Familiarity with breeding habitat improves daily survival in colonial cliff swallows

CHARLES R. BROWN*, MARY BOMBERGER BROWN* & KATHLEEN R. BRAZEAL†

*Department of Biological Sciences, University of Tulsa
†School of Biological Sciences, University of Nebraska, Lincoln

One probable cost of dispersing to a new breeding habitat is unfamiliarity with local conditions such as the whereabouts of food or the habits of local predators, and consequently immigrants may have lower probabilities of survival than more experienced residents. Within a breeding season, estimated daily survival probabilities of cliff swallows, *Petrochelidon pyrrhonota*, at colonies in southwestern Nebraska, U.S.A., were highest for birds that had always nested at the same site, followed by those for birds that had nested there in some (but not all) past years. Daily survival probabilities were lowest for birds that were naïve immigrants to a colony site and for yearling birds that were nesting for the first time. Birds with past experience at a colony site had monthly survival 8.6% greater than that of naïve immigrants. Experienced residents did better than immigrants in colonies with fewer than 750 nests, but in colonies with more than 750 nests, naïve immigrants paid no survival costs relative to experienced residents. Removal of nest ectoparasites by fumigation resulted in higher survival probabilities for all birds, on average, and diminished the differences between immigrants and past residents, probably by improving bird condition to the extent that effects of past experience were relatively less important and harder to detect. The greater survival of experienced residents could not be explained by condition or territory quality, suggesting that familiarity with a local area confers survival advantages during the breeding season for cliff swallows. Colonial nesting may help to moderate the cost of unfamiliarity with an area, probably through social transfer of information about food sources and enhanced vigilance in large groups.

Animals that relocate to new breeding areas face two potential costs. One is a greater risk of mortality during transit in unfamiliar areas (often due to predation, starvation or exposure; e.g. Baker 1978; Gaines & McClenaghan 1980; Garrett & Franklin 1988; Van Vuren & Armitage 1994; Alberts & Altmann 1995; Aars et al. 1999; Stamps 2001). The other is unfamiliarity with the new breeding habitat where an animal settles, which may lead to higher risk of mortality or delays in finding mates and nesting

sites that reduce reproductive success (e.g. Tinkle et al. 1993; Wiggett & Boag 1993; Lozano & Lemon 1999). These costs are often regarded collectively as the costs of dispersal, but there is relatively little empirical information to evaluate their magnitude or importance for most taxa (Aars et al. 1999; Stamps 2001; Weisser 2001). In a few cases, predation rates are higher for newly arrived immigrants (e.g. Metzgar 1967; Ambrose 1972; Isbell et al. 1993; Hoogland et al. 2006), and in other cases, reproductive success or survival of new immigrants is as high or higher than that of more established residents (Berger 1987; Johnson & Gaines 1985, 1987; Krohne & Burgin 1987; Johannesen & Andreassen 1998; Aars et al. 1999; Hoover 2003). Familiarity with a specific territory or breeding site is generally assumed to be advantageous, as experience may confer useful information on the whereabouts of food, habits of local predators and places

Correspondence: C. R. Brown, Department of Biological Sciences, University of Tulsa, Tulsa, OK 74104, U.S.A. (email: charles-brown@ utulsa.edu). M. B. Brown is at the Tern and Plover Conservation Partnership, University of Nebraska, 3310 Holdrege St., Lincoln, NE 68583, U.S.A. K. R. Brazeal is at the Animal Behavior Graduate Group, Section of Neurobiology, Physiology, and Behavior, University of California, Davis, One Shields Avenue, Davis, CA 95616, U.S.A.

to seek shelter, although empirical studies showing apparent benefits of familiarity are usually confounded by effects of age, condition or territory quality (e.g. Shields et al. 1988; Gauthier 1989; Pärt & Gustafsson 1989; Saitou 1991; Isbell et al. 1993; Newton 1993; Lozano & Lemon 1999).

In colonially breeding animals, the ability to find food efficiently and avoid predators at or near a breeding site can be affected by group size. Individual foraging efficiency and the likelihood of escaping predators are often higher in larger colonies than in smaller colonies (reviewed in Brown & Brown 2001), and these group-size effects may interact with experience and familiarity at a site to influence fitness and habitat choice. For example, when many animals are present, immigrants to a site may have less need of personal knowledge of the site because they can rely on others to socially facilitate foraging and predator avoidance. In contrast, in small colonies, an individual's experience with a local area may be more important as compensation for the reduced social benefits of smaller groups. Consequently, a settler's familiarity with a potential colony site may determine in part the size of the colony it chooses and thus may help to create or maintain variation in colony size seen in many populations (Brown et al. 1990; Brown & Brown 2000). While it has been argued theoretically that animals might reduce the postsettlement costs of dispersal by settling with conspecifics and relying on information provided by them (e.g. Shields et al. 1988; Stamps 2001), we are aware of no studies that have shown this empirically.

In this study, we investigated whether past familiarity with a breeding colony site affected within-season survival of nesting cliff swallows, Petrochelidon pyrrhonota, and whether effects of familiarity were influenced by colony size. Adult survival within the breeding season is an important fitness component that varies in this species with the extent of ectoparasitism by blood-feeding bugs and with colony size (Brown & Brown 2004b). Within-season survival is an appropriate measure of fitness, because it pertains to the time of year when the birds are resident in the colonies and thus directly reflects the effects of site familiarity and group size. It is also less sensitive to biases introduced by movement away from a colony site between seasons when animals must often travel long distances to wintering areas. Our objectives were to compare within-season survival probabilities for individuals that were familiar (to varying degrees) with a colony site from past years with those of new immigrants to a site who had previously nested elsewhere, and to determine whether any differences between these classes of birds varied with colony size. Cliff swallows are well suited for such a study, because they nest in colonies of widely different sizes and some individuals are faithful to the same site in successive years while others immigrate to new colony sites between years (Brown & Brown 1996). We also examined potential differences in survival between residents and naïve immigrants during a period of cold weather that reduced food availability for cliff swallows, because at such times, familiarity with foraging habitat might be particularly important (Brown & Brown 1998).

