



Heritable choice of colony size in cliff swallows: does experience trump genetics in older birds?

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The variation in breeding colony size seen in populations of most colonial birds may reflect heritable choices made by individuals that are phenotypically specialized for particular social environments. Although a few studies have reported evidence for genetically based choice of group sizes in birds, we know relatively little about the extent to which animals potentially rely on experience versus innate preferences in deciding how many conspecifics to settle with at different times of their lives. We conducted a cross-fostering experiment in 1997–1998 on cliff swallows, *Petrochelidon pyrrhonota*, in southwestern Nebraska, U.S.A., in which some individuals were reared in colonies that differed in size from those in which they were born. Breeding colony sizes chosen by this cohort of birds were monitored by mark–recapture throughout their lives. A multistate mark–recapture analysis revealed that birds in their first breeding year chose colony sizes similar to those of their birth, regardless of their rearing environment, confirming a previous analysis. Beyond the first breeding year, however, cliff swallows' choice of colony size was less dependent on the size of the colony in which they were born. Birds born in small colonies and reared in large colonies showed evidence of a delayed rearing effect, with these birds overwhelmingly choosing large colonies in later years. Heritabilities suggested strong genetic effects on colony choice in the first year but not in later years. Cliff swallows' genetically based colony size preferences their first year could be a way to ensure matching of their phenotype to an appropriate social environment as yearlings. In later years, familiarity with particular colony sites and available information on site quality may override innate group size preferences when birds choose colonies.

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Most species of colonially nesting birds show wide variation in colony size within populations, the smallest and largest colonies often varying by several orders of magnitude (Brown et al. 1990; Brown & Brown 2001). Hypotheses to explain this variation have invoked (1) uneven distributions of resources that allow individuals to concentrate to varying degrees in areas of high and low resource density, typically regulated by density-dependent dispersal between sites and/or despotic behaviour (Fretwell & Lucas 1970; Robinson 1986; Shields et al. 1988; Brown & Rannala 1995; Bosch & Sol 1998; Davis & Brown 1999; Serrano et al. 2005; Kim et al. 2009), (2) public information in which the presence, number or reproductive success of conspecifics reliably indicates to incoming settlers the suitability of patches of variable quality (Danchin & Wagner 1997; Switzer 1997; Danchin et al. 1998; Erwin et al. 1998; Brown et al. 2000) and (3) genetic or phenotypic

differences among individuals in groups of different sizes that reflect life-history optimization for breeding in small versus large colonies (Brown & Brown 2000; Møller 2002; Brown et al. 2003; Serrano & Tella 2007; Spottiswoode 2007, 2009). Numerous field studies have addressed the former two classes of hypotheses, but relatively little is known about the extent to which variation in breeding colony size reflects individual specialization for degree of sociality (Brown & Brown 2001).

If a bird's choice of group size has been shaped by optimization of particular life-history traits in different social environments, we should see consistent phenotypic differences among individuals in relation to group size, roughly equivalent fitness (over the long term) among settlers in groups of all sizes, and a heritable basis to choice of group size. Recent studies are starting to provide some support for these predictions. For example, susceptibility to ectoparasitism, baseline levels of stress hormones, maternal provisioning of eggs with testosterone, average body size and egg size vary with colony size among individuals of a few bird species (Brown & Brown 1996; Schwabl 1997; Brown et al. 2005a, b; Spottiswoode 2007, 2009), and in other species, individual fitness (as measured by annual reproductive success) is similar among

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colony sizes (reviewed in Brown & Brown 2001). Relatively high heritabilities for choice of breeding colony size have been formally estimated for three species (Brown & Brown 2000; Møller 2002; Serrano & Tella 2007) and suspected to be so for a fourth (Brown et al. 2003; Spottiswoode 2009) on the basis of cross-fostering experiments and offspring/midparent regressions.

Unlike heritable traits such as morphology, which presumably remain relatively constant over an individual's lifetime, colony size selection is a dynamic process that an individual must undertake at least once each year that it breeds. Dispersal between breeding locations (and therefore choice of a new colony) is common in many species, and is often dependent not only on an individual's personal reproductive success but also on the reproductive success of conspecifics in a previous year (Greenwood & Harvey 1982; Brown & Brown 1996; Switzer 1997; Danchin et al. 1998; Clobert et al. 2001). Furthermore, colony sizes may change unpredictably through additions or subtractions of residents, sometimes forcing individuals to relocate and make additional group size choices. On the other hand, experience with the surroundings of a particular colony site (Hoogland et al. 2006; Brown et al. 2008) may compensate individuals for remaining at a site where they might otherwise be ill suited for that colony size. Thus, a given bird potentially must assess colony sizes, and decide whether to join or leave an existing group, relatively frequently both between and within nesting seasons, especially if it lives for several years. Even for those species that clearly show some genetic influences on colony size choice, little is known about how individuals choose group sizes over their lifetimes. Do such decisions remain strongly genetically based at all life stages, or are innate group size tendencies potentially modified by experience in older individuals?

Colonially nesting cliff swallows, *Petrochelidon pyrrhonota*, breed in groups that range from fewer than 10 individuals to several thousand at a single colony site (Brown & Brown 1996). A previous study using over 1900 nestlings partially cross-fostered between nests in small and large colonies in southwestern Nebraska, U.S.A., showed a strong genetic basis to individuals' choice of nesting colony during their first summer as breeding adults (Brown & Brown 2000). Regardless of the colony size in which they were reared, birds chose colony sizes for breeding that matched colony sizes of their birth. The results provided relatively strong experimental evidence that breeding colony choice in cliff swallows is heritable, potentially explaining some of the variation in colony size seen in this population.

Here we extend the earlier study in two major ways. First, we address colony sizes chosen by the experimental birds across their entire lives. The two cohorts of birds in the cross-fostering, born in 1997–1998, were followed annually as part of a long-term mark–recapture project in the study area each summer through 2010. No birds from the cross-fostered cohorts were captured in 2009 or 2010, indicating that virtually all of those birds had reached the end of their lives. Second, the analyses in the earlier report (Brown & Brown 2000) relied entirely on recapture percentages of birds during a single summer. In contrast, multiple years of recapture allow one to formally estimate survival for each group of experimental birds and, more importantly, to estimate the likelihood of a transition from one colony size to another. Multistate capture–recapture models (Nichols & Kendall 1995; Lebreton & Pradel 2002) are designed to estimate the probability that a bird moves from one state (e.g. natal state) to another (e.g. a breeding colony size) after taking into account survival and the likelihood of detection; these statistical methods are particularly useful when individuals are missed in the sampling in some years. In this paper we evaluate whether the same colony selection processes underlie the transition probabilities of cross-fostered birds versus their natal nestmates that were not fostered and how these transitions

potentially change with age. We also examine heritabilities of colony size choice for birds in their first breeding season versus for those birds in later years.

The cross-fostering design of this study had several inherent advantages. By directly comparing experimental groups that shared the same birth or rearing colonies, we avoided statistical problems associated with regression to the mean, which potentially affects strictly observational heritability studies (Kelly & Price 2005). Also, by comparing birds born in one colony size but reared in a different size to ones born and reared in the same colony size, any effect of uncertainty in parentage (e.g. extrapair paternity resulting from birds perhaps being sired by nonresidents in a colony; Brown & Brown 1996) was the same among the groups being compared and thus did not affect our results. Finally, because the groups being compared were of roughly equivalent sample size and these birds encountered the same spatial array of colony sites to choose among in subsequent years, differences between experimental groups could not reflect subsets of colonies to which different groups might have been exposed.

