

Variation in age composition among colony sizes in Cliff Swallows

Charles R. Brown,¹ Erin A. Roche,[†] and Mary Bomberger Brown[‡]

Department of Biological Sciences, University of Tulsa, Tulsa, Oklahoma 74104, USA

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ABSTRACT. Variation in group size is characteristic of most social species. The extent to which individuals sort among group sizes based on age may yield insight into why groups vary in size and the age-specific costs and benefits of different social environments. We investigated the age composition of Cliff Swallow (*Petrochelidon pyrrhonota*) colonies of different sizes over 18 yr at a long-term study site in western Nebraska, USA. Using years elapsed since banding as a relative measure of age for over 194,000 birds, we found that the proportion of age-class-1 swallows (birds banded as nestlings or juveniles or adults in the year of banding) of both sexes increased in larger colonies and at colony sites becoming active later in the summer. Age composition was unrelated to how often a particular colony site was used. The effect of colony size most likely reflected the fact that older birds return to the same colony site in successive years even when the colony size there decreases, and that yearlings and immigrants benefit more from larger colonies than do older, more experienced individuals. The date effect probably resulted in part from later spring arrival by younger and/or immigrant swallows. At fumigated sites where ectoparasitic swallow bugs (*Oeciacus vicarius*) had been removed, age composition did not vary with either colony size or colony initiation date. The patterns reported here appear to be driven partially by the presence of ectoparasites and suggest that the hematophagous bugs influence variation in Cliff Swallow group composition. Our results are consistent with the hypothesis that variation in colony size reflects, in part, age-based sorting of individuals among groups.

RESUMEN. Variación en la composición de la edad entre colonias de diferentes tamaños en *Petrochelidon pyrrhonota*

La variación en el tamaño de grupo es una característica de la mayoría de las especies sociales. La forma en la cual los individuos se distribuyen entre grupos de diferentes tamaños, basado en la edad, puede dar información sobre la razón del porque los grupos varían en tamaño y los costos específicos a la edad y los beneficios de diferentes entornos sociales. Investigamos la composición de la edad de colonias de *Petrochelidon pyrrhonota* de diferentes tamaños a lo largo de 18 años en un sitio de estudio de largo plazo en el oeste de Nebraska, EEUU. Usando los años transcurridos desde el anillamiento como una medida relativa de la edad de mas de 194,000 aves, encontramos que la proporción de las golondrinas de la clase de edad 1 (aves anilladas como polluelos o juveniles o adultos en el año de anillamiento) de ambos sexos incrementó en las colonias mas grandes y en las sitios de colonia que se activaron mas tarde en el verano. La composición de la edad no se relacionó con la frecuencia de uso de un sitio de colonia particular. El efecto del tamaño de la colonia, probablemente reflejó el hecho que aves mayores retornan al mismo sitio de colonia en años sucesivos, incluso cuando el tamaño de la colonia en dicho sitio disminuye y los individuos de primer año e inmigrantes se benefician mas de colonias mas grandes que los individuos mayores y mas experimentados. El efecto de la fecha probablemente es un producto, en parte, de la llegada de individuos juveniles y/o inmigrantes tarde en la primavera. En sitios fumigados donde los insectos ectoparásitos de golondrinas (*Oeciacus vicarius*) fueron removidos, la composición de la edad no varió consistente con el tamaño de la colonia ni con la fecha de inicio de la colonia. Los patrones reportados aquí, aparentemente son el resultado parcial de la presencia de ectoparásitos y sugieren que los insectos hematófagos influyen la variación en la composición del grupo en *Petrochelidon pyrrhonota*. Nuestros resultados son consistentes con la hipótesis que sugiere que la variación en el tamaño de la colonia refleja, en parte, distribución de individuos entre grupos que esta basada en la edad.

Key words: age distributions, coloniality, ectoparasitism, group size, *Petrochelidon pyrrhonota*, social behavior

Most animal social groups vary extensively in size. Among colonial birds, for example, colonies

often differ in size by several orders of magnitude (Brown et al. 1990, Jovani et al. 2008), but the factors generating this sort of variation remain largely unknown for most species (Brown et al. 2013a). Understanding why groups vary in size may provide clues to why animals aggregate in the first place (Brown and Brown 2001, Safran et al. 2007, Spottiswoode 2009), a central question in behavioral ecology (Alexander 1974, Davies et al. 2012).

¹Corresponding author. Email: charles-brown@utulsa.edu

[†]Current address: USGS Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401, USA.

[‡]Current address: School of Natural Resources, University of Nebraska, Lincoln, Nebraska 68583, USA.

One hypothesis for why breeding colonies vary in size (Brown et al. 1990, 2013a) is that differences among individuals lead to asymmetries in the social environment where each individual performs best (Brown 1982, Ranta and Lindstrom 1990, Høglund et al. 1993, Roche and Brown 2013) and that groups of different sizes thus reflect non-random sorting of individuals. For example, competitively inferior individuals may find more food when foraging alone or in a small group, whereas those of average or above average competitive ability do better in a larger group (Ranta et al. 1993). Individuals may also sort among different group sizes based on personality traits (Dardenne et al. 2013, Roche and Brown 2013), with inherently less aggressive animals aggregating more than more aggressive ones (Pruitt et al. 2011).

One factor likely to potentially influence sorting among groups is an individual's age and experience. In some colonial birds, younger, less experienced individuals are more likely to settle in smaller colonies (Fisher and Waterston 1941, Coulson and White 1956, 1958, Robertson 1986, Kharitonov and Siegel-Causey 1988, Burger and Gochfeld 1990). Perhaps because they are unable to compete for space as effectively with the older birds in the larger colonies, they lose mating opportunities to older males (Morton et al. 1990) or must reside on the colony periphery where predation rates are higher (Coulson 1968, Weatherhead 1983, Brown and Brown 1996). However, in other species, naïve individuals with no experience or information about nesting site quality are often attracted to large existing aggregations of individuals (Burger 1988, Podolsky and Kress 1989, Forbes and Kaiser 1994, Brown and Rannala 1995), and this can lead to younger or immigrant birds being overrepresented in larger colonies.