METHODS

Study Animal and Study Site

Cliff swallows are highly colonial passerines that breed throughout most of western North America (Brown & Brown 1995). They build gourd-shaped mud nests and attach them to the vertical faces of cliff walls, rock outcrops or artificial sites such as the eaves of buildings or bridges. Their nests tend to be stacked closely together, often sharing walls. Cliff swallows are migratory, wintering in southern South America, and have a relatively short breeding season in North America. They begin to arrive at our study site in late April or early May and depart by late July. Most birds rear only one brood. Cliff swallows are associated with a variety of ectoparasites, endoparasites and viruses throughout their range (Monath et al. 1980; Scott et al. 1984; Brown & Brown 1995; Brown et al. 2001; Moore et al. 2007), and the ectoparasitic swallow bug (Hemiptera: Cimicidae: Oeciacus vicarius) can cause widespread nestling mortality and nest failure (Brown & Brown 1986, 1996). The main predators of adult cliff swallows in our study area are American kestrels, Falco sparverius, great horned owls, Bubo virginianus, black-billed magpies, Pica hudsonia, and common grackles, Quiscalus quiscula. Bull snakes, Pituophis catenifer, attack nests in colonies, usually preying on eggs or nestlings but sometimes catching adults inside their nests (Brown & Brown 1996).

Our study site is centred at the Cedar Point Biological Station (41°13′N, 101°39′W) near Ogallala, in Keith County, along the North and South Platte rivers, and also includes portions of Deuel, Garden, and Lincoln counties, southwestern Nebraska, U.S.A. We have studied cliff swallows there since 1982. Approximately 160 cliff swallow colony sites are in our 150×50 km study area, and about one-third are not used in a given year. Colony size varies widely; in our study area, it ranges from 2 to 6000 nests, with some birds nesting solitarily. Over a 25-year period, mean ± SE colony size ($N = 1812$) was 393 ± 15 nests. Each colony site tends to be separated from the next nearest by 1−10 km but in a few cases by more than 20 km. In our study area, the birds nest on both natural cliff faces and artificial structures such as bridges, buildings and highway culverts. The study site is described in detail by Brown & Brown (1996).

Beginning in 1984 and continuing throughout the study, we fumigated selected colonies each year to remove swallow bugs. Nests within colonies were sprayed with a dilute solution of an insecticide, Dibrom, that was highly effective in killing swallow bugs (Brown & Brown 1986, 1996, 2004a). Nests were fumigated weekly to remove any bugs brought into the colony by transient birds. Earlier work (Brown & Brown 2004b) showed that daily survival of cliff swallows was affected by the presence or absence of swallow bugs.

Mist Netting and Capture of Birds

We mist-netted cliff swallows at the study colonies at intervals throughout the nesting season and used the resulting captures and recaptures to estimate daily survival

probability. Colonies were chosen for study based on their accessibility to us, ease of netting and colony size. We tried to maximize the range of colony sizes studied each season. In this study we captured birds at 1−17 colonies annually. All colony sites were in the centre of our study area within a 35 km radius of the Cedar Point Biological Station.

Cliff swallows were mist-netted at colony sites as described in Brown (1998) and Brown & Brown (2004b). Adult birds were captured at each colony on 3−37 days during a season (mean = 7 days). Three capture occasions were the minimum necessary for estimating survival and recapture probabilities (Lebreton et al. 1992). An occasion equated to a single day, with netting usually done for 3−3.5 h per day per site. All birds caught received a numbered U. S. Fish and Wildlife Service band, gender was determined by presence or absence of a brood patch or cloacal protuberance, mass was taken, and, for some, additional procedures were done (e.g. colour-marked, morphological measurements taken, blood sampled). The total sample size of birds in this study, over all years and colonies, was 56 813 adults with known histories, distributed among 184 colonies during 1985−2006 (range 18−2166 birds per colony). If a bird was found at two (or more) colonies in the same year, it was treated as an initial capture at each colony but as a recapture only if it reappeared on a subsequent day at one of the same sites and as a recapture only for that site. Thus, survival was estimated only for presumed resident birds at a site, and individuals moving to a different colony site in a season were treated as permanent emigrants even if we knew of their survival in the study area at large. Most such individuals were transients at a site where they were captured only once. Additional details on study design are given in Brown & Brown (2004b).

Determining Colony Size

Cliff swallow colony size was defined as the maximum number of nests at a site to have contained one or more eggs. Active nests were counted at some sites by periodically checking the nest contents with a dental mirror and flashlight, whereas the colony size at other sites was estimated by counting the total number of intact nests in active sections of the colony. Full details on these methods of determining colony sizes are given in Brown & Brown (1996).

Morphometric Measurements

Fluctuating asymmetry in wing length was used as an index of condition for immigrant and resident cliff swallows (Brown & Brown 2002). The same person in all cases (M.B.B.) measured the length of each unflattened, closed wing from the anterior most part of the wrist joint to the tip of the outermost primary with a stoppered wing ruler. We used only the wings for asymmetry analyses, because fluctuating asymmetry in wings is least sensitive to measurement error (Brown & Brown 2002). Asymmetry was expressed as the unsigned right minus left values. Additional details on cliff swallow asymmetry analyses

including repeatabilities are provided in Brown & Brown (2002). Measurements were taken on a subset of birds caught at each site; we had no knowledge of a bird's status, for example, as a resident or immigrant, at the time of measurement.

Designating Experience Categories

Each individual caught at a colony in a given season was assigned to one of five experience categories denoting what we knew about its past history of colony site use based on its pattern of recaptures (Table 1). Not all categories were represented at each colony site in a given year, although sites minimally had to contain naïve immigrants (category N) and individuals that had always nested at the focal site (category A) to be included in the analyses.

Estimation of Survival

We estimated survival probabilities with the software program MARK (White & Burnham 1999) using the general methods of Lebreton et al. (1992) and Burnham & Anderson (2002). Encounter histories were constructed for all birds caught at least once at each colony. Daily survival was estimated for each colony separately each year because the number of capture occasions, dates of sampling, and intervals between the occasions were different for each site. Each colony in a given year represented a single population and thus the resulting survival estimates for each colony were subject to standard statistical testing. Because we were interested in within-season survival only, each encounter history automatically ended at the conclusion of each breeding season (after the last day of netting at each site). With the exception of the first-year age class (category F), the birds in this study were ones with past histories and thus present in multiple years. A given bird contributed to survival estimation at each colony site that it occupied over the years.

