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Parent–offspring resemblance in colony-specific adult survival of cliff swallows

Charles R. Brown[1] · Erin A. Roche[2] ·
Mary Bomberger Brown[3]

Abstract Survival is a key component of fitness. Species that occupy discrete breeding colonies with different characteristics are often exposed to varying costs and benefits associated with group size or environmental conditions, and survival is an integrative net measure of these effects. We investigated the extent to which survival probability of adult ($\geq$1-year old) cliff swallows (*Petrochelidon pyrrhonota*) occupying different colonies resembled that of their parental cohort and thus whether the natal colony had long-term effects on individuals. Individuals were cross-fostered between colonies soon after hatching and their presence as breeders monitored at colonies in the western Nebraska study area for the subsequent decade. Colony-specific adult survival probabilities of offspring born and reared in the same colony, and those cross-fostered away from their natal colony soon after birth, were positively and significantly related to subsequent adult survival of the parental cohort from the natal colony. This result held when controlling for the effect of natal colony size and the age composition of the parental cohort. In contrast, colony-specific adult survival of offspring cross-fostered to a site was unrelated to that of their foster parent cohort or to the cohort of non-fostered offspring with whom they were reared. Adult survival at a colony varied inversely with fecundity, as measured by mean brood size, providing evidence for a survival–fecundity trade-off in this species. The results suggest some heritable variation in adult survival, likely maintained by negative correlations between fitness components. The study provides additional evidence that colonies represent non-random collections of individuals.

Keywords Cliff swallow · Coloniality · Fitness · Life history ·
Petrochelidon pyrrhonota · Survival · Trade-offs

✉ Charles R. Brown
   charles-brown@utulsa.edu

[1]   Department of Biological Sciences, University of Tulsa, 800 S. Tucker Dr., Tulsa, OK 74104, USA

[2]   U. S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND 58401, USA

[3]   School of Natural Resources, University of Nebraska, Lincoln, NE 68583, USA

Introduction

Annual survival, as reflected in breeding lifespan, is one of the major components of individual fitness in natural populations (Roff 1992; Stearns 1992), especially among iteroparous organisms. In birds, lifespan often contributes more to differences in individual fitness than fecundity (Clutton-Brock 1988; Newton 1989), and survivorship may be the best single surrogate for fitness among organisms in general (Pfister 1998; Crone 2001). Understanding the factors that promote variation in survival is thus important in making inferences about potential selection pressures and consequent evolutionary responses.

In colonial animals that are often distributed unevenly across a landscape at discrete breeding sites, one potentially important determinant of survival (and thus of fitness) is the colony occupied. Colonies may differ in size, physical environment for nesting, local food availability, the phenotypic composition of the residents breeding there, or in other ways that influence fitness (Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990; Brown and Brown 2001). Survival is an integrative measure of the different costs and benefits of coloniality, most of which are measured in different currencies (e.g., likelihood of predation vs. food intake rates) and may vary widely across, for example, colonies of different sizes (Brown and Brown 1996, 2004). Thus, understanding how and why survival varies among groups of individuals occupying different sites is key if we are to identify the selective advantages of group living.

Like other traits strongly associated with fitness, survival often has been shown to have low heritability (Gustafsson 1986; Mousseau and Roff 1987; Campbell 1997; Merilä and Sheldon 1999; Papaïx et al. 2010). This result is assumed to reflect reduced additive genetic variance for traits under strong selection and at evolutionary equilibrium (Barton and Turelli 1989; Price and Schluter 1991). However, various factors can, at least in theory, maintain moderate levels of additive genetic variance for fitness-related traits, including polygenic mutation, spatiotemporally fluctuating selection, and negative correlations between fitness components (Mousseau and Roff 1987; Fuiman and Cowan 2003; Coltman et al. 2005; Vehviläinen et al. 2008). Perhaps as a result, some empirical studies have provided evidence that survival can have a moderately high heritability and thus be subject to selection (Chambers et al. 1996; Campbell 1997; Kenway et al. 2006; Blomquist 2010; Dégremont et al. 2010).