METHODS

Study Animal

The cliff swallow is a colonial, insectivorous passerine that breeds throughout western North America, building gourd-shaped mud nests underneath rocky ledges on the walls of cliffs, beneath the eaves of buildings or bridges, or inside highway culverts. The nests tend to be stacked together closely, often sharing walls (Brown & Brown 1995, 1996). Cliff swallows winter in southern South America, begin arriving in our Nebraska study area in late April or early May, generally rear only one brood, and depart on autumn migration by late July (Brown & Brown 1996).

Study Site

Our study area included cliff swallow colonies located along the North and South Platte Rivers centred near Ogallala, in Keith and Garden Counties, Nebraska, from 1997 to 2010. Groups of nesting swallows using the same bridge or culvert and showing at least occasional interactions were considered to belong to the same colony (Brown & Brown 1996). Colonies in this area included natal colonies of birds in the cross-fostering experiment (Brown & Brown 2000) and those subsequently used by the cross-fostered birds for breeding (Fig. 1). The study area and colony sites are described in detail by Brown & Brown (1996, 2000). Selected colony sites in the study area were fumigated to remove haematophagous swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*) as part of other research on this population, using methods described previously (Brown & Brown 1986, 1996, 2004a).

Field Methods

In 1997 and 1998, we performed a partial cross-fostering experiment in which we exchanged newly hatched chicks with similarly aged chicks in colonies of different sizes. At relatively small colonies, a subset of nestlings was transported to nests with similarly aged broods at relatively large colonies, where they were exchanged with nestlings that were reciprocally moved to the nests in the small colonies (Brown & Brown 2000). We ensured that cross-fostered nestlings were reared in broods of the same size in which they had hatched. Nestlings were transferred at approximately 5 days of age, the youngest age at which cliff swallows can be banded (with U. S. Fish and Wildlife Service bands) for permanent identification (Brown & Brown 2000).

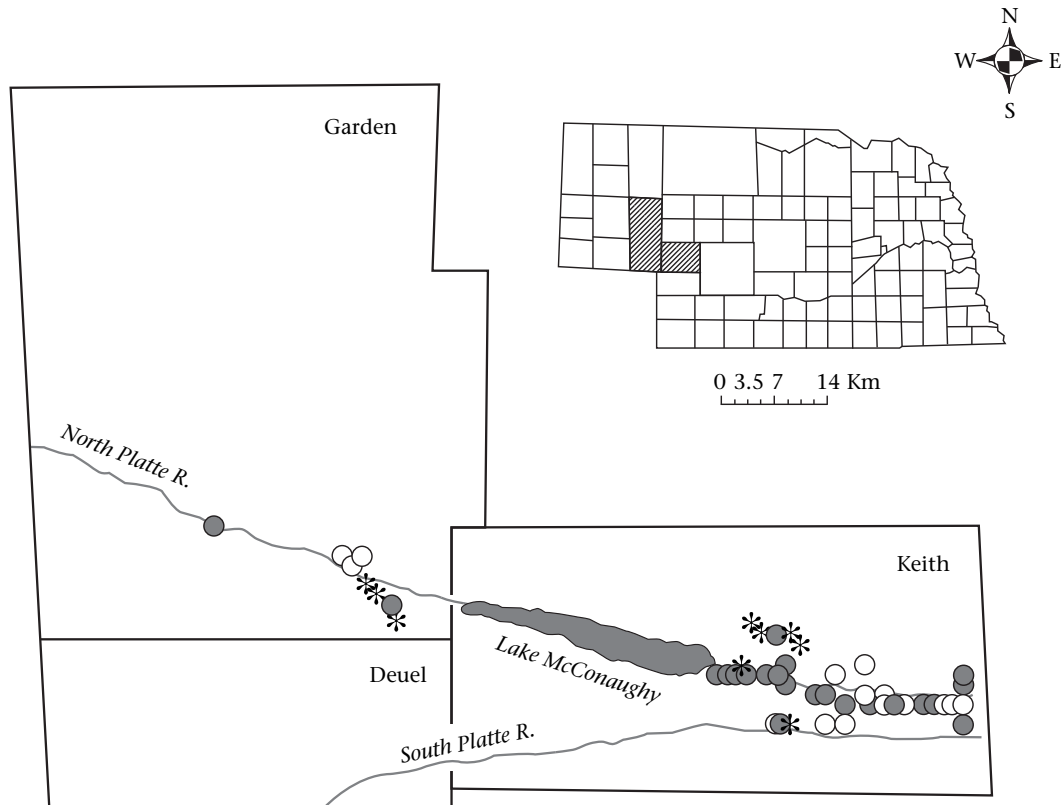


Figure 1. Cliff swallow colonies within the southwestern Nebraska study area, 1997–2010. Asterisks designate natal colonies used in the original cross-fostering experiment in 1997 and 1998, while closed circles designate colony sites used for breeding by cliff swallows in the cross-fostering experiment in years after the natal year (natal sites in later years were also used for breeding by some birds). Open circles designate colony sites at which no birds from the cross-fostering experiment were captured but were still within the minimum convex polygon described by where cross-fostered birds settled.

The breeding colony choices of the cliff swallows in the cross-fostering experiment, both those fostered and their ‘control’ broodmates that were not fostered, were recorded upon subsequent recapture in the study area from 1998 to 2010 (Table 1). We monitored the settlement of breeding cliff swallows at sites each year through systematic mist netting at 25–40 sites per season (Brown & Brown 2004b). Cliff swallows were captured by putting nets across the entrances of highway culverts or along the sides of bridges that contained swallow colonies. Swallows were caught as they exited their nests. Sex of adult birds was determined by presence of a cloacal protuberance or brood patch (Brown & Brown 1996). We rotated among the accessible colonies, netting at each colony several times each season. The spatial distribution of these colony sites is shown in Fig. 1, which illustrates the minimum convex polygon (using Hawth’s analysis tools in ArcGIS 9.3; Beyer 2004) circumscribed by all known sites used by birds in the cross-fostering experiment at any time during their lives. The capture of birds is described in detail by Brown (1998) and Brown &

Brown (2004b). Colony sizes were determined in late June at each site, after all birds had settled, using a combination of active nest counts and estimation based on the number of birds present (see Brown & Brown 1996).

The pattern of multiple recaptures of individuals within a season allowed us to assign a bird as a resident breeder at a given colony. For cliff swallows caught at multiple colony sites within a season, we categorized a bird as resident at a colony if it was (1) caught at the same colony multiple times prior to 20 June (an arbitrary date but one chosen as representative of when postbreeding colony visits by transient individuals typically begin each year) or (2) caught previously at a different colony but switched to its resident colony prior to 20 June and was caught at least twice there. Cliff swallows caught at multiple colonies after 20 June were not assumed to be residents at any of those colonies, because of the widespread presence of transient individuals at most sites late in the nesting season (Brown 1998; Brown & Brown 2004a; Brown et al. 2007).

Table 1

Sample sizes (number of nestlings) and the number of birds recaptured as breeders in the different rearing groups of the cliff swallow cross-fostering experiment each year

Rearing group*		Number of nestlings		Number recaptured as breeding adults													
Birth	Rearing	1997	1998	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	
Large	Large	LL	329	160	119	104	54	31	30	13	12	5	4	2	1	0	0
Large	Small	LS	321	164	129	102	62	28	20	11	5	3	4	3	0	0	0
Small	Large	SL	325	166	119	113	59	29	22	7	8	4	3	1	0	0	0
Small	Small	SS	344	157	126	100	45	26	18	12	7	6	1	1	1	0	0

* Small colonies had <500 nests; large colonies had ≥500 nests.