In this study, we explore how age composition varies among colonies of Cliff Swallows (*Petrochelidon pyrrhonota*), one of the most highly social land birds in North America (Brown and Brown 1996). Using data collected over 18 yr from colonies that varied in size from two to 3000 nests (plus solitarily nesting individuals), we examine the effect of colony size, colony initiation date, and site-use history on the proportions of different age classes constituting a colony. Because infestations of blood-sucking ectoparasites are known to af-

fect nest-site selection in some species (Møller et al. 1990), we also evaluate, using a long-term fumigation experiment, to what extent parasites potentially influence the birds' age distributions among colony sizes. We use the results to better understand the extent of age-related sorting among colonies, the role of ectoparasites in colony choice, and the implications of different age compositions for the evolution of coloniality.

METHODS

Study site. We have studied Cliff Swallows since 1982 in the western Great Plains centered near the Cedar Point Biological Station (41°13' N, 101°39' W) in Keith County, southwestern Nebraska, along the North and South Platte rivers and including portions of Deuel, Garden, Lincoln, and Morrill counties (Brown and Brown 1996, Brown et al. 2013a). Cliff Swallows construct gourd-shaped mud nests, often in dense, synchronously breeding colonies. In our study area, the swallows nest mostly on the sides of bridges, in box-shaped road culverts, or underneath overhangs on the sides of cliffs. Colony size varies widely, ranging from two to a maximum of 6000 nests (mean = 404 ± 13 [SE], $N = 2318$ colonies) in our study area, with some birds nesting solitarily (Brown et al. 2013a). Cliff Swallows first arrive in southwestern Nebraska in mid- to late April and initiate egg-laying from May through late June. Most nestlings have fledged by mid- to late July.

Field methods. We conducted an intensive mark-recapture program that began in 1982, with Cliff Swallows captured in mist nets at different colony sites throughout the study area each year (Brown and Brown 1996, 2004a, Roche et al. 2013). We visited sites regularly to capture and recapture nesting adults, and generally visited larger colonies more often than smaller ones. Mist-nets were erected across culvert entrances to capture birds as they exited the colony, dropped over the sides of bridges from above to capture birds as they flushed from their nests, or installed with pulleys on tall poles next to bridges to capture individuals as they approached or left their nests. All birds captured were sexed, weighed, and given a United States Geological Survey band if not already

banded. For subsets of individuals in some years, ectoparasites were sampled, morphometric measurements (wing, tail, tarsus, and bill) taken, blood collected, or the birds' white foreheads marked with colored paint (Brown and Brown 1996, 2009, Brown et al. 2013b). Birds first captured as juveniles in the year of fledging were not used in these analyses unless caught (as an adult) in a later year.

As part of other research (Brown and Brown 1986, 2004b), some colony sites were fumigated each year to remove ectoparasitic swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*), the major nest parasite of Cliff Swallows. Nests were lightly sprayed with a dilute solution of Dibrom, a contact insecticide that is highly effective against swallow bugs. Fumigated colonies were considered separately in all analyses, and comparison of patterns in fumigated and non-fumigated colonies was used to investigate the effect of ectoparasites on colony age composition.

Colony size at each site each year (SIZE) refers to the number of active nests (with ≥ 1 egg) and was determined by checking the contents of nests with a dental mirror and flashlight inserted into each nest's mud neck or from the estimated number of birds present during alarm responses (Brown and Brown 1996, Brown et al. 2013a). A colony's initiation date (DATE) was when breeding birds were first seen at a colony site and subsequently remained there daily. We monitored colony sites frequently by driving among them throughout the nesting season, and if initiation date could not be determined exactly or estimated to the nearest 3 d, that colony was excluded from our analyses. Colony site use (USE) was defined as the proportion of years a site was occupied by at least one pair of birds and calculated only for colony sites with ≥ 10 yr of occupancy data.

Colonies at a given colony site in different years were considered independent units of analysis because colony size at a site and the birds resident there often varied from year to year. A colony site refers to a physical structure at a particular locale where birds nested, whereas a colony refers to a collection of individuals at a given site (Brown et al. 2013a). Colony sites tended to be spatially clustered along physiographic landscape features, such as the South Platte River near Roscoe, the Union Pacific Railroad tracks near Keystone, or the

Ash Hollow area in Garden County. We made seven cluster designations (REGION) based on these natural groupings to account for potential differences in netting effort among the groups of colonies (Brown and Brown 2000). Because some clusters were visited more often than others in the course of other research activities, the extent of banding of colony residents may have varied among clusters, potentially influencing the relative ages (see below) recorded among the birds captured there. To control for any non-independence brought about by shared site effects, we incorporated colony site (SITE) and REGION as random effects in our analyses (see below).

Designating relative age. Age in these analyses refers to minimum age since the year of first banding and is thus a relative measure. Each bird captured as an adult was given a relative age score, with adults in the year of banding receiving a "1," those the next year after being banded a "2," and so on. Birds of known age when first banded (i.e., nestlings or juveniles) were given their exact age (to the nearest year) if later caught as a breeding adult. Because so many breeding adults in our colonies were captured each year (Table 1), most that were unbanded in a given year were locally hatched yearlings or immigrants from outside the study area (who are also likely yearlings; Brown and Brown 1996, Brown 1998). Comparison of annual survival and recapture for birds of relative age (as defined here) and those of actual known age showed similar results, indicating that relative age is a useful index of true age (Roche et al. 2013). Other long-term studies of swallows have also treated adults caught unbanded in a given year as yearlings (Møller 1994, Saino et al. 2004). We began mark-recapture as early as 1982, but we used no years prior to 1994 in these analyses to allow time for banded individuals (of different relative ages) to accumulate in the population.

Statistical methods. The proportion of each age class (1, 2, 3, 4, 5, and ≥ 6 yr) by sex was expressed as the number of birds of that age divided by the total number of birds of each sex caught at a colony site per year. Colony size was log-transformed and all covariates were standardized to a mean of zero and a standard deviation of 1 (e.g., $[(x - x_{\text{mean}})/x_{\text{sd}}]$).