In this study, we examine the extent to which the colony an individual was born in influences its later survival as an adult. The cliff swallow (*Petrochelidon pyrrhonota*) is a colonially nesting songbird that occupies colonies that range from a few to thousands of nests at a single site (Brown et al. 2013a). Many of the costs and benefits of coloniality vary with group size in cliff swallows (Brown and Brown 1996, 2004), as in other species (Hoogland and Sherman 1976; Snapp 1976; Hoogland 1981; Wiklund and Andersson 1994; Serrano et al. 2005; Spottiswoode 2009). However, for both cliff swallows and other colonial animals we still know relatively little about how annual survival varies with colony size or with other characteristics of breeding sites independent of group size. For example, when inexperienced or inferior individuals colonize some sites or when birds settle in areas with reduced food availability or high ectoparasite load (Robinson 1985; Loye and Carroll 1991; Brown et al. 2014; Hoi et al. 2014), their offspring may be disadvantaged through inadequate provisioning, and this could lead to long-term negative effects on them as adults (Loison et al. 1996; Hastings and Testa 1998; Rose et al. 1998).

We take advantage of a cross-fostering study of cliff swallows (Brown and Brown 2000; Roche et al. 2011), in which nestlings were switched between colony sites soon after

hatching and their survivorship and colony choice monitored throughout their lives. This allowed us to examine survival of both the birds born and reared at their natal site and those reared elsewhere, and determine, at a colony-specific level, whether there was parent–offspring resemblance in survival probabilities. We focused on adult survival—that is, for birds after they attained 1 year of age—and thus compared parental and offspring generations at the same life stage. By measuring survival only as adults, we also removed any confounding natal dispersal biases (Brown and Brown 1992) or other effects such as ectoparasite load known to influence first-year (juvenile) survival (Brown and Brown 1986, 1996). In addition to investigating parent–offspring resemblance in survival, we examined how any systematic differences in survival might be maintained by a survival–fecundity trade-off. The results offer insight into causes of variation in this fitness component across colonies and the extent to which adult survival might be heritable.

Methods

Study population

We have studied cliff swallows since 1982 in the western Great Plains, USA, in a study area of 200×50 km, centered near the Cedar Point Biological Station (41°13′N, 101°39′W) in Keith County, western Nebraska, along the North and South Platte rivers and including portions of Deuel, Garden, Lincoln, and Morrill counties (Brown and Brown 1996). Cliff swallows construct gourd-shaped mud nests, often in dense, synchronously breeding colonies. In our study area the birds nest mostly on the sides of bridges, in box-shaped road culverts, or underneath overhangs on the sides of cliffs (Brown et al. 2013a). A colony was defined as groups of nests whose owners at least occasionally interacted during foraging or in alarm responses at predators, and typically all nests on a given bridge or culvert were considered a single colony (Brown and Brown 1996). Each colony was usually separated from the next nearest by 1–10 km. Colony size varies widely; in our study area it ranges from 2 to 6000 nests (mean $\pm$ SE, 404 ± 13, $n = 2318$ colonies), with some birds nesting solitarily. Cliff swallows in Nebraska typically lay 3–4 eggs and usually rear a single brood (Brown and Brown 1996, 2015). The breeding season generally extends from early May to late July. The birds are migratory and spend the winter in northeastern Argentina, Uruguay, and southwestern Brazil (Brown and Brown 1995), although the wintering range of our specific population is unknown.

Cross-fostering study

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 and Brown 2000). We ensured that cross-fostered nestlings were reared in broods of the same size in which they had hatched. Nestlings were fostered at approximately 5 days of age, the youngest age at which cliff swallows can be banded (with US Fish and Wildlife Service bands) for permanent identification (Brown and Brown 2000). The spatial distribution of the colony sites used in the cross-fostering study is shown in Roche et al. (2011).