Multistate Mark–Recapture Analyses

We fitted multistate recaptures-only models in program MARK (White & Burnham 1999; White et al. 2006) using R-MARK (R Development Core Team 2007; Laake & Rexstad 2008) to estimate the between-year movement probability of 1966 individually marked cliff swallows hatched in 1997–1998 and followed through 2010. The individuals in this analysis, all hatched at 10 natal colonies (8, 82, 98, 109, 154, 170, 193, 220, 950 and 1005 nests in size), were all of known age (1319 hatching in 1997 and 647 in 1998), and therefore, the first appearance of a bird in each capture history occurred during its hatching year. We truncated capture histories following 2008 because none of the birds included in this analysis were detected in 2009 or 2010 (Table 1). This resulted in capture histories with 12 encounter occasions.

Multistate models examine the probability that an animal moves between particular states (ψ) while concurrently estimating survival (S) and detection (p) probability (Hestbeck et al. 1991; Brownie et al. 1993). Multistate models are an extension of Cormack–Jolly–Seber models (Cormack 1964; Jolly 1965; Seber 1965), in which ‘apparent survival’ is decomposed into its dual components: (1) the probability that an animal survives from time t to time $t + 1$, given that it is in state r at time t , and (2) the conditional probability that an animal in state r at time t is in state s (i.e. the animal has moved to a new state) at time $t + 1$, given that the animal is still alive at time $t + 1$. Key assumptions of multistate models are that all mortality occurs prior to movement and all individuals move at the same time (Cooch & White 2010).

Based on previous analyses and classifications of cliff swallow colony size (Brown & Brown 1996) and the distribution of birds banded and recaptured at the colony sites in this study (Fig. 1), we established three colony size categories to which each natal and breeding colony was assigned: small (S), <100 nests; medium (M), 100–499 nests; and large (L), ≥ 500 nests. Nine different combinations for a bird’s birth and rearing colony size classes were thus possible (SS, SM, SL, MS, MM, ML, LS, LM, LL); however, two combinations were not represented (MS, SM), as we did no reciprocal cross-fostering between small and medium colonies. Hereafter, we refer to these seven groups as ‘rearing groups’. We initially began our analyses with these seven rearing groups, but later collapsed medium colonies with small ones to form a new ‘small’ category consisting of 1–499 nests. This resulted in four rearing groups (Table 1), was better supported by Akaike’s Information Criterion, AIC (see below), and matched the grouping structure used in the earlier analysis (Brown & Brown 2000). In the case of cross-fostered individuals, birth and rearing colony sizes were different: for example, SL denoted an individual born in a small colony but fostered to a large colony, while SS denoted a non-fostered individual (with one or more cross-fostered nestmates) that was born and reared in a small colony.

The earlier analysis (Brown & Brown 2000) used a within-year colony ranking to describe colony size, the rationale being that birds might be more likely to rank-order colonies from small to large and choose a colony size relative to other colony sizes available that season. For the present analysis, we calculated an intra-class correlation coefficient (Zar 1996) for both colony size and colony rank (using the previous criteria for ranking) for all individuals in this data set. Although both were significantly repeatable for an individual, actual colony size showed greater within-individual consistency ($r_I = 0.56$, $P < 0.0001$) than colony rank ($r_I = 0.43$, $P < 0.0001$), so for these analyses a bird’s actual colony size (total number of active nests at the site) was used in classifying birds into colony size classes. The main advantage of using actual colony size is that it did not require grouping colonies into arbitrary spatial clusters for ranking (as in Brown & Brown 2000).

We defined four separate states in our multistate models. The first, state 1, represented the natal state for each cliff swallow, regardless of the colony size at which it was born and reared. States 2–4 corresponded to the three colony size categories that a cliff swallow could choose as a breeder: small, medium or large. In this way we could determine the effects of birth and rearing colony sizes on movement probabilities between a bird’s natal state (i.e. state 1) and breeding colony size (i.e. states 2–4). Because movement from a breeding state (i.e. states 2–4) back to a natal state was impossible, we set the probability of moving to state 1 as equal to 0; this eliminated four unique state-to-state movements (1–1, 2–1, 3–1, and 4–1). We used combinations of rearing group*state interactions to assess the effect of birth versus rearing environment on movement among colony size states.

Overdispersion may result if a capture–recapture data set does not meet the variance assumptions inherent in the binomial distribution used in mark–recapture analysis, usually brought about by trap dependence in captures or the presence of transient individuals (Pradel et al. 1997, 2005). Using the fully parameterized model, we assessed the degree of overdispersion in our data by conducting a median \hat{c} test in program MARK (Cooch & White 2010). Although these data were not heavily overdispersed, with a $\hat{c} = 1.09$, we adjusted the variance in movement probabilities through quasilikelihood (Burnham & Anderson 2002). All models tested were ranked using Akaike’s Information Criterion (AIC) corrected for small sample size and overdispersion (QAIC_c).

Because we were primarily interested in estimating the colony-to-colony movement of cliff swallows and how that movement was related to a bird’s rearing group, we began by simplifying our models for detection while leaving survival and movement probability models fully parameterized. With only two cohorts included in our analysis, and because cliff swallows appear to show mist-net avoidance as they get older (C. R. Brown, unpublished data), we expected any temporal variation to also covary with age. We considered models in which detection probabilities were unique and variable by year (i.e. each year received a unique parameter, ‘ t ’), followed a log-linear trend based on age (Age), were constant across age and time but varied by rearing group (reargrp), or contained either additive or multiplicative interactions of rearing group with year or Age.

Once we simplified the model parameterization for detection, we reduced model complexity in the parameterization of apparent survival (S). We considered models in which apparent survival varied by rearing group (reargrp), state, two age classes (first year and beyond the first year) and a log-linear effect of age (Age). In addition, some survival models had additive or multiplicative interactions of rearing group with state, age class and Age.

Once identifying the best reduced parameterized model for both detection and apparent survival, we built and tested different models to examine whether individuals in the four rearing groups (Table 1) behaved differently in their selection of breeding colony size at different ages (first breeding year versus all subsequent years combined). Specifically, we predicted that if colony choice is genetically based, cross-fostered individuals should show the same movement probabilities as those both born and reared at the birth colony (i.e. rearing group SL = SS, LS = LL; Nature, Table 2, model 2), whereas if rearing environment is more important, we should see the reverse (SL = LL, LS = SS; Nurture, Table 2, model 5). Alternatives were that movement probabilities would differ among all rearing groups (Table 2, model 1, also the full model for ψ) or would not be influenced by rearing group (Table 2, model 6).

To investigate the effect of sex, we identified our best supported model and then added sex as a covariate to that model. Because the model with sex was identical in structure to the top-ranked model except for one additional parameter, following Arnold (2010), we considered sex to be a potentially ‘uninformative parameter’ if it

failed to lower the AIC. One solution to cases like this is to discard the model with the uninformative parameter and not use it in consideration of model weights (Arnold 2010), which we elected to do.