In earlier analyses, we identified six survival and recapture models that were fitted to the data at each colony; these six models are described in Brown & Brown

Table 1. Summary of the five experience categories used to describe the extent of a cliff swallow's familiarity with a colony site

Category	Description
N	*Naïve* immigrants that had nested, minimally, at one other colony site in past years but were not known to have nested at the focal site
A	Birds that had *always* used the focal site, not known to have nested elsewhere
P	Birds that had used the focal site in the immediate *past* year, but had occupied other sites in years before that
E	Birds that had used the focal site 2 or more years earlier but had nested *elsewhere* in the immediate past year
F	One-year old birds (banded as nestlings or juveniles the year before) breeding for their *first* time at the focal site

(2004b). The models incorporated different degrees of time dependence in both the survival and recapture parameters. We used age-dependent survival models to control for the presence of transients at a site and to estimate survival of the residents (Pradel et al. 1997; Brown & Brown 2004b). Before comparing the fit of the candidate set of models, we performed a goodness-of-fit test for each colony's data set using the program RELEASE (Burnham et al. 1987). This evaluated how well the data met the variance assumptions inherent in the binomial distribution used in capture−mark−recapture analysis. We assessed the goodness of fit of the most highly parameterized model in our candidate set by calculating a combined chi-square value based on Tests 3m, 2ct and 2cl in RELEASE (Pradel et al. 2005). The total chi-square value allows estimation of a variance inflation factor, $\hat{c}$, as χ^2/df, which was used in MARK to adjust the Akaike information criterion (AIC; Burnham & Anderson 2002) through quasilikelihood (QAIC). Further details are provided in Brown & Brown (2004b).

Comparing Experience Categories

Model fit at each colony initially was assessed by the AIC (or QAIC) in an earlier study without categorizing birds by their degree of past familiarity with a site (Brown & Brown 2004b). The model with the lowest AIC was considered the best model. Using the survival and recapture structure from this model, we estimated daily survival from a series of eight models that differed only in the way that birds of different experience categories were grouped. Because we were primarily interested in how naïve birds performed relative to experienced residents, in all cases we had two groups with category N birds (new immigrants at a site) always separate from category A birds (residents that had always been there). Categories P, E and F were then placed in either of the two groups in these combinations: N/APEF, NF/APE, NFE/AP, NFEP/A, NPE/AF, NP/AEF, NE/APF, NFP/AE. We also included a model without a group effect in which survival of all birds in all categories was considered identical. Parameter estimates for each experience category were generated from all nine models, and daily survival for each category at a colony site averaged among all models using MARK. Model averaging weights the parameter estimate from a given model by the likelihood of that model being the 'best' one. We did not divide our data set into more than two groups, because of relatively small sample sizes at most colonies for birds in categories P, E and F.

We estimated daily survival during a cold weather event in 2004 at one colony where netting spanned both the period before and after the cold weather. Using the parameter structure from the best-fitting two-group model (see above), we constructed a model with survival during the intervals prior to the cold weather as different from the interval spanning the cold weather period, and compared this model to one that considered survival constant throughout the season. Parameter estimates from these two models were averaged for experienced residents (category A) and naïve immigrants (category N).

Statistical Analyses

After we generated point estimates of survival probabilities for different experience categories at each colony, we found that the distributions were not normal, and no transformations successfully normalized them. We thus used nonparametric statistical tests for most of our analyses. To assess the separate effects of several independent variables on survival differences between groups of birds, we ranked all quantitative variables and used the rank-transformed values (Montgomery 2001) in an analysis of covariance (ANCOVA), respectively. Statistical analysis of the per-colony survival probabilities was done with SAS (SAS Institute 1990). Survival probabilities (± 1 SE) are reported.

RESULTS

Survival in Relation to Experience at a Site

Among the 152 nonfumigated colonies in 1985−2006, average survival for experienced birds (category A) was higher than that for naïve immigrants (category N) at 87 (57.2%); significantly more sites had greater survival for experienced birds than for immigrants (binomial test: $P = 0.044$). The mean difference in daily survival (category A minus category N) across all nonfumigated colonies differed significantly from 0 (one-sample t test: $t_{151} = 2.18$, $P = 0.031$). A similar comparison for 32 fumigated colonies showed 22 (68.8%) with higher average survival for experienced birds (binomial test: $P = 0.025$), but the mean difference in daily survival at fumigated sites did not differ significantly from 0 (one-sample t test: $t_{31} = 1.05$, $P = 0.30$).

Averaged over all nonfumigated colonies, experienced residents that had always nested at the same colony site had a 1.2% higher daily survival probability than naïve immigrants (Fig. 1a). Individuals with some (but not exclusive) experience at a site showed daily survival probabilities higher than those of naïve immigrants but lower than those of perennial residents; those present at a site the previous year had higher average survival than ones that had only been present 2 or more years earlier (Fig. 1a). First-time breeders (yearlings) had the lowest daily survival (Fig. 1a). Daily survival probabilities per colony for nonfumigated sites differed significantly between the experience categories (Kruskal−Wallis ANOVA: $\chi^2_4 = 12.4$, $P = 0.014$; Fig. 1a).