The cross-fostering design of this study had several inherent advantages. By directly comparing rearing groups that either (1) shared the same birth colony but were reared apart or (2) were both born and reared in the same natal colony, we avoided statistical problems associated with regression-to-the-mean that potentially affects strictly observational studies of parent–offspring resemblance (Kelly and Price 2005). Also, by comparing birds born but reared in a different colony to ones born and reared in the same colony, any effect of uncertainty in parentage (e.g., extra-pair paternity resulting from birds perhaps being sired by non-residents of a colony; Brown and Brown 1996) was the same among the rearing groups being compared and thus did not affect our results. Finally, because the groups being compared encountered the same spatial array of colony sites to choose among in subsequent years, differences between rearing groups could not reflect varying subsets of colonies to which the groups were exposed or differences in dispersal distances as adults (see Results).

Field methods

We monitored the survival of cliff swallows each year through 2013 via systematic mist-netting at 25–40 colony sites per season (Brown and Brown 2004; Roche et al. 2013). Birds 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. We rotated among the accessible colonies, netting at each several times each season. The capture of birds is described in detail by Brown (1998), Brown and Brown (2004) and Roche et al. (2013). No birds from the cross-fostering cohorts were detected after 2008; thus, we assumed that we followed these individuals for their entire lives.

Brood sizes at each colony in the cross-fostering study were recorded at the time we selected nests for fostering and included some nests not chosen because brood sizes did not match those at foster colonies. Brood size refers only to the number of nestlings found in nests prior to fostering, that is, at about 5 days of age. Here we use data on brood sizes only for the colonies in the 1997–1998 cross-fostering study, and we did not know subsequent brood sizes for any of the nestlings in that study as adults.

Colony size was the number of active nests at a site, determined by checking nest contents and scoring any nest with ≥1 egg or nestling as active (Brown and Brown 1996). We quantified the relative age compositions of the breeders in the colonies in the cross-fostering study using mark-recapture as described by Brown et al. (2014). The number of newly banded adults at a site in a year served as a relative index of the number of yearling breeders. Many of the unbanded adults in our study population each year were first-year birds (Brown et al. 2014). We used the percentage of first-year breeders at a colony as a relative index of parental age among the colonies in the cross-fostering study.

To examine whether fostered and non-fostered adults may have dispersed to breed at different distances relative to their rearing sites (and thus affected apparent-survival estimation), we calculated settlement distances for the 414 birds from the cross-fostering study that were caught at least once in their second year as a breeder or beyond. The linear distance in kilometers between the colony site where a bird was reared and the site chosen as a breeder was determined from aerial maps. For birds caught in multiple years as adults from the second year or beyond, only the first site for each individual during this period was used in the analysis.

Mark-recapture analysis

For each nestling in the cross-fostering experiment, we created a capture history that indicated whether the bird was encountered (captured) as an adult somewhere in the study

area each year. Capture histories for nestlings began in the first year as an adult. Birds banded as a nestling but never encountered again were excluded; thus, this analysis was restricted to adult (breeder) survival only. Breeding adults in the cross-fostering colonies were given capture histories beginning in those years. This enabled us to compare adult survival probabilities of the cross-fostered nestlings to that of the adults (i.e., their parental cohort) occupying both the birth and foster colonies of the nestlings and ensured that survival was estimated for the parental and offspring generations at the same life stage (from ≥1-year of age for all).