Colony Size Regression Analysis

Because a multistate movement analysis by definition includes some individuals captured on multiple occasions, we also examined whether there was an effect of rearing group on choice of colony size after accounting for annual changes in average colony size in the study area and for the repeated measures of the same individuals. We built linear mixed models using package nlme in program R, version 2.12.2 (R Development Core Team 2007; Pinheiro et al. 2011) to investigate the degree to which choice of breeding colony size by cliff swallows could be explained by natal year, breeding year, swallow age (first-year versus all other ages combined) and rearing group. The repeated measurements of colony size for individual cliff swallows allowed us to include a random effect of individual nested within colony site. Models were built using forward selection, adding one covariate at a time to a null model (i.e. colony size regressed on an intercept and a random effects only model) and retaining each covariate in our linear model only if it resulted in a reduced AIC score.

Estimating Heritability

We estimated heritability of colony size choice with midparent regression (Falconer & Mackay 1996) using an individual's birth colony size as its midparent value. Heritability estimates were calculated for cross-fostered and nonfostered birds, and for birds in their first breeding year and in all other years combined. Regressions were done with a mixed model in R (package nlme), in which nest identity was included as a random effect in calculating heritability for the first breeding season (to account for multiple individuals from the same brood) and individual nested within nest identity for heritability in later years (to account for repeated measures of the same individuals). Unlike in Brown & Brown (2000), in which heritabilities were calculated on colony ranks (that also required arbitrarily defining spatial clusters of breeding colonies), for these analyses we used actual breeding colony size with no spatial restrictions based on where breeding colonies were located.

RESULTS

Annual Detection and Apparent Survival

The annual likelihood of detecting a cliff swallow (p) decreased with a bird's age following a log-linear trend ($\beta_{p-Age} -0.33$; 95%

confidence interval, CI: $-0.40, -0.26$; Table 2, model 1). For example, the likelihood of detecting a cliff swallow in its second year ($p = 0.72$; 95% CI: 0.68, 0.76) was $1.7\times$ higher than in its sixth year ($p = 0.41$; 95% CI: 0.36, 0.46). Annual apparent survival (S) increased with age in a log-linear trend ($\beta_{S-Age} 0.15$; 95% CI: 0.06, 0.25) and also varied with a bird's colony size state. An individual's survival was between 1.3 and $1.5\times$ higher by age 5, depending on the size of the colony at which it was a resident ($S_{small} = 0.61$, 95% CI: 0.47, 0.73; $S_{medium} = 0.68$, 95% CI: 0.61, 0.75; $S_{large} = 0.71$, 95% CI: 0.66, 0.76), than during its first year ($S = 0.46$, 95% CI: 0.43, 0.49). In general, the survival of adult cliff swallows was lowest when an individual was a resident breeder in a small colony (average S over all ages = 0.64; 95% CI: 0.48, 0.77), while survival rates for birds residing at medium (average $S = 0.72$; 95% CI: 0.62, 0.79) and large colonies (average $S = 0.74$; 95% CI: 0.67, 0.80) were equivalent.

Our most highly parameterized global model (Table 2, model 4) included 59 parameters: 16 survival parameters (four rearing groups by four states), 11 detection parameters (one parameter per year, 1998–2008) and 32 movement parameters (4 rearing groups by 8 unique state-to-state movements). The best model with a reduced parameterization for detection consisted of 50 parameters and reduced QAIC_c by 0.735 points relative to the fully parameterized model (Table 2, model 3 versus model 4). The top model with the lowest parameterization of apparent survival consisted of 39 parameters and reduced QAIC_c by 27.50 points relative to the fully parameterized model (Table 2, model 1 versus model 4).

Movement among Colony Sizes

The state-to-state movement probabilities of cliff swallows varied according to their rearing group and age and the colony sizes that they moved between (Table 2, model 1). Although the best supported model suggested that movement probability was uniquely different for each rearing group, there was also evidence that cliff swallows were more likely to move to colonies that were similar in size to their birth colony than they were to move to colonies that were similar in size to their rearing colony; the Nature model (Table 2, model 2) outcompeted the Nurture model (Table 2, model 5) by 141.52 QAIC_c points.

Comparison of movement probabilities between rearing groups for birds during their first breeding season (1998 for the 1997 cohort, 1999 for the 1998 cohort) revealed trends consistent with a greater effect of birth colony size than rearing colony size (Fig. 2). The probability of a bird born and reared in a large colony (LL) settling in a small colony was low (<0.02) and essentially identical to that for birds born in a large colony but reared in small colony (LS; Fig. 2a). Birds born in a small colony but reared in a large colony (SL) were more likely to settle in a small colony than were birds

Table 2

Set of models used to test hypotheses and estimate apparent survival (S), detection (p) and movement probabilities (ψ) of 1966 cliff swallows from different rearing groups in a cross-fostering experiment in southwestern Nebraska, U.S.A., 1997–2010*

Model	S	p	ψ	k	ΔQAIC_c	w_i	QDev
1	Age+state	Age	Reargrp*state-to-state	39	0.0000†	0.9999	1600.20
2	Age+state	Age	Nature*state-to-state	23	19.7297	0.0001	1652.53
3	Reargrp*state	Age	Reargrp*state-to-state	50	27.4987	0.0000	1605.11
4	Reargrp*state	t	Reargrp*state-to-state	59	28.2341	0.0000	1587.25
5	Age+state	Age	Nurture*state-to-state	23	161.353	0.0000	1794.15
6	Age+state	Age	State-to-state	15	183.3104	0.0000	1832.30

* Parameters with interactions are joined by '*', whereas parameters having parallel (additive) relationships are joined by '+'; 't' specifies that survival/detection/movement varied by year; 'Age' was a continuous covariate, represented by a linear trend based on age in years; reargrp: the four rearing groups; state: colony size; state-to-state: a unique parameter estimation for each movement between colony size states; nature: rearing groups were combined by birth colony size; nurture: rearing groups were combined by rearing colony size. Akaike's Information Criterion (AIC) values were corrected for small sample size and overdispersion ($\hat{c} = 1.09$), yielding quasi-AIC (QAIC_c) values. ΔQAIC_c values and model weights (w_i) were used to rank models.

† QAIC_c = 7870.9161.