For fumigated colonies, experienced residents averaged only 0.2% higher daily survival than naïve residents (Fig. 1b). Individuals with some (but not exclusive) experience at a site had higher daily survival on average than either perennial residents or naïve immigrants, and first-year birds had a daily survival equivalent to that of perennial residents (Fig. 1b). However, daily survival probabilities per colony for fumigated sites did not differ between the experience categories (Kruskal−Wallis ANOVA: $\chi^2_4 = 8.1$, $P = 0.09$; Fig. 1b).
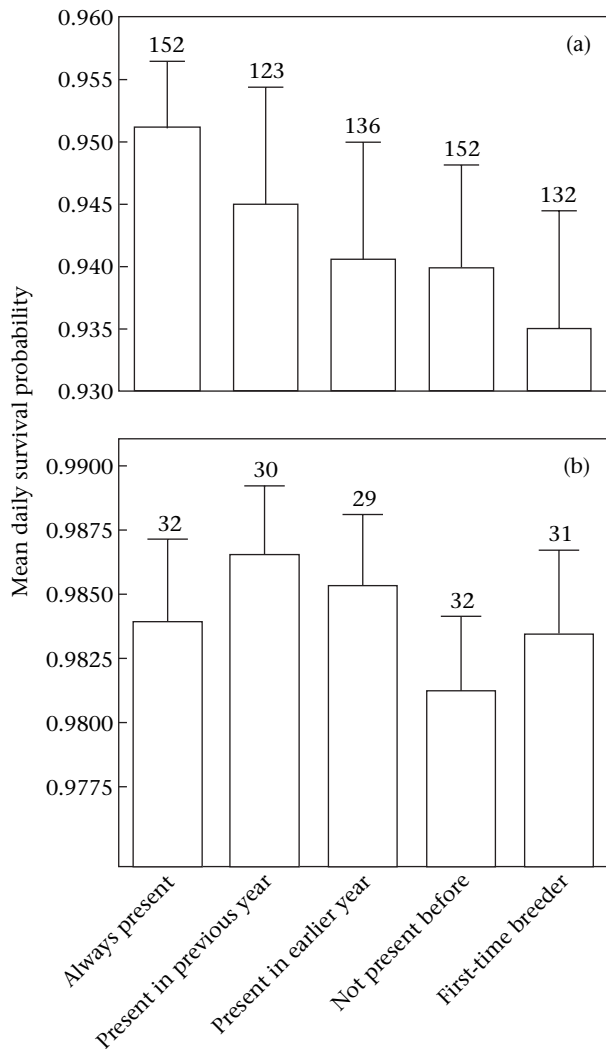
Figure 1. Daily survival probability ($\phi \pm$ SE) per colony for cliff swallows that had always been present at the same breeding colony (category A), those present there in the previous year but elsewhere in an earlier year (category P), those that were elsewhere the previous year but present at the focal site in an earlier year (category E), naïve immigrants that had not been present before (category N), and first-time (yearling) breeders (category F), at nonfumigated (a) and fumigated (b) colonies. Values are means across colonies. Sample sizes (number of colonies) are shown above bars. Survival probabilities were estimated with the software program MARK through model averaging (see text). Note the differences in scale of the Y axes.

Factors Affecting Differences in Survival

The magnitude of the survival difference between immigrants and experienced residents at a colony was unaffected by whether a colony was fumigated or not, the colony site itself, or the sample size (number of birds) of category A (typically smaller than that for category N at most sites; ANCOVA, Table 2). Year and colony size (see below) had a significant effect on the extent of the survival difference between experienced residents and naïve immigrants at a colony site (Table 2). The average difference between survival of experienced residents and naïve immigrants (category A minus category N) per site varied

Table 2. Analysis of covariance to detect effects of variables potentially affecting the extent of the difference between daily survival probabilities of experienced residents versus naïve immigrant cliff swallows at a colony site ($N = 184$ colonies)

Variable	F	df	P
Fumigated or not	0.18	1	0.67
Year	1.88	21	0.017
Colony site	0.00	29	0.97
Sample size*	0.41	1	0.52
Colony size (site)†	2.01	1	0.004

*Of group containing experienced residents.
†Effect of colony size was nested within colony site because of potential covariation between colony size and a physical site (Brown & Brown 2004b).

from -0.0283 (in 2002) to 0.1515 (in 1998). However, we did not find climatic correlates or other relationships that explained this yearly variation. We did not separate our analyses by sex, as gender has no effect on daily survival probability in this population of cliff swallows (Brown & Brown 2004b).

While the magnitude of the survival difference between experienced residents versus naïve immigrants did not vary with fumigation status at a site (Table 2), cliff swallows at fumigated sites had higher absolute daily survival probabilities on average than did birds at nonfumigated sites (see Fig. 1). Daily survival probability of experienced residents differed significantly between fumigated and nonfumigated colonies (Wilcoxon two-sample test: $Z = 2.91$, $P = 0.004$), as did daily survival probability of naïve immigrants ($Z = 3.45$, $P = 0.0006$).

Effect of Colony Size

Colony size affected the magnitude of the survival difference between naïve immigrants and experienced residents at a site, when colony size was nested within colony site in an ANCOVA (Table 2). This effect seemed to be mostly because the largest colonies had little survival advantage for experienced residents (Fig. 2). For example, in colonies with more than 750 nests ($N = 44$), the average daily difference in survival probabilities (category A minus category N) was -0.0052, whereas in colonies with fewer than 750 nests ($N = 144$), the average difference was 0.0243. However, for smaller colonies, there was no significant correlation between the survival difference and colony size (Spearman rank correlation: $r_S = 0.13$, $P = 0.11$; Fig. 2).

Effect of Bad Weather

In 2004, a 4-day period during 17−20 June was unusually cold and rainy, reducing the availability of flying insects, and these conditions caused the starvation of thousands of nestling cliff swallows and smaller numbers of adults in our study area. At one colony of about 600 nests, the estimated daily survival probability during the cold weather for naïve immigrants was 0.8605 ± 0.0124
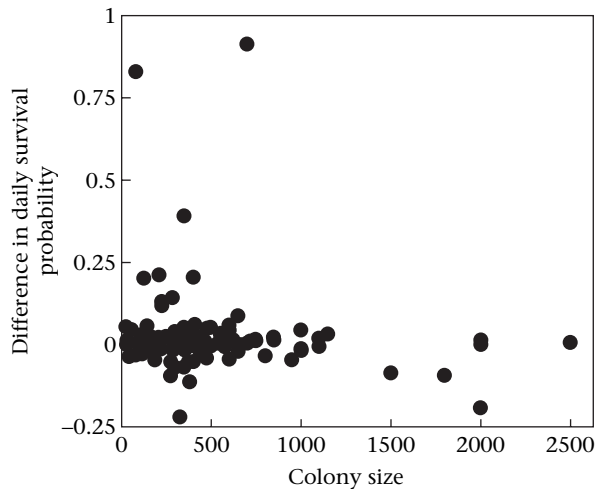
Figure 2. Difference in daily survival probability between experienced residents versus naïve immigrants at a cliff swallow colony site in relation to colony size (number of active nests). A positive difference means that experienced residents had higher survival, and a negative difference means that immigrants had higher survival. Only nonfumigated colonies are shown.

and for experienced residents 0.9480 ± 0.0001. Prior to the bad weather, immigrants and residents at this site had estimated daily survival probabilities of 0.9465 ± 0.0260 and 0.9917 ± 0.0245, respectively.

