrelated to colony size. In general, late breeding birds were the heaviest, while those breeding mid-season were the lightest. Among other factors, the body mass of small passerines during brood feeding should be a function of workload (e.g., brood size or age), food availability, and individual quality (Witter and Cuthill 1993). Parents lose mass during the feeding period, but some of this loss is likely to be an adaptation to minimize the energetic cost of brood provisioning (Norberg 1981). Moreover, high quality birds may shed greater mass, without incurring greater risk, because of their superior foraging abilities. Similarly, greater mass loss may be favored when the abundance and predictability of prey is high (Witter and Cuthill 1993). Consequently, we propose that the greater mass of late breeders reflected a combination of lower food abundance, lighter workload due to smaller broods, and lower quality. Age-related differences in the life history trade-off between current and future reproduction may have also contributed, as younger birds may be predicted to breed later and maintain higher body condition than older birds (Partridge 1989). Indeed, in the cliff swallow, late laying females were also heavier than their earlier laying colony-mates and this disparity may have contributed to their greater likelihood of survival to the following breeding season (Brown and Brown 1999).

The complexities of interpreting variation in body mass (and condition) are fascinating (Witter and Cuthill 1993) but reveal the difficulties of drawing conclusions about quality from associations between mass, timing of breeding, and colony size. In the absence much more detailed information, less dynamic phenotypic traits, such as structural size and wing length, are likely to provide more helpful insights into variation in quality. These morphological traits clearly indicate that phenotypes were not distributed randomly with respect to either relative laying date or colony size.

Escalating social cost of breeding in larger colonies

All else being equal, as colonies establish and grow in size, competition for local resources should become more intense, and possibly lead to local resource depletion (Alexander 1974; Brown and Brown 2001). In cliff

swallows, for example, travel distances from colony to foraging patches and the total area over which residents forage increase with colony size (Brown and Brown 1996). In our population, there is also some evidence that foraging efficiency may have decreased with colony size as both chick condition and survival declined over the season and with colony size (Santema et al. 2009).

Ectoparasites have also been shown to increase in abundance with colony size in a range of other Hirundines (Hoogland and Sherman 1976; Møller 1987; Shields and Crook 1987) and are known to adversely affect nestling growth and survival (Hoogland and Sherman 1976; Shields and Crook 1987; Brown and Brown 1996; Davis and Brown 1999). Indeed, in the cliff swallow, ectoparasitism by the swallow bug (*Oeciacus vicarius*) represents the major cost of coloniality and is responsible for most of the seasonal increase in nestling loss (Brown and Brown 1996, 1999). While we did not quantify ectoparasite abundance in this study, infestations of a blood-feeding hemipteran were commonly observed on nestlings and their impact on reproductive performance may have been greater in larger colonies.

However, this “social costs” hypothesis was not supported by our experimental findings. The performance of delayed pairs appeared to be unrelated to colony size, in terms of both clutch size (Fig. 2b) and nest success (Fig. 2d), while the social costs hypothesis would predict their performance to be lower in the large colonies. Having said this, the sample of experimental colonies was very small ($n=4$), so comparisons between colony level variables (such as colony size) have little statistical power (as opposed to within-colony comparisons between delayed and non-delayed pairs). Therefore, we cannot exclude the possibility that social costs contributed to the steeper seasonal decline observed in larger colonies, but we can conclude that social costs were not solely responsible for this effect.

Compensatory benefits of late nesting in larger colonies

Even if the social costs are higher, lower quality and/or younger birds might favor joining larger colonies if there are compensatory benefits. For example, predation risk for adults is anticipated to decline with colony size, through earlier predator detection, more intense communal defense, and dilutions effects (Alexander 1974; Brown and Brown 2001; but see Varela et al. 2007). Consistent with this idea, daily survival probability during the breeding season has been shown to increase with colony size in the cliff swallow (Brown and Brown 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. Younger individuals may have relatively more to gain from these anti-predation mechanisms because of their inexperience. Similarly, younger or lower quality birds may gain disproportionately from the benefits of social foraging if these benefits are of less importance to more experienced or higher quality individuals (Brown and Brown 1996).

Conclusions

The experimental delays in conjunction with our morphometric measurements suggest that the steeper decline in reproductive performance observed in the larger colonies resulted from a preference by younger and/or lower quality birds to settle in larger colonies. This preference may arise because these phenotypes gain disproportionately from social benefits of coloniality such as predator avoidance or enhanced foraging efficiency. Greater social costs may also have contributed to the steeper performance decline in large colonies, though this remains unclear. In conjunction with further experimental delays, additional data on parental age, food availability, ectoparasite abundance, adult survival rates (both within and between season), and chick growth in relation to relative laying date and colony size would help to assess the relative importance of these processes.

Regardless of the mechanism, our findings have significant implications for the study of colonial breeding. Many previous studies have sought to investigate the evolution of coloniality by examining how costs, benefits, and reproductive output vary with colony size (Brown and Brown 2001). This approach has been useful, but variation between individuals within colony has often been overlooked, focusing instead on estimating colony averages (Danchin and Wagner 1997; Safran et al. 2007). Our findings show that the composition of phenotypes within colonies varied with colony size, particularly among later nesting birds. This would confound comparisons between reproductive performance and colony size, even if sampling was conducted throughout the season. In theory, experimental manipulation of colony size may solve this problem by decoupling the association between colony size and phenotype, but in practice these manipulations are likely to be unsuccessful, because of post-manipulation movements, and highly disruptive.

The non-random distribution of phenotypes also suggests that 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, higher quality birds arriving early may favor smaller colonies, distributing themselves quite evenly across most suitable sites. However, lower quality and/or

later arrivals may prefer larger colonies (for reasons discussed above), resulting in a more skewed distribution of colony sizes. Relating the settlement decisions of individual phenotypes to temporal changes in colony characteristics (such as size and composition of nesting stages) may be a rewarding (if challenging) approach to developing a more comprehensive understanding of coloniality and variation in colony size (Brown and Brown 2001; Safran et al. 2007).

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