Use of beta regression is recommended when response data are highly skewed or heterodastic

Table 1. Sample sizes (total number of colony sites, colony size range, and total birds caught) for each year in a study of age composition of Cliff Swallow colonies. Total number of colony sites and total birds are also separated by fumigated (parasite-free) and non-fumigated colonies.

Year	Total number of colony sites (fumigated, non-fumigated)	Colony size range (number of nests)	Total birds captured (fumigated, non-fumigated) ^a
1994	25 (1, 24)	19–2300	10,320 (3382, 6938)
1995	36 (2, 34)	4–1900	12,043 (5600, 6443)
1996	22 (2, 20)	3–1200	7700 (3079, 4621)
1997	22 (2, 20)	4–1200	7493 (3293, 4200)
1998	28 (3, 25)	1–1400	8775 (3746, 5029)
1999	24 (2, 22)	3–1800	10,034 (5425, 4609)
2000	33 (3, 30)	10–3000	12,238 (5897, 6341)
2001	28 (4, 24)	15–2100	10,505 (6304, 4201)
2002	24 (3, 21)	95–2500	12,634 (6752, 5882)
2003	28 (2, 26)	27–1500	13,022 (6724, 6298)
2004	30 (2, 28)	3–3000	14,786 (6334, 8452)
2005	25 (2, 23)	25–1810	10,932 (6136, 4796)
2006	27 (2, 25)	16–1800	10,256 (4671, 5585)
2007	29 (2, 27)	15–2000	9320 (4025, 5295)
2008	22 (2, 20)	2–1800	9071 (4874, 4197)
2009	23 (2, 21)	1–2120	11,133 (5980, 5153)
2010	28 (2, 26)	8–2500	12,359 (6513, 5846)
2011	22 (2, 20)	15–1765	12,028 (5674, 6354)
Total			194,649 (94,409, 100,240)

^aBirds captured at multiple colonies in a single year counted multiple times.

(Smithson and Verkuilen 2006). Although we also attempted to model our data with a traditional binomial regression, model fit statistics (such as the Bayesian P value) did not support the use of the latter. Specifically, we assumed

$$y_i \sim \beta(\mu_i, \tau),$$

where y_i is the proportion of either male or female swallows caught at a site in a given year falling into a particular age class (thus i indexes all sex by year by colony-site combinations, $N = 712$) and is assumed to follow a beta distribution (β) with mean μ and precision τ (i.e., $1/\text{variance}$). When modeling response variables using the beta distribution, one assumes values fall in the open standard unit interval (0,1), meaning that any 0 or 1 proportions that appear in the data must be transformed to fall between 0 or 1 (Cribari-Neto and Zeileis 2010), or a zero-one inflated beta regression may be used (Wieczorek et al. 2012). To account for a few cases (for age class 1) where a single age class made up the entire colony for one of the sexes (corresponding to an observed proportion of 1),

we transformed our response variable following Smithson and Verkuilen (2006):

$$y'_i = \frac{(y_i * (N_i - 1) + 0.5)}{N_i},$$

where y is the original proportion, in this case the proportion of the total number of individuals in a particular age class, and N is the total count of individuals for each sex by site-year combination i .

We modeled μ as a function of covariates using a logit-link. We fit separate fixed-effect (β) intercepts for each combination of sex and fumigation (e.g., female age class proportion at a fumigated colony, female age class proportion at a non-fumigated colony, and so on), and allowed full interactions between the two categorical covariates and the three continuous covariates. Age-class data were collected over the course of 18 yr at 57 colony sites distributed in seven separate colony clusters. Thus, some of the variability in age proportions might be due to spatial and temporal heterogeneity. However, we were not interested in the individual contributions of each component (i.e., the effect of each year on the proportion of age class 1) and thus included

SITE nested within REGION and year (YEAR) as random effects (ϵ). We modeled the age class proportion as

$$\begin{aligned} \text{logit}(\mu_i) = & \beta_0 + \beta_{\text{DATE}_{j(i),k(i)}} * x_{\text{DATE}_i} \\ & + \beta_{\text{SIZE}_{j(i),k(i)}} * x_{\text{SIZE}_i} + \beta_{\text{USE}_{j(i),k(i)}} \\ & * x_{\text{USE}_i} + \epsilon_{\text{YEAR}_i} + \epsilon_{\text{REGION}(\text{SITE})_i}, \end{aligned} \quad (1)$$

where β_0 , β_{DATE} , β_{SIZE} , and β_{USE} are the regression coefficients for each SEX (j indexes factor level) by FUM (k indexes factor level) combination depending on the values of x_{DATE} , x_{SIZE} , and x_{USE} for each sex by year by colony-site observation (i). Following Kéry and Schaub (2011), we represent the extra variation associated with site nested within cluster $\epsilon_{\text{REGION}(\text{SITE})_i}$ and year ϵ_{YEAR_i} for each sex by year by site observation (i) as:

$$\epsilon_{\text{REGION}(\text{SITE})} \sim N(0, \sigma_{\text{SITE}}^2),$$

$$\sigma_{\text{SITE}}^2 \sim N(0, \sigma_{\text{REGION}}^2),$$

and

$$\epsilon_{\text{YEAR}} \sim N(0, \sigma_{\text{YEAR}}^2).$$

We conducted analyses using JAGS v. 2.3.0 (Plummer 2003) with R package R2jags (R Development Core Team 2012, Su and Yajima 2012). We used priors that were intended to be uninformative for all parameters. For fixed covariate coefficients, we specified uninformative normal prior distributions with mean 0 and variance 1000; variances were assigned uniform priors ranging from 0 to 100 on the sigma scale (Kéry and Schaub 2011). We ran three Markov chain Monte Carlo (MCMC) chains for 20,000 iterations, 10,000 of which we discarded as “burn-in” and then “thinned” every two iterations. We visually monitored chains for convergence and used the Gelman-Rubin \hat{R} statistic for confirmation (Gelman and Rubin 1992, Gelman and Hill 2007), judging that convergence was acceptable when \hat{R} for each parameter was ≤ 1.1 . We assessed model fit using posterior predictive checks and report pos-

terior medians and 95% credible (confidence) intervals.