Because we did not know the identities of the parents of the cross-fostered nestlings (parents were not known for specific nests), we estimated colony-specific, cohort-level survival for all adults occupying each colony in the cross-fostering experiment. We also estimated the equivalent colony-specific survival for three groups: (A) nestlings born and reared at their birth colony (i.e., those not fostered); (B) nestlings from a given birth colony fostered (and reared) elsewhere; and (C) nestlings from elsewhere fostered into (and reared) at a given foster colony. Sample sizes of birds caught beyond their first year (as adults) were too small to make finer divisions in the dataset and still achieve colony-specific survival estimates. The total number of birds used for estimating survival for group A ranged from 14 to 331 per colony; for group B, 15 to 323 per colony; and for group C, 34 to 326 per colony. The number of individuals in the parental cohort at a colony ranged from 13 to 2649. The total number of colonies for which parental cohort survival and survival for at least two of groups A, B, or C could be estimated was 10. One colony had too few recaptures of group C, and another of group A, for estimating survival. Two colony sites were used in the cross-fostering in both 1997 and 1998, and these were treated as independent colonies each year, owing to differences in colony size and residents present among years (Brown et al. 2014). Although we had additional colonies (in earlier years) not part of the cross-fostering study for which adult survival was measured, we chose not to include those due to pronounced annual variability in survival for our population (Brown and Brown 1996). Using only the 1997–1998 cohorts meant that survival for all birds was measured over the same set of annual conditions and did not include the effects of a severe weather-related mortality event that occurred in 1996 (Brown and Brown 1998).

The package RMark in program R (Laake 2013; R Core team 2014) was used to create models and generate estimates of survival probabilities. We were interested in directly comparing colony-specific adult survival for groups of nestlings and their parental cohorts over the same time period, so we used the same model structure for each cohort-level survival estimate. For each of the three groups (A, B, C), we constructed a "full" model in which apparent survival (φ) was parameterized with an additive effect of swallow age (i.e., first-year or older than first-year) and interactions of initial banding year, colony, and in the case of the offspring analyses, whether or not an individual was fostered. Sample sizes for colony-specific survival were not sufficient for modelling time-dependent survival or age beyond two age classes (<1 and ≥1 year), so we used a model that estimated survival as constant across years within the adult (≥1 year) age class. This yielded average survival for each colony-specific cohort and allowed us to compare relative survival among groups. Recapture probability was modelled as fully time-dependent [i.e., a unique detection probability was estimated for each year of the analysis; see Roche et al. (2013)] but, because of sample size, did not vary with group, age, or colony.

Because this study focused only on survival, we did not investigate or attempt to model colony choice by these cohorts; this topic is extensively investigated elsewhere (Roche et al. 2011). Colony-specific sample sizes were not sufficient to examine the effect of breeding colony size on survival using multi-state models for birds beyond the first year,

and thus we were forced to assume in our analyses that breeding colony size beyond the first year does not affect adult survival. We examined only the effect of birth and foster colony sizes. Analyses did not incorporate an effect of sex, as we earlier found that models with sex as a covariate were a poorer fit to this dataset than models without sex (Roche et al. 2011).

Multiple regression analyses using colony-specific survival probabilities, as estimated from program MARK, were performed in SAS using Proc GLM (SAS Institute 2004).

Results

The colony-specific adult survival probability for nestling cliff swallows born and reared in the same colony varied directly with the colony-specific survival probability of the adults in that colony (the parental cohort; Fig. 1a), with parental-cohort survival ($\beta = 0.704$, $SE = 0.249$, $P = 0.030$) and natal colony size ($\beta = 0.001$, $SE = 0.000$, $P = 0.030$) being significant predictors of offspring survival as adults. A similar result held for nestlings from a given colony that were fostered and reared elsewhere: adult survival of these birds (Fig. 1b) also varied significantly with survival of the parental cohort from their birth colony ($\beta = 1.245$, $SE = 0.412$, $P = 0.019$). Colony size of the birth colony had no influence on adult survival of the birds fostered from that colony ($\beta = 0.000$, $SE = 0.000$, $P = 0.29$).

In contrast, the colony-specific adult survival probability of birds born elsewhere and fostered into a colony was not significantly related to either the survival of their foster-parent cohort (Fig. 2a; $\beta = -0.281$, $SE = 0.695$, $P = 0.70$) or the size of the colony to which they were fostered ($\beta = 0.000$, $SE = 0.000$, $P = 0.78$). Adult survival of fostered nestlings was also unrelated to the colony-specific adult survival probability of non-fostered nestlings with whom they were reared (i.e., nestlings born and reared in the foster colony; Fig. 2b, $\beta = -0.432$, $SE = 0.683$, $P = 0.55$).