Fluctuating Asymmetry as a Measure of Condition

At 17 colonies ranging in size from 98 to 1600 nests, we had wing measurements for both naïve immigrants and experienced residents; combined sample sizes across all colonies were 1054 and 1320 birds for category N and category A, respectively. There was no significant difference in unsigned wing asymmetry between immigrants and residents at any of the colonies (Wilcoxon two-sample test for each colony: $P \geq 0.09$ in all cases).

DISCUSSION

The analyses reported here reveal a survival cost for immigrant cliff swallows occupying a breeding colony site for the first time. Experienced birds that always used the same site had about 1% higher daily survival, on average, than naïve immigrants. Translating the seemingly small difference in daily survival probability (using Powell (2007)'s delta method) revealed that monthly survival of experienced residents was 8.6% greater than that of naïve immigrants (see Brown & Brown 2004b). There was no evidence that the difference between immigrants and residents could be caused by differential quality or condition of the two classes of birds (see Lozano & Lemon 1999; Dufty & Belthoff 2001; Ims & Hjermann 2001), as we found no differences between them in wing fluctuating asymmetry. These results could not be explained by

differences in territory quality among immigrants and residents, because cliff swallows do not defend territories.

As in most studies of survival in open populations, our results cannot distinguish mortality from permanent emigration. Although emigration within the nesting season is likely to be less than that occurring between seasons, cliff swallows that permanently left a colony site during the season would be treated as dead in our statistical estimation of survival. We addressed this in part by specifically testing for the presence of transient individuals in our analyses and deriving survival estimates only for nesting birds in each colony (Pradel et al. 1997). However, this solution still does not account for birds that may have been resident at a colony for part of a season but emigrated from the site before the season ended, which occurs occasionally when a nest fails and owners abandon a colony completely (Brown & Brown 1996). Thus, our daily survival probabilities are underestimates to some degree. Nevertheless, the daily survival estimates we present are relative indexes of survival as long as emigration from a site does not covary with whether a bird has prior experience there (Brown & Brown 2004b).

Experience at a Site and Survival

Daily survival probability in cliff swallows is potentially affected by many factors, yet it provides a useful integrative measure of how these factors collectively affect fitness (Brown & Brown 2004b). Among the more important effects on survival are an individual's ability to find food (especially during cold weather events), the ectoparasitic swallow bugs and predation (Brown & Brown 1996, 2004b). How might experience at a site influence these effects on survival?

Cliff swallows feed on patches of swarming insects that are spatiotemporally variable over brief periods such as a single morning (Brown & Brown 1996). Birds use information from knowledgeable colony members in order to locate swarms on a short-term basis (Brown 1986; Brown & Brown 1996). The habitat surrounding a colony site and the terrain over which birds forage is quite variable from site to site (Brown et al. 2002), and it is probable that swallows learn in general where insects are more likely to be found near a specific colony site (e.g. around windbreaks or bare earth, which promotes formation of thermals; Brown & Brown 1996). During spells of cold weather that may often last 2–3 days in our study area and that restrict flying-insect availability, the birds must resort to foraging over lakes and rivers (where a few insects can still be found), and these bodies of water are often situated some distance from a colony site. Past familiarity with a breeding colony site probably enables an individual to find these foraging sites more quickly, and the resulting increase in foraging success may affect survival, especially in cold weather. In support of this, we found that experienced residents at one site had a 4.4% reduction in daily survival probability during a cold weather event, compared to a 9.1% reduction for naïve immigrants during that same period.

Cliff swallows are attacked by both avian predators and snakes in our study area (Brown & Brown 1996). While predation events are not common at most sites, they are frequent enough, on average, to increase per capita risk in the larger colonies despite greater levels of vigilance and the dilution effect there (Brown & Brown 1987, 1996). The avian predators tend to hunt in predictable ways; for example, black-billed magpies usually perch on the same part of a bridge under which cliff swallows nest, and fly out at incoming and outgoing swallows. The habits of local predators may be more familiar to birds that have perennially nested at a given colony site, and the unfamiliarity of naïve immigrants with local predator hunting strategies could contribute to their lower daily survival probabilities.

Experience at a site may also help cliff swallows avoid exposure to ectoparasites such as swallow bugs (and the viruses they carry; Monath et al. 1980; Scott et al. 1984; Brown et al. 1995, 2001; Moore et al. 2007) and thereby improve survival prospects. At many colonies, not all existing nests are used in a given year; ones from the past year tend to be more infested with swallow bugs than ones not used in the last year. Familiarity with what part of a colony site was used last year may help direct a bird when it first arrives away from nests likely to be infested and cause it to settle in nests or parts of the colony site where parasites are less numerous.

Removal of nest ectoparasites by fumigation resulted in higher survival probabilities for all birds, on average, and diminished the differences between immigrants and past residents. This finding might suggest that the extent of nest parasitism by blood-feeding bugs at a site directly interacts with past experience to influence daily survival. However, a more likely conclusion is that removal of parasite-related stress on nesting cliff swallows (e.g. Brown & Brown 1986, 1996) increases overall survival probability to such a large degree (Brown & Brown 2004b), probably by improving bird condition and altering time and energy budgets, that effects of past experience are relatively less important and harder to detect.

Effects of Colony Size

Cliff swallows, like most colonial animals, receive social benefits of living in colonies. These have been studied extensively (Brown & Brown 1996), and the most important ones are related to food finding. Birds use each other to find the locations of insect swarms, mostly by following successful individuals from their nests to a foraging site (Brown 1986, 1988; Brown & Brown 1996). At other times, birds give special calls to alert others that food has been found (Stoddard 1988; Brown et al. 1991). Swallows in larger colonies also detect incoming predators at greater distances, giving colony residents time to take evasive action (Brown & Brown 1987). Both food-finding and predator-related benefits increase with colony size (Brown & Brown 1996).