RESULTS

The total number of captures ranged from 11,739 to 21,272 per year, with a total sample size of 194,649 birds. Study colonies ranged in size annually from 2 to 3000 nests plus solitary nesters, and the total number of sites studied was 22–36 per year (Table 1).

For fumigated colonies, all covariates for both sexes had coefficients with credible intervals that overlapped zero (Fig. 1), suggesting little support for an effect of any of these variables. Thus, we do not present additional results for fumigated sites and conclude that colony age composition was not influenced by colony size, colony initiation date, or the proportion years a site was used at colony sites where parasites were removed.

For non-fumigated colonies, credible intervals for the colony size covariate did not overlap zero for any age class proportion (Figs. 2A and B). As colony size increased, the proportion of age-class-1 swallows (of both sexes) in the colony increased, whereas the proportions of the other age classes decreased (Figs. 3A and B). There was probably no difference in the effect of colony size between age classes 4, 5, and ≥ 6 because the credible intervals for those overlapped each other (Figs. 2A and B).

Colony initiation date was associated with the proportion of each age class for all except age-classes 5 and ≥ 6 females (credible intervals did not overlap 0; Figs. 2C and D). Age class 1 again exhibited an association opposite that of the other age classes. For colonies initiated later in the season, the proportion of age-class-1 individuals increased (Figs. 2C and D), whereas the proportion of swallows in all other age classes decreased (Figs. 3C and D). The credible intervals (for both sexes) of the regression parameters overlapped for most age classes, suggesting little difference in the magnitude of the date effect for the older age classes (Figs. 2C and D).

The proportion of years a colony site was used had relatively little effect on age composition (Figs. 2E and F). Only one credible interval (for age-class-1 females) did not overlap zero (and only barely so), suggesting that this covariate was poorly supported relative to colony size and colony initiation date for non-fumigated colonies.

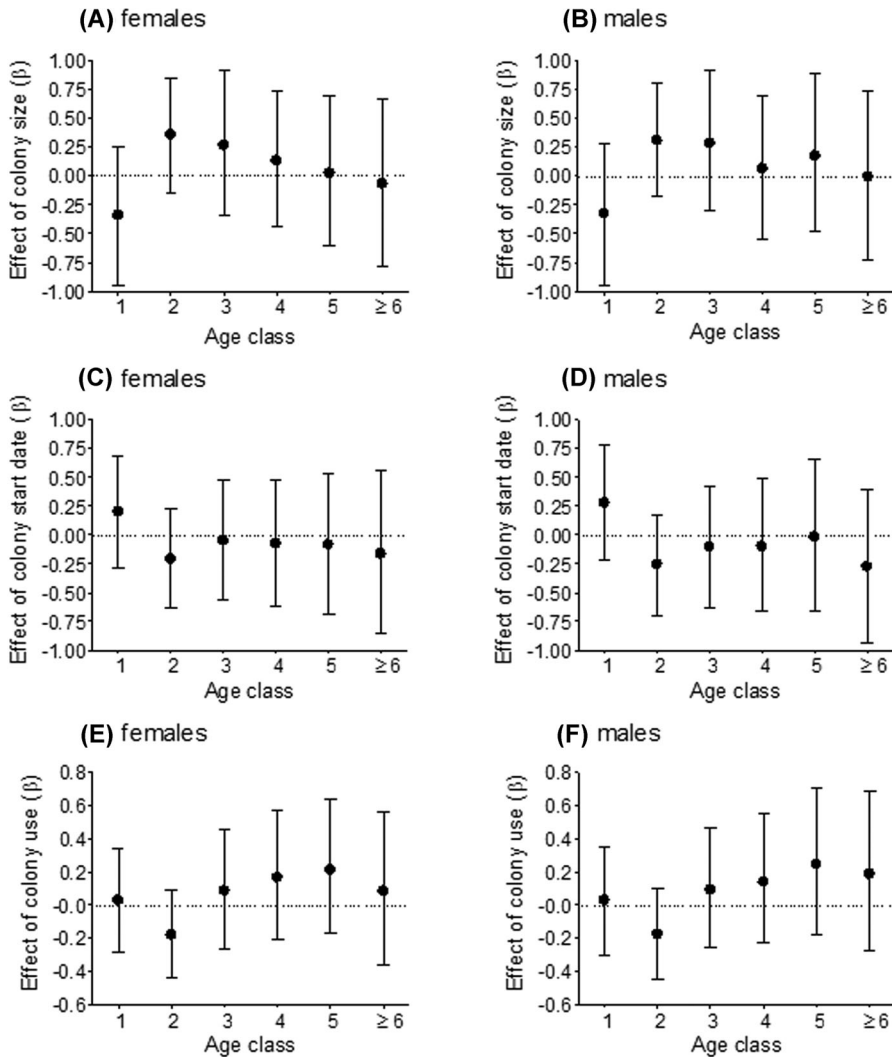


Fig. 1. Beta regression coefficients (\pm 95% credible intervals) for effects of colony size on proportion of age classes of (A) female and (B) male Cliff Swallows, for effects of colony initiation date on proportion of age classes of (C) females and (D) males, and for effects of colony site use on proportion of age classes of (E) females and (F) males in fumigated colonies.

DISCUSSION

We found that the age compositions of Cliff Swallow colonies differed principally because age-class-1 birds seemed to choose colony sizes and colony phenology unlike older age classes. As colonies increased in size and sites became active later in the season, the proportion of age-class-1 birds at those sites increased, whereas the inverse occurred for the remaining age

classes. These patterns held while statistically controlling for other variables that might have also influenced age compositions. The presence of ectoparasitic bugs appeared, in part, to be driving the differing age compositions because we found no evidence for age-based sorting among colony sizes at fumigated sites.