A negative relationship existed between a colony's average brood size and subsequent parental-cohort survival per colony (Fig. 3). Subsequent adult survival was significantly predicted by mean brood size in 1997–1998 ($\beta = -0.184$, $SE = 0.041$, $P = 0.003$), independent of colony size in those years ($\beta = 0.000$, $SE = 0.000$, $P = 0.29$).

While the percentage of age-1 breeders ranged from 30.8 to 83.3 % among the 10 colonies used in the cross-fostering study, parental cohort survival did not vary significantly with either the percentage of age-1 breeders at the site ($\beta = -0.089$, $SE = 0.138$, $P = 0.54$) or with colony size during the cross-fostering years ($\beta = 0.000$, $SE = 0.000$, $P = 0.98$). The multiple regression coefficients for the effect of parental cohort and colony size on offspring survival, and the effect of mean brood size on parental-cohort survival (above), remained the same in direction and significance ($P < 0.05$) when the percentage of age-1 breeders in the natal (birth) colony or in the foster colony was included in each analysis.

Cross-fostering per se had no effect on colony-specific adult survival of cliff swallows: average survival ($\pm SE$) for fostered offspring was 0.634 (± 0.0329) and for non-fostered offspring, 0.636 (± 0.0224). Settlement distances for ≥ 2-year old birds relative to their rearing site also did not differ. Fostered offspring ($n = 207$) settled at colonies a mean ($\pm SE$) 2.87 (± 0.37) km (range 0.0–42.8 km) from their rearing site, versus 2.96 (± 0.45) km (range 0.0–57.5 km) for non-fostered offspring; the difference was not significant ($Z = -1.20$, $P = 0.23$, Wilcoxon test).

Fig. 1 Colony-specific cliff swallow annual adult survival (±SE) over all years, 1998–2008, for **a** nestling cohorts reared in their birth colony and **b** nestling cohorts from a given birth colony fostered to and reared in other colonies, in relation to colony-specific adult survival probability (±SE) of the parental cohort from that birth colony. *Line* indicates best-fit least-squared regression


(a) nestlings reared in birth colony

(b) nestlings reared in foster colony
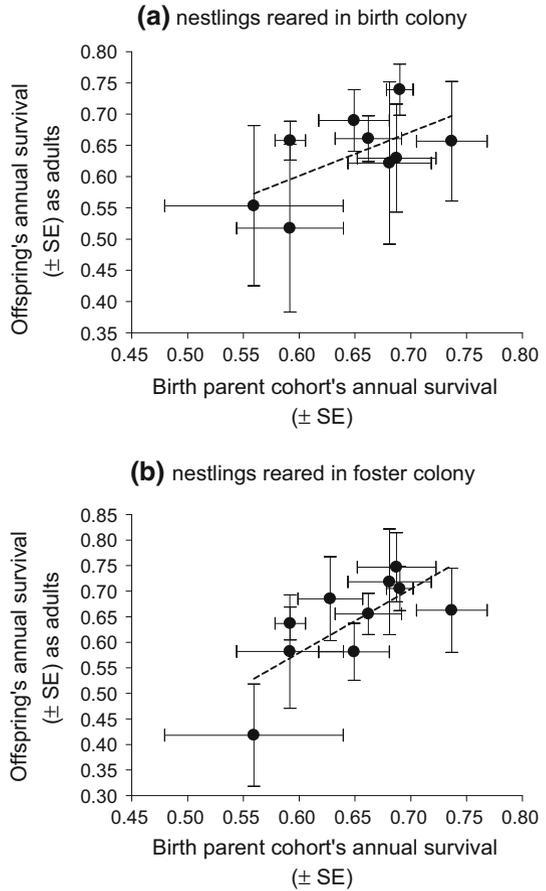
## Discussion

These results show strong parent–offspring resemblance in adult survival for cliff swallows. The variation in survival across sites suggests that an individual's expected lifespan can be determined in large part by birth colony. A strength of this analysis is that survival was measured for both parental and offspring cohorts at the same life stage (survival for those reaching 1 year of age) and during the same years, the latter an important consideration given the annual variation in cliff swallow survival probabilities in our study area (Brown and Brown 1996).