The ability to gain information on food sources from conspecifics and to avoid predators through group vigilance could compensate naïve immigrants for their unfamiliarity with a colony site, and this might be most pronounced in the largest colonies where these social effects are greatest. In support, we found no survival disadvantage for naïve immigrants (and conversely, no survival advantage for experienced residents) in the larger colonies (those with more than 750 nests). With fewer conspecifics in smaller colonies, a naïve immigrant might be more exposed to predators and would not as efficiently locate food, impacting daily survival probability and contributing to the disadvantage suffered by immigrants in some of the smaller colonies.

Cliff swallows in colonies of different sizes show various phenotypic differences that suggest a sorting of birds among colonies (Brown & Brown 1996, 2000; Brown et al. 2005). Thus, a possible alternative interpretation of our results is that individuals immigrating into the larger colonies are of higher quality or in better condition than ones immigrating into small colonies. If so, the smaller survival differences between immigrants and experienced residents in the largest colonies might not be directly attributable to sociality. However, we found no evidence of differences in quality between classes of birds or colony sizes. Wing asymmetry, an index of an individual's past exposure to ectoparasites and thus its probable condition (Brown & Brown 2002), did not differ between immigrants and experienced residents in any colony, large or small.

Survival of Birds with Mixed Experience and Yearlings

Comparison of survival probabilities of birds resident at the same colony site the previous year (but not in years before that) with those that had been resident there in an earlier year (but not the previous year), seems to suggest that familiarity with the site from the previous year is more useful than more dated information from earlier years, especially at nonfumigated sites (Fig. 1). Cliff swallows with mixed experience but that were residents the year before averaged only 0.6% lower daily survival than perennial residents, whereas those with familiarity strictly from earlier years showed survival probabilities more similar to those of naïve immigrants. Local conditions such as foraging terrain and habits of local predators possibly change enough with time that familiarity from 2 or more years ago is less likely to result in useful information than when birds have been there more recently. Still, even outdated familiarity with a site conferred higher survival prospects, on average, than did unfamiliarity at many colony sites.

Birds in their first breeding year have no past experience at any site, and perhaps as a result they are the ones most likely to fall victim to predators (Brown & Brown 1996). They may also be more likely to starve in bad weather. We thus might expect daily survival of first-time breeders (category F) to be even lower than that of naïve immigrants (all of whom were at least 2 years old; category N). This proved to be the case, with yearling breeders showing the lowest daily survival probabilities of all classes among nonfumigated sites (Fig. 1a).

The lower survival for yearlings suggests that one potentially confounding variable in our other analyses might be age, especially if survival tends to increase with age. We addressed this in part by using only birds known to be at least 2 years old in comparing naïve immigrants and experienced residents. Yet, if daily survival also systematically varies among birds older than 2 years (for reasons unrelated to the colony site occupied) and perennial residents are on average older than immigrants, survival differences between categories or colony sizes could reflect an age structure of the subsets of birds being compared. However, previous work has shown that larger colonies contain younger birds, on average, than smaller ones (Brown & Brown 1996). This suggests that the greater survival of immigrants in large colonies, relative to small colonies, cannot be due to older birds either being overrepresented in large colonies or being overrepresented among residents. Thus, an effect of age per se on daily survival beyond the second year is unlikely to explain our results.

Site Familiarity and Coloniality

If naïve immigrant cliff swallows pay a survival cost related to their unfamiliarity with a new colony site, why do birds immigrate to a different colony site at all? Some birds in our population perennially use the same site, while others regularly move to different sites in different years. Clearly, if an immigrating bird chooses one of the largest colonies, it is less likely to suffer a reduction in its survival prospects, and this may represent a major benefit of coloniality for individuals that immigrate. For birds in the larger colonies, sociality moderates the postsettlement costs of dispersal, and in so doing, may make dispersal more advantageous in certain circumstances. If such benefits of sociality are widespread, this may be a basis for why many colonial species show 'conspecific attraction' (e.g. Burger 1988; Shields et al. 1988; Smith & Peacock 1990; Reed & Dobson 1993; Brown & Rannala 1995; Serrano et al. 2001; Stamps 2001), in which naïve (often young) animals prefer to settle in groups. Those cliff swallows choosing small colonies may pay a more substantial cost of immigrating than those that choose large colonies. Although the reasons for immigration remain unclear in many cases for cliff swallows, the ability to join a large colony and do well despite being unfamiliar with the local conditions represents a previously unknown benefit of coloniality for at least some individuals in the population. For this reason, we might also predict greater rates of immigration to large colonies, although this prediction has not been explicitly tested for cliff swallows. In addition, the apparent advantages of familiarity with a site may help maintain the existence of small cliff swallow colonies, where experienced birds can do well despite the reduced social benefits and perhaps avoid the inevitable costs of large groups (e.g. ectoparasitism).

Identifying the costs and benefits of colonial breeding has been a goal of behavioural ecologists for decades (e.g. Hoogland & Sherman 1976; Snapp 1976; Wiklund & Andersson 1994; Brown & Brown 1996, 2001; Safran 2004), but we still do not completely understand the complexities of how these costs and benefits interact to affect the fitness of animals in differently sized groups. The analyses reported here reveal yet another complexity for the well-studied cliff swallow. Earlier work showed that birds in larger colonies have higher daily survival probabilities on average (Brown & Brown 2004b), but it now appears that a bird's past history at a site may be partly responsible for this pattern. Lower survival probabilities for immigrants in smaller colonies reduce average survival for those sites, whereas all birds do well in large colonies. This finding underscores the importance of considering the identity and past experience of the individuals that constitute each breeding colony when studying the effects of group size on fitness.

A number of studies have measured how animals settling in new areas (dispersers) perform, but these comparisons are usually relative to philopatric individuals in a different area who do not move (e.g. Pärt & Gustafsson 1989; Pärt 1991; Van Vuren & Armitage 1994; Spear et al. 1998; Aars et al. 1999). Furthermore, most studies are necessarily confounded by dispersers often being younger than philopatric animals and sometimes being forced to settle for territories of poorer quality by virtue of the more suitable habitat being saturated with incumbents (Greenwood 1980; Waser & Jones 1983; Isbell et al. 1993). This study of cliff swallows is one of the few we are aware of to measure the performance of immigrants and residents at the same site simultaneously and suggests that familiarity with a local area, per se, can be important and have a major effect on survival. An important question yet to be addressed is how the degree of familiarity with a local colony site affects other components of fitness such as reproductive success and how coloniality in turn influences this interaction.