Heritability and experience. Some colonial species exhibit choice of colony size that has been shown, or has been suggested, to

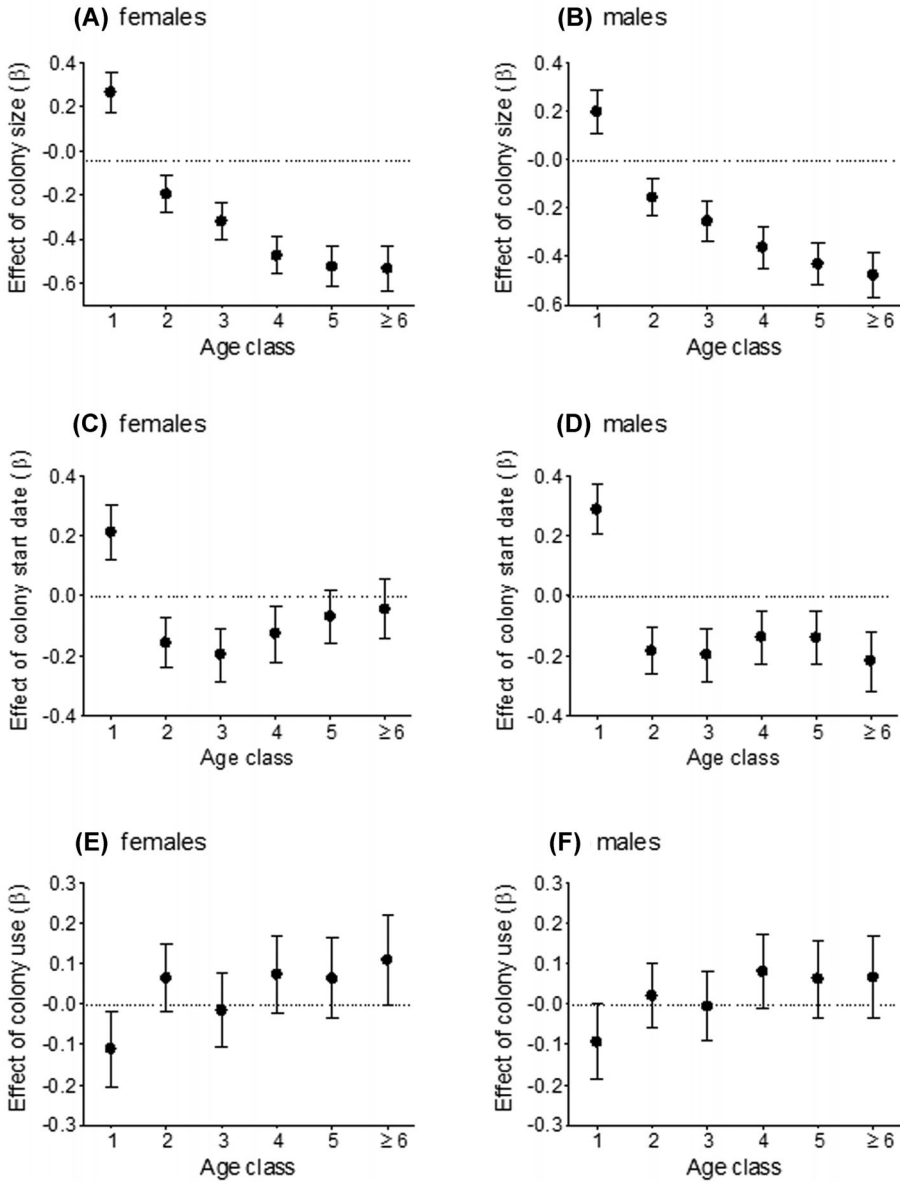


Fig. 2. Beta regression coefficients (\pm 95% credible intervals) for effects of colony size on proportion of age classes of (A) female and (B) male Cliff Swallows, for effects of colony initiation date on proportion of age classes of (C) females and (D) males, and for effects of colony site use on proportion of age classes of (E) females and (F) males in non-fumigated colonies.

be genetically based (Brown and Brown 2000, Møller 2002, Brown et al. 2003, Serrano and Tella 2007, Spottiswoode 2009). Cross-fostering experiments with Cliff Swallows indicate that choice of colony size is at least in part heritable,

with birds cross-fostered between colonies of different sizes more likely to settle as breeding adults their first year in a colony of a size matching that of their hatching site (their parents' colony size) than that of the colony where

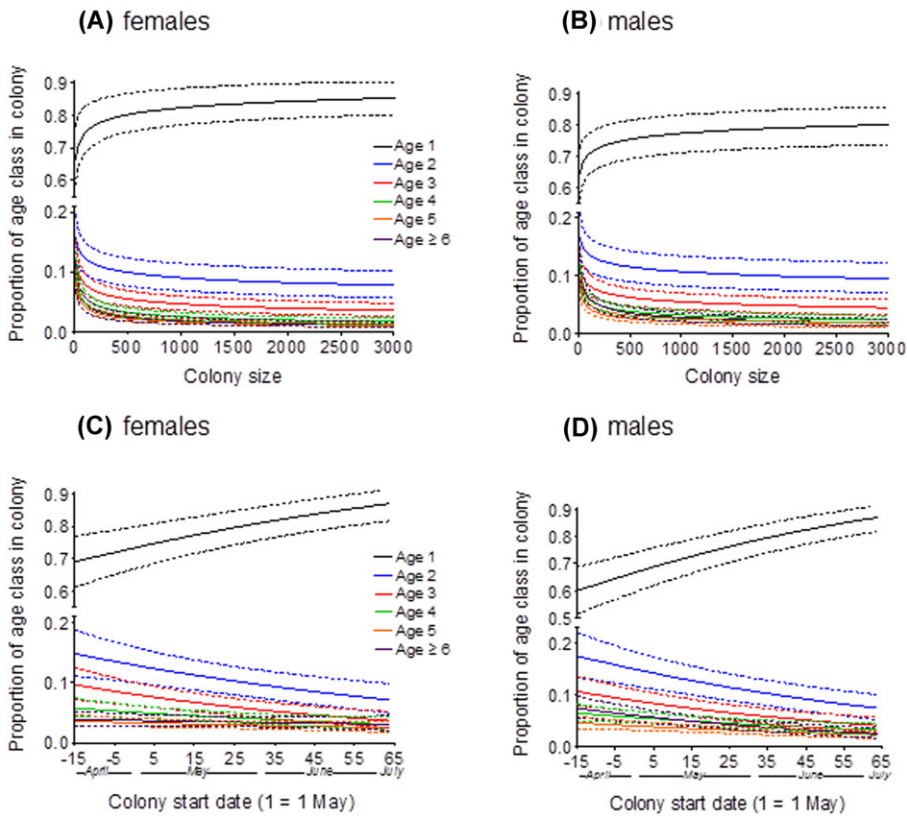


Fig. 3. Predicted proportions (solid lines) and 95% credible intervals (dotted lines) of each age class, derived from beta regression, in relation to Cliff Swallow colony size (number of nests) for (A) females and (B) males, and in relation to colony initiation date for (C) females and (D) males in non-fumigated colonies.

they were reared (Brown and Brown 2000). Fully heritable colony-size choice should lead to relatively stable and similar age proportions among different colony sizes, all else being equal. Thus, if colony-size variation reflects a stable polymorphism with respect to group size, why would larger colonies have disproportionately more younger birds?