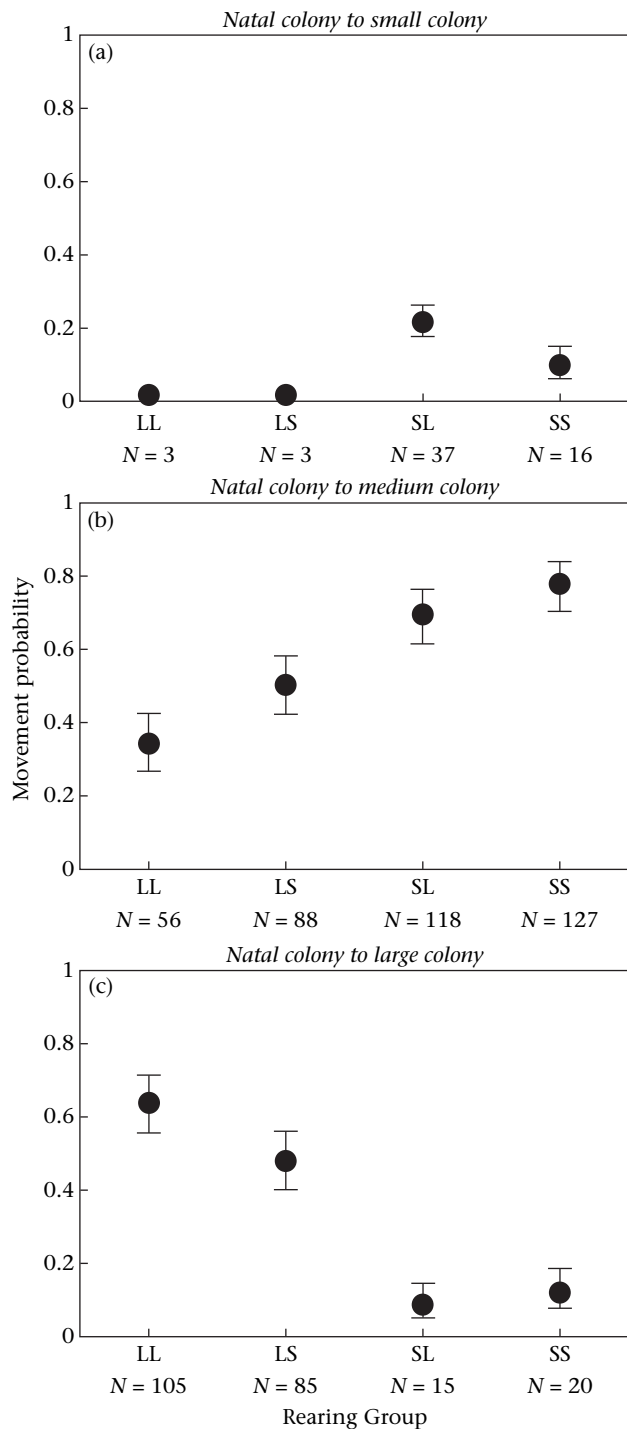


Figure 2. Movement probabilities of cliff swallows from their natal site to their first breeding site in their first season as breeders for the four rearing groups (LL: large natal colony and large rearing colony; LS: large natal colony and small rearing colony; SL: small natal colony and large rearing colony; SS: small natal colony and small rearing colony). Cliff swallows could move from the natal colony to breed at colonies that were (a) small (<100 nests), (b) medium (100–499 nests) and (c) large (≥ 500 nests). Closed circles represent movement probabilities and vertical lines represent 95% confidence intervals; the number of observed state-to-state movements (N) are shown beneath each rearing group designation. All estimates were made using the following model: $S(\text{Age} + \text{state}), p(\text{Age}), \psi(\text{rearing group} * \text{state-to-state})$; see Table 2.

born and raised in a small colony (SS; Fig. 2a). The same birth-colony-based pattern was seen among the rearing groups in their selection of large colonies their first year: groups LL and LS were more similar to each other than to the other groups, while SL and SS

birds showed much lower but roughly equivalent likelihoods of moving to large colonies (Fig. 2c). Selection of medium-sized colonies was least likely for birds born and reared in small colonies (SS), while the cross-fostered birds showed intermediate tendencies to select medium-sized colonies their first year (Fig. 2b).

For birds beyond their first year, there was a clear tendency for those breeding in medium and large colonies to remain in colonies of those sizes (Fig. 3e, g) or to move from a small or medium colony to a large colony (Fig. 3a, d), regardless of their original rearing group. There was little movement to small colonies by breeders of any category in subsequent years, with movement probabilities inestimable due to so few birds undertaking those transitions in some cases (Fig. 3c, f, i). Colony choice by breeders in later years may have partly reflected a changing distribution of colony sizes in the study area (Fig. 1), with the percentage of small colonies (and the percentage of the population occupying them) declining from 1998 through 2008 and that for large colonies increasing (Fig. 4).

Effect of Sex

When sex was added as a covariate to the top model (Table 2, model 1) used in estimating movement probabilities, the resulting model ($S(\text{Age} + \text{state}), p(\text{Age}), \psi(\text{rearing group} * \text{state-to-state} + \text{sex})$), with $k = 40$, had a $\Delta\text{QAIC}_c = 1.9077$, $w_i = 0.2781$, and $\text{QDev} = 7791.85$. Because this model was both a poorer fit to the data and was within 2.0 QAIC_c of the top model from which it was derived, we considered sex uninformative and concluded that male and female cliff swallows showed no difference in choice of breeding colony size. Analyses were thus not separated further by sex.

Factors Affecting Colony Size Choice

When controlling for repeated measures among individuals and annual population-wide changes in colony size (Fig. 4), differences in the breeding colony sizes chosen by cliff swallows based on rearing group persisted. In addition to rearing group, size choice was significantly related to breeding year and a bird's age (Table 3), when colony ($\text{SD}_{\text{intercept}} = 261.88$) and individual nested within colony ($\text{SD}_{\text{intercept}} = 212.19$, $\text{SD}_{\text{residual}} = 392.16$) were modelled as random effects. Natal year (1997, 1998) had no significant effect, suggesting that birds in these two cohorts selected colonies on a similar basis.

Heritability Estimates

Using midparent regressions, we estimated heritability of choice of breeding colony size for cross-fostered birds and those not cross-fostered in both a bird's first breeding season and in later breeding seasons combined (Table 4). Heritabilities for both age classes were relatively large and differed significantly from zero. Heritabilities for cross-fostered and nonfostered birds were roughly equivalent in the first breeding season and were positive, indicating that all birds in the first year were choosing colonies that matched the size of their parents' colonies (Table 4). These heritabilities were similar to those for the first breeding season calculated using colony ranks (Brown & Brown 2000). For birds beyond the first year, however, cross-fostered birds showed a highly significant negative heritability, indicating an avoidance of colony sizes similar to those of their birth sites (Table 4).

To explore the reversal in heritability for cross-fostered birds in later seasons, we investigated whether two perennially fumigated colony sites in the study area might be preferentially attracting birds because they were free of ectoparasites. These two colony sites, denoted 05 and 97, were fumigated each year of the study. Site 05, containing 1000–1800 nests annually, was clearly favoured by