References

Aars, J., Johannesen, E. & Ims, R. A. 1999. Demographic consequences of movements in subdivided root vole populations. *Oikos*, **85**, 204−216.

Alberts, S. C. & Altmann, J. 1995. Balancing costs and opportunities: dispersal in male baboons. *American Naturalist*, **145**, 279−306.

Ambrose, H. W., III. 1972. Effect of habitat familiarity and toe-clipping on rate of owl predation in *Microtus pennsylvanicus*. *Journal of Mammalogy*, **53**, 909−912.

Baker, R. R. 1978. *The Evolutionary Ecology of Animal Migration*. London: Hodder & Stoughton.

Berger, J. 1987. Reproductive fates of dispersers in a harem-dwelling ungulate: the wild horse. In: *Mammalian Dispersal Patterns: the Effects of Social Structure on Population Genetics* (Ed. by B. D. Chepko-Sade & Z. T. Halpin), pp. 41−54. Chicago: University of Chicago Press.

Brown, C. R. 1986. Cliff swallow colonies as information centers. *Science*, **234**, 83−85.

Brown, C. R. 1988. Enhanced foraging efficiency through information centers: a benefit of coloniality in cliff swallows. *Ecology*, **69**, 602−613.

Brown, C. R. 1998. *Swallow Summer*. Lincoln, Nebraska: University of Nebraska Press.

Brown, C. R. & Brown, M. B. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology*, **67**, 1206−1218.

Brown, C. R. & Brown, M. B. 1987. Group-living in cliff swallows as an advantage in avoiding predators. *Behavioral Ecology and Sociobiology*, **21**, 97−107.

Brown, C. R. & Brown, M. B. 1995. Cliff swallow (*Hirundo pyrrhonota*). In: *The Birds of North America. No. 149* (Ed. by A. Poole & F. Gill), Philadelphia: Academy of Natural Sciences. Washington, D.C.: American Ornithologists' Union.

Brown, C. R. & Brown, M. B. 1996. *Coloniality in the Cliff Swallow: the Effect of Group Size on Social Behavior*. Chicago: University of Chicago Press.

Brown, C. R. & Brown, M. B. 1998. Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution*, **52**, 1461−1475.

Brown, C. R. & Brown, M. B. 2000. Heritable basis for choice of group size in a colonial bird. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 14825−14830.

Brown, C. R. & Brown, M. B. 2001. Avian coloniality: progress and problems. *Current Ornithology*, **16**, 1−82.

Brown, C. R. & Brown, M. B. 2002. Ectoparasites cause increased bilateral asymmetry of naturally selected traits in a colonial bird. *Journal of Evolutionary Biology*, **15**, 1067−1075.

Brown, C. R. & Brown, M. B. 2004a. Empirical measurement of parasite transmission between groups in a colonial bird. *Ecology*, **85**, 1619−1626.

Brown, C. R. & Brown, M. B. 2004b. Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behavioral Ecology and Sociobiology*, **56**, 498−511.

Brown, C. R. & Rannala, B. 1995. Colony choice in birds: models based on temporally invariant site quality. *Behavioral Ecology and Sociobiology*, **36**, 221−228.

Brown, C. R., Stutchbury, B. J. & Walsh, P. D. 1990. Choice of colony size in birds. *Trends in Ecology & Evolution*, **5**, 398−403.

Brown, C. R., Brown, M. B. & Shaffer, M. L. 1991. Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, **42**, 551−564.

Brown, C. R., Brown, M. B. & Rannala, B. 1995. Ectoparasites reduce long-term survival of their avian host. *Proceedings of the Royal Society of London, Series B*, **262**, 313−319.

Brown, C. R., Komar, N., Quick, S. B., Sethi, R. A., Panella, N. A., Brown, M. B. & Pfeffer, M. 2001. Arbovirus infection increases with group size. *Proceedings of the Royal Society of London, Series B*, **268**, 1833−1840.

Brown, C. R., Sas, C. M. & Brown, M. B. 2002. Colony choice in cliff swallows: effects of heterogeneity in foraging habitat. *Auk*, **119**, 446−460.

Brown, C. R., Brown, M. B., Raouf, S. A., Smith, L. C. & Wingfield, J. C. 2005. Steroid hormone levels are related to choice of colony size in cliff swallows. *Ecology*, **86**, 2904−2915.

Burger, J. 1988. Social attraction in nesting least terns: effects of numbers, spacing, and pair bonds. *Condor*, **90**, 575−582.

Burnham, K. P. & Anderson, D. R. 2002. *Model Selection and Multimodel Inference: a Practical Information−Theoretic Approach*. 2nd edn. New York: Springer.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. 1987. *Design and Analysis Methods for Fish Survival Experiments Based on Release−Recapture*. Bethesda, Maryland: American Fisheries Society Monograph 5.

Dufty, A. M., Jr & Belthoff, J. R. 2001. Proximate mechanisms of natal dispersal: the role of body condition and hormones. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 217−229. Oxford: Oxford University Press.

Gaines, M. S. & McClenaghan, L. R. 1980. Dispersal in small mammals. *Annual Review of Ecology and Systematics*, **11**, 163−196.

Garrett, M. G. & Franklin, W. L. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. *Journal of Mammalogy*, **69**, 236−250.

Gauthier, G. 1989. The effect of experience and timing on reproductive performance in buffleheads. *Auk*, **106**, 568−576.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140−1162.

Hoogland, J. L. & Sherman, P. W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecological Monographs*, **46**, 33−58.

Hoogland, J. L., Cannon, K. E., DeBarbieri, L. M. & Manno, T. G. 2006. Selective predation on Utah prairie dogs. *American Naturalist*, **168**, 546−552.

Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology*, **84**, 416−430.