One potential explanation is that first-year survival is greater for Cliff Swallows reared in larger colonies. If increased juvenile survival results in proportionately more “large-colony” phenotypes among the age-class-1 birds each year and these birds return to large colonies, large colonies would necessarily contain a greater fraction of age-class-1 individuals than smaller colonies. However, first-year survival probabilities do not vary with colony size (Brown and Brown 1996). Thus, greater use of large colonies

by age-class-1 birds is not simply a demographic consequence of differential survival.

The colony age compositions in our study support the recent finding that heritable colony size choice begins to break down for older age classes of Cliff Swallows (Roche et al. 2011). As birds become older they seem, in general, less likely to continue to match their birth-colony size in selecting colonies, being less sensitive to colony size *per se* and perhaps relying more on experience with a particular site (Brown et al. 2008). A colony site with a large colony when used in the successive year tends to become smaller in size, whereas a site with a small colony is often not used at all in the successive year (Brown et al. 2013a). Thus, large-colony phenotypes are more likely than small-colony phenotypes, when re-using the same colony site, to occupy a colony that was smaller in size the

next year. A consequence of this is that smaller colonies will contain proportionately more of the older age classes.

Date-related effects. Independent of any effects of colony size, the date when Cliff Swallows first occupied a site in the spring was also associated with the colony's age composition. The earliest colonies contained proportionately more older Cliff Swallows and fewer age-class-1 birds than colonies at sites that became active later in the summer. This may reflect slightly later arrival of yearlings and/or immigrants in the study area, which other data (especially for males) suggest (Brown and Brown 1996), or that spring arrival in general varies inversely with age in Cliff Swallows. Once colonies initiate, birds settle synchronously within a span of 7–10 d at most sites and, after that time, additional birds do not recruit to a site even though space is almost always available, probably because starting late in a colony often results in nest failure due to heavy swallow-bug parasitism (Brown and Brown 1996; see below). Thus, later spring arrival by age-class-1 birds means the earlier-starting colonies are not available to them as potential settlement options.

Radio-tracking has revealed that Cliff Swallows spend variable amounts of time visiting different colony sites and presumably assessing them before settling in the spring (Brown and Brown 1996). Age-class-1 birds might settle at later colonies in part because they take longer to assess sites and select one. Not being experienced as a breeder at a particular site or having directly observed the reproductive success of other birds at certain colony sites the year before (Brown et al. 2000, 2008), both yearlings and immigrants have less information available to them. The consequence could be a longer pre-settlement period as they visit different sites before eventually either choosing one or forming an entirely new colony *en masse*.

Birds of age class 1 could also have been underrepresented in small colonies and in earlier-starting ones simply because residents of those sites aggressively excluded them. However, we have never observed anything to indicate that residents at a colony attempt to regulate colony size in any way. Nest owners defend their own nest, but do not try to prevent others from nest-building nearby. Birds at a nest often allow others to begin nest construction directly above or beside their nest, often sharing mud walls.

Furthermore, all colony sites have substantial unused suitable nesting substrate where additional nests could be constructed (Brown and Brown 1996). Thus, age-class-1 Cliff Swallows are not prevented from using certain colonies by either aggressive defense or lack of space and, as such, their avoidance of certain colonies must reflect active choice not to settle there.

Site use. One hypothesis to explain the evolution of avian coloniality is that individuals assess the quality of habitat patches and traditionally aggregate in areas where reproductive success is relatively high (Shields et al. 1988, Danchin and Wagner 1997). This hypothesis predicts that high-quality sites will attract settlers each year, leading to perennial use and increases in colony size over time. If this hypothesis applied to Cliff Swallows, we would expect perennially used colony sites to accumulate larger proportions of older birds, as previous residents continue to return there each year, and that more erratically occupied sites would have a greater proportion of younger or immigrant individuals who have not nested before (Forbes and Kaiser 1994).

We found little indication that the proportion of years a site was used influenced colony age composition, once controlling for colony size and colony initiation date. Our results suggest that the proportion of age-class-1 females might have been greater at sites used less often, but there was no effect for age-class-1 males. Among older (≥ 2 yr) age classes, colony site use had no effect on age composition, suggesting that older Cliff Swallows do not preferentially settle in more regularly used sites. These analyses thus provide no support for the hypothesis that Cliff Swallow coloniality results from the traditional aggregation of (sometimes the same) individuals in areas of high-quality habitat.

Age-specific costs and benefits of coloniality. Although some of the increase in age-class-1 proportions in larger colonies may be explained by older individuals re-using the same site that hosts a smaller colony in the successive year (see above), the apparent sorting of younger or immigrant Cliff Swallows into larger colonies may also reflect age-specific differences in the costs and benefits associated with particular colony sizes. Increasing evidence now indicates that animals in different-sized breeding colonies often exhibit age-related or phenotypic differences that may change the payoffs expected

from a given group size (Brown and Brown 1996, 2001, Spottiswoode 2007, 2009, Pruitt et al. 2011, Dardenne et al. 2013).