Variation in offspring survival can sometimes reflect maternal effects that are mediated through parental provisioning, hormone allocation, or vertical antibody transmission, and these often vary with the mother's age (Bernardo 1996; Hastings and Testa 1998; Mousseau and Fox 1998; Lindström 1999; Spencer and Verhulst 2007). However, most reported maternal effects on survival are relatively short term, usually most apparent either immediately post-natal or expressed over the first year or less of the offspring's life (Kern et al. 2007; Räsänen and Kruuk 2007; Reed et al. 2009; reviewed in Bernardo 1996). Longer-term maternal effects appear rare in birds and have been documented mostly in

Fig. 2 Colony-specific cliff swallow annual adult survival (±SE) over all years, 1998–2008, for nestling cohorts reared in a given foster colony in relation to **a** the colony-specific adult survival probability (±SE) of the parental cohort from that foster colony and **b** the colony-specific adult survival probability (±SE) of the non-fostered cohort from that colony with whom the foster offspring were reared. *Line* indicates best-fit least-squared regression
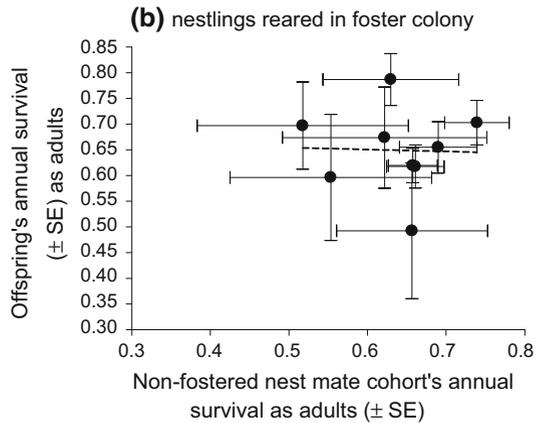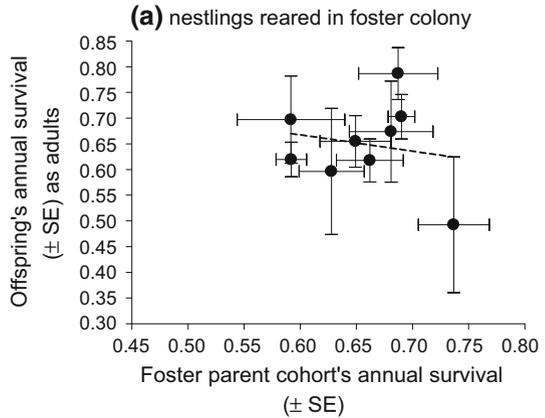
Fig. 3 Colony-specific cliff swallow annual adult survival (±SE) over all years, 1998–2008, for parental cohorts from the cross-fostering colonies in relation to mean brood size for each colony in 1997–1998 (±SE; number of nestlings surviving to 5 days of age). Survival was estimated beginning in the year that brood size was measured. *Line* indicates best-fit least-squared regression
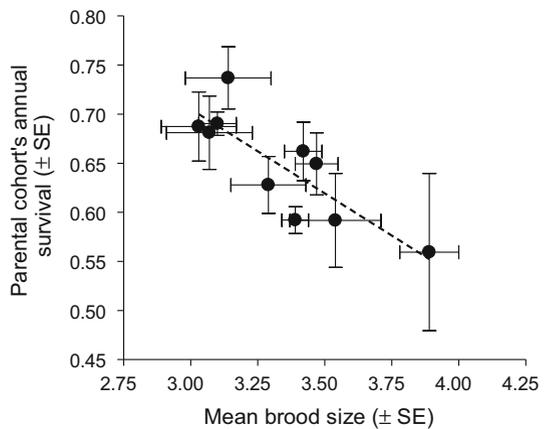
polygynous mammals where early maternal provisioning is important especially for sons (Loison et al. 1996; Post et al. 1997; Rose et al. 1998). Because cliff swallows are socially monogamous and sexually monomorphic, our results were probably not caused by the