Ims, R. A. & Hjermann, D. Ø. 2001. Condition-dependent dispersal. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 203−216. Oxford: Oxford University Press.

Isbell, L. A., Cheney, D. L. & Seyfarth, R. M. 1993. Are immigrant vervet monkeys, *Cercopithecus aethiops*, at greater risk of mortality than residents? *Animal Behaviour*, **45**, 729−734.

Johannesen, E. & Andreassen, H. P. 1998. Survival and reproduction of resident and immigrant female root voles (*Microtus oeconomus*). *Canadian Journal of Zoology*, **76**, 763−766.

Johnson, M. L. & Gaines, M. S. 1985. Selective basis for emigration of the prairie vole, *Microtus ochrogaster*: open field experiment. *Journal of Animal Ecology*, **54**, 399−410.

Johnson, M. L. & Gaines, M. S. 1987. The selective basis for dispersal of the prairie vole, *Microtus ochrogaster*. *Ecology*, **68**, 684−694.

Krohne, D. T. & Burgin, A. B. 1987. Relative success of residents and immigrants in *Peromyscus leucopus*. *Holarctic Ecology*, **10**, 196−200.

Lebreton, J. D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67−118.

Lozano, G. A. & Lemon, R. E. 1999. Effects of prior residence and age on breeding performance in yellow warblers. *Wilson Bulletin*, **111**, 381−388.

Metzgar, L. H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). *Journal of Mammalogy*, **48**, 387–391.

Monath, T. P., Lazuick, J. S., Cropp, C. B., Rush, W. A., Calisher, C. H., Kinney, R. M., Trent, D. W., Kemp, G. E., Bowen, G. S. & Francy, D. B. 1980. Recovery of Tonate virus (''Bijou Bridge'' strain), a member of the Venezuelan equine encephalomyelitis virus complex, from cliff swallow nest bugs (*Oeciacus vicarius*) and nestling birds in North America. *American Journal of Tropical Medicine and Hygiene*, **29**, 969–983.

Montgomery, D. C. 2001. *Design and Analysis of Experiments*. 5th edn. New York: J. Wiley.

Moore, A. T., Edwards, E. A., Brown, M. B., Komar, N. & Brown, C. R. 2007. Ecological correlates of Buggy Creek virus infection in *Oeciacus vicarius*, southwestern Nebraska, 2004. *Journal of Medical Entomology*, **44**, 42–49.

Newton, I. 1993. Age and site fidelity in female sparrowhawks, *Accipiter nisus*. *Animal Behaviour*, **46**, 161–168.

Pärt, T. 1991. Philopatry pays: a comparison between collared flycatcher sisters. *American Naturalist*, **138**, 790–796.

Pärt, T. & Gustafsson, L. 1989. Breeding dispersal in the collared flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. *Journal of Animal Ecology*, **58**, 305–320.

Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *Condor*, **109**, 950–955.

Pradel, R., Hines, J. E., Lebreton, J.-D. & Nichols, J. D. 1997. Capture–recapture survival models taking account of transients. *Biometrics*, **53**, 60–72.

Pradel, R., Gimenez, O. & Lebreton, J.-D. 2005. Principles and interest of GOF tests for multistate capture–recapture models. *Animal Biodiversity and Conservation*, **28**, 189–204.

Reed, J. M. & Dobson, A. P. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology & Evolution*, **8**, 253–256.

Safran, R. J. 2004. Adaptive site selection rules and variation in group size of barn swallows: individual decisions predict population patterns. *American Naturalist*, **164**, 121–131.

Saitou, T. 1991. Comparison of breeding success between residents and immigrants in the great tit. *Acta Congressus Internationalis Ornithologici*, **20**, 1196–1203.

SAS Institute. 1990. *SAS/STAT User's Guide, Version 6*. Cary, North Carolina: SAS Institute.

Scott, T. W., Bowen, G. S. & Monath, T. P. 1984. A field study of the effects of Fort Morgan virus, an arbovirus transmitted by swallow bugs, on the reproductive success of cliff swallows and symbiotic house sparrows in Morgan County, Colorado, 1976. *American Journal of Tropical Medicine and Hygiene*, **33**, 981–991.

Serrano, D., Tella, J. L., Forero, M. G. & Donazar, J. A. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology*, **70**, 568–578.

Shields, W. M., Crook, J. R., Hebblethwaite, M. L. & Wiles-Ehmann, S. S. 1988. Ideal free coloniality in the swallows. In: *The Ecology of Social Behavior* (Ed. by C. N. Slobodchikoff), pp. 189–228. San Diego: Academic Press.

Smith, A. T. & Peacock, M. M. 1990. Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology*, **4**, 320–323.

Snapp, B. D. 1976. Colonial breeding in the barn swallow (*Hirundo rustica*) and its adaptive significance. *Condor*, **78**, 471–480.

Spear, L. B., Pyle, P. & Nur, N. 1998. Natal dispersal in the western gull: proximal factors and fitness consequences. *Journal of Animal Ecology*, **67**, 165–179.

Stamps, J. A. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 230–242. Oxford: Oxford University Press.

Stoddard, P. K. 1988. The ''bugs'' call of the cliff swallow: a rare food signal in a colonially nesting bird species. *Condor*, **90**, 714–715.

Tinkle, D. W., Dunham, A. E. & Congdon, J. D. 1993. Life history and demographic variation in the lizard *Sceloporus graciosus*: a long-term study. *Ecology*, **74**, 2413–2429.

Van Vuren, D. & Armitage, K. B. 1994. Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? *Oikos*, **69**, 179–181.

Waser, P. M. & Jones, W. T. 1983. Natal philopatry among solitary mammals. *Quarterly Review of Biology*, **58**, 355–390.

Weisser, W. W. 2001. The effects of predation on dispersal. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 180–188. Oxford: Oxford University Press.

White, G. C. & Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, S120–S139.

Wiggett, D. R. & Boag, D. A. 1993. Annual reproductive success in three cohorts of Columbian ground squirrels: founding immigrants, subsequent immigrants, and natal residents. *Canadian Journal of Zoology*, **71**, 1577–1584.

Wiklund, C. G. & Andersson, M. 1994. Natural selection of colony size in a passerine bird. *Journal of Animal Ecology*, **63**, 765–774.