Because enhanced foraging efficiency through information sharing (Brown 1986, 1988) is a major benefit of coloniality for Cliff Swallows, birds in larger colonies find more food than those in smaller colonies (Brown and Brown 1996). In addition, prior experience with the area surrounding a specific colony site confers survival advantages independent of colony size *per se* (Brown et al. 2008). Thus, birds unfamiliar with any colony site (because they have either not nested anywhere before or have immigrated from some distance away) may rely more heavily on foraging information provided by conspecifics, whereas those already experienced with where to find insects at a site from an earlier year may have less need for, or benefit less from, information from conspecifics. Consequently, we would expect younger, less experienced birds to prefer larger colonies (Brown and Brown 1996), whereas older birds would be more likely to settle in a smaller colony at a site with which they were familiar. Our data support this scenario. Older birds (≥ 2 yr old) may also maintain consistent associations with other individuals with whom they have nested in the past (even when changing colony sites), as found in colonial Bank Swallows (*Riparia riparia*; Szabó and Szép 2010). If so, this would promote older individuals settling collectively at a site, contributing in part to the patterns we observed.

Costs of coloniality could also drive age-related sorting by colony size. Because ectoparasitic swallow bugs increase with colony size and are a major cost of breeding in large groups for Cliff Swallows (Brown and Brown 1986, 1996, 2004b), any bird experienced in finding food (i.e., an older bird) should choose as small a colony as possible to minimize the costs of swallow bug parasitism.

Effects of ectoparasites. That a colony's age composition was unrelated to colony size for birds at fumigated colonies indicates that the presence of ectoparasites is, to some degree, driving age-related colony choice. In the absence of ectoparasites, all birds regardless of age seemed to not be sensitive to colony size (or even colony-initiation date) in making settlement decisions. We believe this result reflects primarily the longer period of time over which settlement occurs at fumigated colony sites. Under natural

conditions, because swallow bugs begin feeding and breeding as soon as Cliff Swallows occupy a site (Brown and Brown 1996) and their populations increase with time, later nests at a site suffer disproportionately from the effects of bugs. This probably constrains birds from settling after the first arrivals at a given site and results in relatively synchronous settlement of colony residents (Brown and Brown 1996, 2014). However, with the experimental removal of bugs and their deleterious effects, the settlement window is essentially all summer, and allows any bird regardless of age or arrival date to colonize any fumigated site. Egg-laying dates at fumigated colonies extend over a much longer span of the nesting season (Brown and Brown 1996). These results underscore the complex ways that swallow bugs influence Cliff Swallow colony dynamics (Brown et al. 2013a).

The next step in studying the mechanisms generating differences in Cliff Swallow colony age compositions is to follow individually marked birds over their lives, as recently done for a small sample of cross-fostered individuals (Roche et al. 2011), and determine to what extent colony size choice is related to age, experience at a site, or phenotypic condition as a measure of the relative costs and benefits a bird can expect from a given group size. These analyses are beyond the scope of this study, but are currently underway using a total sample size of over 229,000 Cliff Swallows from the Nebraska study area.

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LITERATURE CITED

- ALEXANDER, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5: 325–383.
- BROWN, C. R. 1986. Cliff Swallow colonies as information centers. *Science* 234: 83–85.
- . 1988. Enhanced foraging efficiency through information centers: a benefit of coloniality in Cliff Swallows. *Ecology* 69: 602–613.
- . 1998. Swallow summer. University of Nebraska Press, Lincoln, NE.
- , AND M. B. BROWN. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). *Ecology* 67: 1206–1218.
- , AND ———. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, IL.
- , AND ———. 2000. Heritable basis for choice of group size in a colonial bird. *Proceedings of the National Academy of Sciences USA* 97: 14825–14830.
- , AND ———. 2001. Avian coloniality: progress and problems. *Current Ornithology* 16: 1–82.
- , AND ———. 2004a. Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behavioral Ecology and Sociobiology* 56: 498–511.
- , AND ———. 2004b. Empirical measurement of parasite transmission between groups in a colonial bird. *Ecology* 85: 1619–1626.
- , AND ———. 2014. Breeding time in a migratory songbird is predicted by drought severity and group size. *Ecology* 95, in press.
- , ———, AND K. R. BRAZEAL. 2008. Familiarity with breeding habitat improves daily survival in colonial Cliff Swallows. *Animal Behaviour* 76: 1201–1210.
- , R. COVAS, M. D. ANDERSON, AND M. B. BROWN. 2003. Multistate estimates of survival and movement in relation to colony size in the Sociable Weaver. *Behavioral Ecology* 14: 463–471.
- , M. B. BROWN, AND E. DANCHIN. 2000. Breeding habitat selection in Cliff Swallows: the effect of conspecific reproductive success on colony choice. *Journal of Animal Ecology* 69: 133–142.
- , ———, AND E. A. ROCHE. 2013a. Spatial and temporal unpredictability of colony size in Cliff Swallows across 30 years. *Ecological Monographs* 83: 511–530.
- , ———, AND ———. 2013b. Fluctuating viability selection on morphology of Cliff Swallows is driven by climate. *Journal of Evolutionary Biology* 26: 1129–1142.
- , AND B. RANNALA. 1995. Colony choice in birds: models based on temporally invariant site quality. *Behavioral Ecology and Sociobiology* 36: 221–228.
- , B. J. STUTCHBURY, AND P. D. WALSH. 1990. Choice of colony size in birds. *Trends in Ecology and Evolution* 5: 398–403.
- BROWN, J. L. 1982. Optimal group size in territorial animals. *Journal of Theoretical Biology* 95: 793–810.
- BROWN, M. B., AND C. R. BROWN. 2009. Blood sampling reduces annual survival in Cliff Swallows. *Auk* 126: 853–861.
- BURGER, J. 1988. Social attraction in nesting Least Terns: effects of numbers, spacing, and pair bonds. *Condor* 90: 575–582.
- , AND M. GOCHFELD. 1990. The Black Skimmer: social dynamics of a colonial species. Columbia University Press, New York, NY.
- COULSON, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature* 217: 478–479.
- , AND E. WHITE. 1956. A study of colonies of the Kittiwake *Rissa tridactyla* (L.). *Ibis* 98: 63–79.
- , AND ———. 1958. The effect of age on the breeding biology of the Kittiwake *Rissa tridactyla*. *Ibis* 100: 40–51.
- CRIBARI-NETO, F., AND A. ZEILEIS. 2010. Beta regression in R. *Journal of Statistical Software* 34: 1–24.
- DANCHIN, E., AND R. H. WAGNER. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12: 342–347.
- DARDENNE, S., S. DUCATEZ, J. COTE, P. PONCIN, AND V. M. STEVENS. 2013. Neophobia and social tolerance are related to breeding group size in a semi-colonial bird. *Behavioral Ecology and Sociobiology* 67: 1317–1327.
- DAVIES, N. B., J. R. KREBS, AND S. A. WEST. 2012. An introduction to behavioural ecology, 4th ed. Wiley Blackwell, Chichester, UK.
- FISHER, J., AND G. WATERSTON. 1941. The breeding distribution, history and population of the Fulmar (*Fulmarus glacialis*) in the British Isles. *Journal of Animal Ecology* 10: 204–272.
- FORBES, L. S., AND G. W. KAISER. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. *Oikos* 70: 377–384.
- GELMAN, A., AND J. HILL. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York, NY.
- , AND D. B. RUBIN. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7: 457–511.
- HOGLUND, J., R. MONTGOMERIE, AND F. WIDEMO. 1993. Costs and consequences of variation in the size of Ruff leks. *Behavioral Ecology and Sociobiology* 32: 31–39.
- JOVANI, R., R. MAVOR, AND D. ORO. 2008. Hidden patterns of colony size variation in seabirds: a logarithmic point of view. *Oikos* 117: 1774–1781.
- KÉRY, M., AND M. SCHAUB. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, MA.
- KHARITONOV, S. P., AND D. SIEGEL-CAUSEY. 1988. Colony formation in seabirds. *Current Ornithology* 5: 223–272.
- MØLLER, A. P. 1994. Sexual selection and the Barn Swallow. Oxford University Press, Oxford, UK.