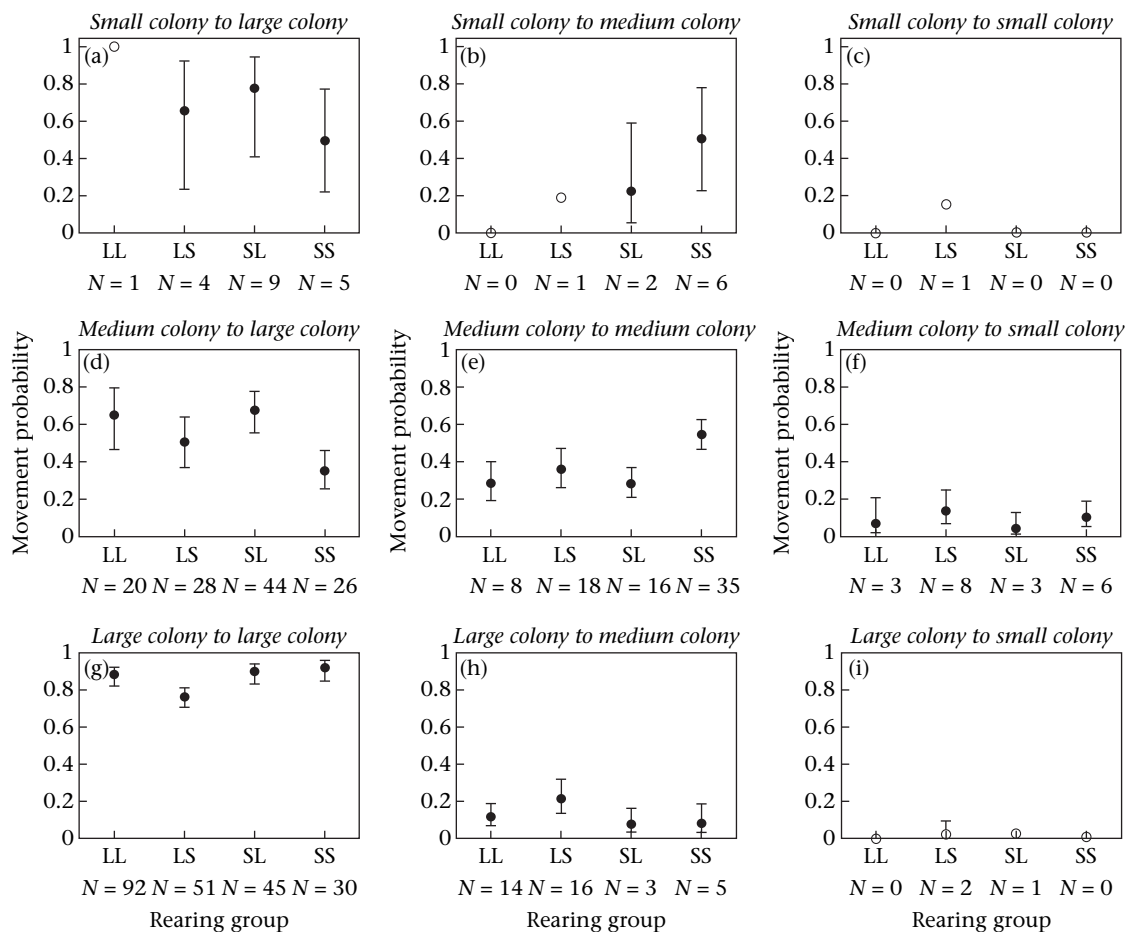


Figure 3. Movement probabilities of cliff swallows during breeding seasons beyond their first year for the four rearing groups (LL: large natal colony and large rearing colony; LS: large natal colony and small rearing colony; SL: small natal colony and large rearing colony; SS: small natal colony and small rearing colony). Cliff Swallows bred in small (<100 nests), medium (100–499 nests), or large (≥ 500 nests) colonies and could thus undergo one of nine state-to-state movements in a later breeding year (a–i). Closed circles represent movement probabilities and vertical lines represent 95% confidence intervals; the number of observed state-to-state movements (N) are shown beneath each rearing group designation. Open circles represent movement probabilities for which confidence intervals could not be estimated because of insufficient sample sizes. All estimates were made using the following model: $S(\text{Age} + \text{state}), p(\text{Age}), \psi(\text{rearing group} * \text{state-to-state})$; see Table 2.

many of the birds born in large colonies (rearing groups LL, LS) at all ages (Fig. 5a). Interestingly, however, birds born in small colonies but reared in large colonies (rearing group SL), while largely avoiding site 05 their first year, chose it overwhelmingly in later years (Fig. 5a). Site 97, which was smaller than 05 during the earlier years of this study (varying from a low of 220 nests in 1997 to a high of 1810 nests in 2005), was more attractive in later breeding seasons to birds associated in some way with small colonies (SS, SL, LS) than to birds not associated at all with small colonies (LL; Fig. 5b).

DISCUSSION

The most striking result of this study was that cliff swallows' heritable tendencies in choice of breeding colony size, shown earlier for birds in their first breeding season (Brown & Brown 2000) and confirmed by these analyses, appeared to wane as birds aged. While all birds, regardless of birthplace or rearing environment, tended to select larger colonies as they got older, those born in small colonies but reared in large colonies showed a much stronger likelihood of choosing large colonies in later years than did their counterparts born and reared in small colonies, implying a delayed rearing effect. Any such influence of rearing environment seemed to apply mostly to birds born in small

colonies and reared in large colonies, and not as strongly to individuals born in large colonies and reared in small colonies. These results suggest that choice of breeding colony size in cliff swallows is complex and may include both genetic and environmental influences at different times in an individual's life.

Colony Size Choice as Life-history Optimization

The prevailing explanation for genetically based variation in choice of colony size in birds is that inherent ability to perform in different social environments has led to selection for individuals that match their phenotype to the appropriate group size (Brown & Brown 2000, 2001; Møller 2002; Brown et al. 2003; Serrano & Tella 2007; Spottiswoode 2007, 2009). Consistent phenotypic differences among individuals in different-sized colonies support this hypothesis: for example, sociable weavers, *Philetairus socius*, adjust egg size based on the colony size they occupy, perhaps in response to an individual's ability to compete for food in different-sized groups (Spottiswoode 2009), and in lesser kestrels, *Falco naumanni*, competitively inferior individuals choose smaller colonies where the costs of overcoming aggression by dominant birds are reduced (Serrano & Tella 2007).

Cliff swallows also show phenotypic differences among colonies, consistent with some degree of individual specialization for

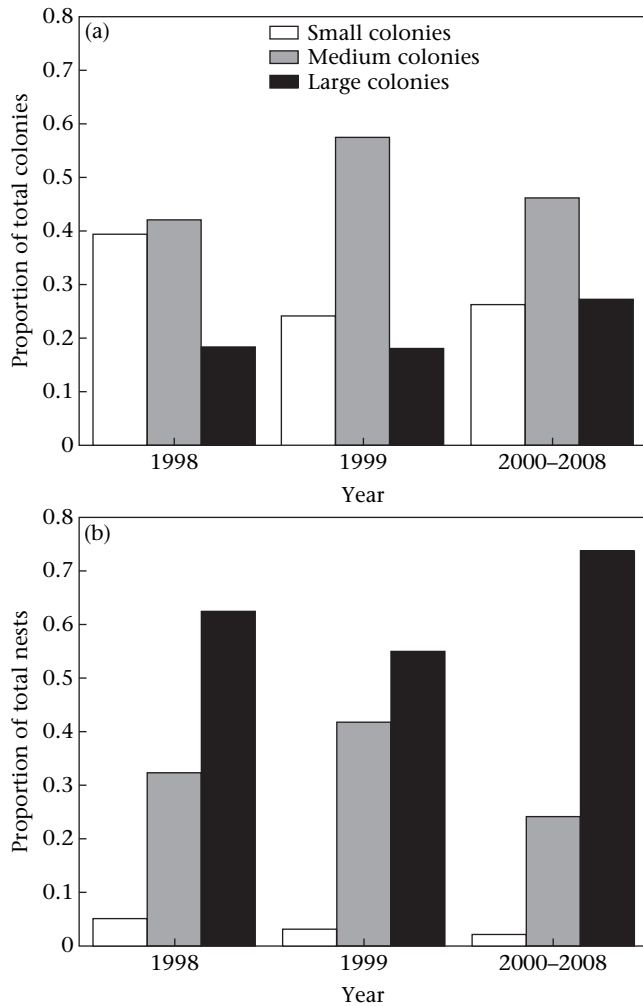


Figure 4. (a) Proportion of colonies available to cliff swallows in their first breeding season (1998 or 1999) and in later seasons (2000–2008) in relation to whether colonies were small (<100 nests), medium (100–499 nests), or large (≥500 nests). (b) Proportion of total cliff swallow nests in the population within each size class.

Table 3

Parameter estimates and significance levels resulting from an ANOVA of the top linear mixed effects model for choice of breeding colony size in cliff swallows, 1997–2008*

Parameter	df	Value	SE	F	P
Intercept	1	885.48	269.48	44.67	<0.001
Breeding year	10			44.75	<0.001
1999		278.19	53.63		
2000		326.83	76.38		
2001		501.83	81.97		
2002		565.02	83.58		
2003		477.92	93.85		
2004		397.35	105.23		
2005		687.10	120.94		
2006		502.69	145.66		
2007		387.83	174.32		
2008		568.36	302.54		
Rearing group	3			31.47	<0.001
LS		−315.00	283.90		
SL		−296.37	37.48		
SS		−523.13	284.21		
Age class	1			15.85	<0.001
		−139.84	56.49		
Natal year	1			1.85	0.17
		−65.78	48.40		

* Rearing groups included the four groups described in Table 1. The two age classes were first breeding year and after the first breeding year.

Table 4

Midparent heritability estimates (h^2) for choice of breeding colony size in cliff swallows that were part of a cross-fostering experiment (offspring's natal colony size was used as the midparent value)

Category	h^2	SE	P
First year: cross-fostered birds (N=346)	0.4134	0.0443	<0.0001
First year: nonfostered birds (N=327)	0.4332	0.0469	<0.0001
After first year: cross-fostered birds (N=387)	−0.2453	0.0712	0.0007
After first year: nonfostered birds (N=392)	0.4152	0.0716	<0.0001

certain colony sizes. Earlier work found that individuals settling in large colonies were more likely to be infested with fleas than those at smaller sites, either because these birds were inherently more likely to contract parasites or because they had visited more sites (where fleas can be acquired) before settling (Brown & Brown 1996). Hormonal profiles also differ for cliff swallows in small versus large colonies. Birds are predisposed to choose certain colonies based on whether their baseline levels of corticosterone and testosterone are above or below average, implying that individual differences in stress responses and competitive ability mediated by hormones may influence performance in different social environments (Brown et al. 2005a, b; Smith et al. 2005).

The strong preference shown by first-year breeders for colonies that were similar in size to their birth colonies, even when cross-fostered to colonies of different sizes (Brown & Brown 2000; this study), is consistent with genetically based phenotypic differences among individuals in their ability to function in different social environments. The heritabilities for choice of breeding colony size in the first year were higher than those reported for many other behavioural traits (Mousseau & Roff 1987), and the first-year heritabilities were essentially the same among the different rearing groups regardless of how the estimates were derived (e.g. midparent versus single parent, colony ranks versus actual colony size; see Brown & Brown 2000). The previous study ruled out maternal effects as a likely cause of this pattern, given that single father-offspring heritabilities tended to be higher than mother-offspring heritabilities (Brown & Brown 2000). Natal philopatry as an explanation for high first-year heritability was also rejected; the same degree of heritable preferences were seen among birds not using natal sites for breeding (Brown & Brown 2000).

Age-related Changes in Colony Size Choice

Cliff swallows may use a simple rule of thumb during their first breeding season: settle at sites similar in size to those their parents chose. In the absence of better information, a first-year breeder that adopts this rule may maximize its chances of living in a social environment that will be broadly appropriate to its particular constellation of life-history attributes. The clear avoidance by cross-fostered birds of colony sizes similar to those where they were reared (Figs 2, 5) indicates that rearing environment has comparatively little influence on first-year settlement decisions.

However, genetically based preferences were not maintained throughout an individual's breeding life. By the second breeding season, cross-fostered birds of each rearing combination had begun to diverge from the choices made by their nonfostered counterparts, particularly those birds born in small colonies but reared in large colonies (Fig. 5a). Some evidence suggested that all birds (including nonfostered ones) became more homogeneous in colony size choice in years after their first breeding season (Fig. 3).

Several factors may account for the waning influence of birth colony size in later settlement decisions. Other studies of this cliff swallow population have shown that familiarity with a given colony site from a past year confers survival advantages within

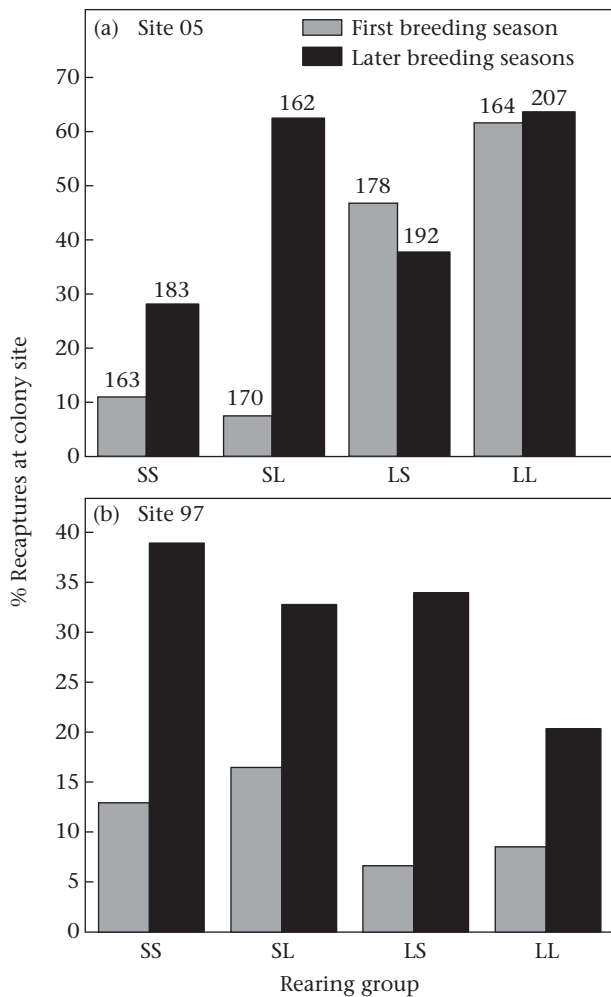


Figure 5. Percentage of cliff swallows in the different rearing groups (LL: large natal colony and large rearing colony; LS: large natal colony and small rearing colony; SL: small natal colony and large rearing colony; SS: small natal colony and small rearing colony) recaptured at two colony sites (a) 05 and (b) 97 in the study area that were fumigated each year to remove ectoparasites and where birds had high reproductive success. Numbers above bars in (a) show the total number of recaptures of each rearing group; some individuals in later years were counted multiple times if caught in multiple years.

a breeding season (Brown et al. 2008). Thus, being familiar with where to find food near a site in bad weather, what predators are likely to be present there, or which parts of the site were previously infested with ectoparasites may lead to fitness advantages that override the benefits of particular colony sizes and could cause an individual to settle at the same site the next year even when the colony size there differs from a bird's genetic template. Cliff swallows also gather information and apparently assess the success of different sites within a year, as do other species (Danchin et al. 1998; Doligez et al. 1999). This probably occurs through extensive prospecting during postbreeding visits at different colony sites at the end of each nesting season (Brown 1998). Sites where residents have high reproductive success one year tend to attract more birds (and grow in size) the next year (Brown et al. 2000). Birds do not presumably have access to this information their first year.

The choice of two fumigated colonies by relatively large numbers of birds in later breeding seasons is consistent with widespread site assessment. The removal of ectoparasites at a cliff swallow colony increases nesting success dramatically, contributing in part to greater survivorship of both offspring and breeding

adults (Brown & Brown 1986, 1996, 2004b). The potential attraction of birds from nearby colonies to these successful sites can serve to increase colony size there from year to year and contribute to our measuring average increases in colony sizes chosen by all birds over time (Figs 3, 5). In contrast, sites where large numbers of nests fail tend to be abandoned entirely the next season (Brown & Brown 1996; C. Brown, personal observation).