- . 2002. Parent-offspring resemblance in degree of sociality in a passerine bird. *Behavioral Ecology and Sociobiology* 51: 276–281.
- , K. ALLANDER, AND R. DUFVA. 1990. Fitness effects of parasites on passerine birds: a review. In: *Population biology of passerine birds* (J. Blondel, A. Gosler, and J.-D. Lebreton, eds.), pp. 269–280. Springer-Verlag, Berlin, Germany.
- MORTON, E. S., L. FORMAN, AND M. BRAUN. 1990. Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. *Auk* 107: 275–283.
- PLUMMER, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop of Distributed Statistical Computing (DSC 2003)*, Vienna, Austria.
- PODOLSKY, R. H., AND S. W. KRESS. 1989. Factors affecting colony formation in Leach's Storm-Petrel. *Auk* 106: 332–336.
- PRUITT, J. N., G. ITURRALDE, L. AVILES, AND S. E. RIECHERT. 2011. Amazonian social spiders share similar within-colony behavioural variation and behavioural syndromes. *Animal Behaviour* 82: 1449–1455.
- R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing, version 2.12.2. R Foundation for Statistical Computing, Vienna, Austria.
- RANTA, E., AND K. LINDSTROM. 1990. Assortative schooling in three-spined sticklebacks? *Annals Zoologici Fennici* 27: 67–75.
- , H. RITA, AND K. LINDSTROM. 1993. Competition versus cooperation: success of individuals foraging alone and in groups. *American Naturalist* 142: 42–58.
- ROBERTSON, G. 1986. Population size and breeding success of the Gentoo Penguin, *Pygoscelis papua*, at Macquarie Island. *Australian Wildlife Research* 13: 583–587.
- ROCHE, E. A., AND C. R. BROWN. 2013. Among-individual variation in vigilance at the nest in colonial Cliff Swallows. *Wilson Journal of Ornithology* 125:685–695.
- , ———, AND M. B. BROWN. 2011. Heritable choice of colony size in Cliff Swallows: does experience trump genetics in older birds? *Animal Behaviour* 82: 1275–1285.
- , ———, ———, AND K. M. LEAR. 2013. Recapture heterogeneity in Cliff Swallows: increased exposure to mist nets leads to net avoidance. *PLoS ONE* 8: e58092.
- SAFRAN, R. J., V. A. J. DOERR, P. W. SHERMAN, E. D. DOERR, S. M. FLAXMAN, AND D. W. WINKLER. 2007. Group breeding in vertebrates: linking individual- and population-level approaches. *Evolutionary Ecology Research* 9: 1163–1185.
- SAINO, N., T. SZEP, M. ROMANO, D. RUBOLINI, F. SPINA, AND A. P. MØLLER. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecology Letters* 7: 21–25.
- SERRANO, D., AND J. L. TELLA. 2007. The role of despotism and heritability in determining settlement patterns in the colonial Lesser Kestrel. *American Naturalist* 169: E53–E67.
- SHIELDS, W. M., J. R. CROOK, M. HEBBLETHWAITE, AND S. S. WILES-EHMANN. 1988. Ideal free coloniality in the swallows. In: *The ecology of social behavior* (C. N. Slobodchikoff, ed.), pp. 189–228. Academic Press, San Diego, CA.
- SMITHSON, M., AND J. VERKUILEN. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods* 11: 54–71.
- SPOTTISWOODE, C. N. 2007. Phenotypic sorting in morphology and reproductive investment among Sociable Weaver colonies. *Oecologia* 154: 589–600.
- . 2009. Fine-scale life-history variation in Sociable Weavers in relation to colony size. *Journal of Animal Ecology* 78: 504–512.
- SU, Y. S., AND M. YAJIMA [online]. 2012. R2jags: a package for running jags from R. R package version 0.03-08. <http://CRAN.R-project.org/package=R2jags> (Accessed 5 June 2014).
- SZABÓ, Z. D., AND T. SZÉP. 2010. Breeding dispersal patterns within a large Sand Martin (*Riparia riparia*) colony. *Journal of Ornithology* 151: 185–191.
- WEATHERHEAD, P. J. 1983. Two principal strategies in avian communal roosts. *American Naturalist* 121: 237–243.
- WIECZOREK, J., C. NUGENT, AND S. HAWALA. 2012. A Bayesian zero-one inflated beta model for small area shrinkage estimation. *Proceedings of the 2012 Joint Statistical Meetings, American Statistical Association, Alexandria, VA.*