The picture that emerges, then, is that colony choice by older breeders (≥ 2 years old) may be based on both an individual's own experience and history at a given site and its assessment of how birds at neighbouring colonies have fared. These considerations may override genetic predispositions for certain colony sizes for many birds after they have nested once and gained breeding experience somewhere. The precise trade-offs between colony choice based on benefits associated with a particular site versus those associated with, for example, an individual's genetically based hormonal response to stressful events remain to be determined. Perhaps site characteristics or familiarity with a colony site from a past year dictates colony choice as long as colony size remains within a rather broad range and does not deviate excessively (in either direction) from an individual's genetic template.

Interestingly, the opposite pattern, in which heritabilities were low for first-time breeders but increased for older birds, was observed in lesser kestrels (Serrano & Tella 2007). This seems to be because younger birds in this species are actively prevented from settling in the larger, more established colonies by despotic behaviour of established residents (Serrano et al. 2003, 2004). Only after they become older and more competitive can they gain breeding space in larger colonies. A similar situation may apply in black-headed gulls, *Chroicocephalus ridibundus* (Péron et al. 2010). This scenario seems unlikely to explain settlement patterns in cliff swallows, as no colony-level despotic behaviour occurs, and yearlings of some rearing groups (LL, LS) routinely chose and successfully settled in large colonies their first year.

The evidence for an effect of rearing environment was asymmetric in that small-colony birds reared in large colonies (SL) seemed more likely to choose large colonies in their later breeding seasons than large-colony birds reared in small colonies (LS) were to choose small colonies. This probably follows in part from larger colonies generally being those that were perennially successful; if all birds were selecting based largely on conspecifics' reproductive success at a site rather than on size per se, we would see SL birds gravitating to large colonies and LS birds largely staying put in later years. Nevertheless, the SL birds' SS counterparts (born and reared in small colonies), while also tending to be more likely to choose large colonies in later breeding seasons than during the first year, did not settle overwhelmingly in large colonies. This marked difference among rearing groups suggests that being reared in the large-colony social environment predisposes even birds that may be small-colony phenotypes to later choose large groups. How this rearing effect comes about and its significance under natural conditions are unclear. Perhaps the juvenile birds' staying in and around the colony site where they are reared for several days after they fledge (Brown & Brown 1996, 2004b) and interacting with the many colony residents there primes them to be attracted to large groups later in life. The SL birds' repeated choice in later years of one of the largest sites (05) in the study area (Fig. 5a) was probably responsible for the reversal in heritability values (Table 4) between the first and later breeding seasons in cross-fostered birds.

Generating and Maintaining Colony Size Variation

A challenge in studying colony size variation in natural populations is identifying the factors that both cause colonies to vary in size between sites and maintain continued size variation in

a population (Brown & Brown 2001). Heritable choice of colony size could account for maintenance of colonies of different sizes if genetic polymorphisms for different group sizes exist and if fitness is equivalent among the morphs (Serrano & Tella 2007). We do not have complete fitness estimates available for cliff swallows occupying colonies of different sizes at different times of their lives, and thus we do not know how genetically based preferences for certain group sizes are maintained. However, that these heritable tendencies persist at least for birds during their first year suggests that choice of certain group sizes does not consistently lead to lower or higher fitness.

Birds in our population are faced with the potential choice of many different colony sizes in a given year (Brown & Brown 1996). Individuals may not always have control over the colony size at the site they choose, especially if other birds depart from a site or settle there after an individual moves in (Sibly 1983; Kharitonov & Siegel-Causey 1988; Brown et al. 1990; Girard & Yesou 1991). However, unpredictability of colony size is not likely to be a major factor in cliff swallow decision making, mainly because many sites are settled simultaneously and synchronously by most colony residents, with late waves of settlers uncommon at most sites.

A colony size continuum is maintained only by the presence of colonies intermediate in size between small and large. Interestingly, medium-sized colonies attracted birds from both small and large colonies and from all rearing groups at a relatively high frequency in the first breeding season. This may reflect partly that we were forced to use a fairly wide range of breeding colony sizes as our 'medium' category, given the distribution of our capture data among sites. Medium-sized colonies near the low end may have essentially provided a small-colony environment, while those at the high end may have been more similar, socially, to large colonies. Our sample sizes were insufficient to statistically distinguish between birds reared in small versus medium natal colonies, and the fact that some birds were born in natal colonies as large as 220 nests yet were still necessarily classified as small-colony individuals, may have helped generate the observed patterns in choice of medium-sized sites.

Beyond the first year, however, medium colonies seemed to become less attractive for all rearing groups, and large colonies became more attractive, based on individual movement probabilities to those sites (Fig. 3). To what degree this reflected actual choice of large colonies versus increased availability of large colonies in the study area is unclear. Apparent use of large colonies may have increased over time in part because the cross-fostering experiment was conducted in the immediate aftermath of a significant population-wide mortality event. About half of the cliff swallows in the study area succumbed to lack of food brought about by unusually cold weather in May 1996 (Brown & Brown 1998), the summer before this study started. Average colony sizes were smaller in 1997, 1998 and 1999 than in the previous decade, with the population not fully recovering in size until about 2002 (C. Brown, unpublished data). Thus, even if all else were equal, birds might have settled in larger colonies later in the study because colonies at most sites tended to increase gradually in size during the 1997–2002 period. Natural events such as these may episodically reshuffle the colony size distribution within populations and further complicate the measurement of colony size preference by individuals.

Colony size variation within populations may be maintained by spatiotemporal fluctuations between fitness and group size, perhaps brought about by unpredictable changes in the risk of predation or parasitism in different social environments (Serrano & Tella 2007). This hypothesis predicts that there is no 'best' colony size and that environmental factors affecting colony site quality and the frequency distributions of phenotypes across colonies might vary among years (Møller 2002), such that fitness and genetic correlations with particular colony sizes change regularly. No direct

tests of these predictions have been done for any species to date. This cross-fostering study was not designed to investigate temporal variation in fitness associated with group size; other analyses using a much larger mark–recapture data set (>100 000 birds) are planned for this purpose.

Perhaps variation in colony size with its associated phenotypic variation among residents of different colonies reflects some degree of behavioural plasticity ('noise') around adaptive fitness averages, and that differences among individuals are part of wider behavioural tendencies (e.g. syndromes or personalities; Serrano & Tella 2007). That these behavioural tendencies tend to have a genetic basis that can be mediated by the neuroendocrine system (Koolhaas et al. 1999; van Oers et al. 2005, 2011; Goodson et al. 2009; Lea et al. 2010) is consistent with our demonstration of a heritable basis to colony size selection in cliff swallows for younger birds (Brown & Brown 2000; this study), greater plasticity by older birds (this study) and systematic hormonal differences between birds in groups of different size (Brown et al. 2005a, b; Smith et al. 2005; Raouf et al. 2006).

The results presented here indicate that choice of colony size in cliff swallows is a complex process and that these birds probably integrate multiple kinds of information or cues (both genetic and experiential) in making settlement decisions. The value of long-term study of individuals over their lifetimes is well illustrated by the differences we found in how yearlings versus older birds select colonies. The high heritability of colony size choice reported for birds in their first breeding season (Brown & Brown 2000) describes only part of how cliff swallows choose colony sizes. The challenge ahead is to learn the relative contribution of genetics and experience for individuals at different ages and whether colony selection as we currently understand it can account for the existence of colonies ranging in size from 2 to 6000 nests in this Nebraska population of cliff swallows.

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