same kind of long-term maternal effects seen in polygynous species. In addition, more general parental age effects are unlikely, as we found no evidence that the age compositions of the colonies in this study varied enough to systematically affect adult survival of either the parental or offspring cohorts.

We used colony-specific cohort survival estimates in this study because we did not know the individual identities of the parents of the cross-fostered nestlings. Thus, our data do not allow calculation of heritability of survival in the strict sense. However, the nests included in the cross-fostering study were a random sample of those present at each site and should be broadly representative of all parents and offspring from a colony. Given this, the strong direct relationship between cohort-level adult survival probabilities of fostered nestlings and the breeding adults in their birth colony—but no such relationship with the breeding adults in their foster colony—implies a heritable basis for adult survival in cliff swallows. While significant heritabilities for survival have been reported in a few organisms (Chambers et al. 1996; Campbell 1997; Kenway et al. 2006; Blomquist 2010; Dégremont et al. 2010), these are the first data for a colonial species suggesting heritable parent–offspring resemblance in survival.

Trade-offs and sorting among colonies

Mechanisms maintaining additive genetic variance in traits that are strongly related to fitness (such as survival) are unclear (Barton and Turelli 1989; Price and Schluter 1991; Merilä and Sheldon 1999; Vehviläinen et al. 2008). One obvious possibility for cliff swallows, suggested by our data, is that annual survival and annual fecundity represent a multiple-trait trade-off. As annual fecundity as measured by mean brood size at a site increased, survival of breeding adults at that site declined. Survival–fecundity trade-offs have been investigated in many species (Stearns 1992), although compelling evidence for their existence within species remains surprisingly sparse (Fry 2003; Agrawal et al. 2010). Many studies have found either no relationship or positive correlations between survival and fecundity within populations (e.g., Smith 1981; Newton 1989; Waser and Jones 1991; Blondel et al. 1992), including in some swallows (De Steven 1980; Murphy et al. 2000; cf. Bryant 1979). While positive or non-correlations do not rule out a survival–fecundity trade-off, a negative correlation such as that reported here provides excellent evidence for a trade-off (Agrawal et al. 2010). Thus, additive genetic variation for survival in cliff swallows could be maintained, in part, because individuals vary in their fecundity and because adult survival costs are determined by brood size. That fecundity varied enough across sites to generate this trade-off is perhaps surprising, given the low variation in clutch size in this species: 80 % of cliff swallow nests contain 3–4 eggs, and clutch size does not systematically vary with colony size (Brown and Brown 1996). This suggests that most of the site-related variation in fecundity is related to differences among parents in the number of offspring surviving after hatching.

The long-term parent–offspring resemblance in adult survival per colony suggests two questions: (1) do individuals invest proportionately more or less in survival (vs. fecundity) in the same way as do their parents, and (2) do individuals sort among colonies on this basis. We do not have information to evaluate the former possibility, as the reproductive success of the cross-fostered birds as adults was not monitored. However, the results are consistent with other analyses suggesting that cliff swallow colonies represent non-random sorting of individuals among groups (Brown and Brown 1996, 2000; Brown et al. 2014), based on how the costs and benefits of group-living vary among sites. For example, ectoparasite load, risk of starvation, predation, and foraging efficiency vary among

colonies, often in relation to colony size, and all could influence individual performance at a site (Brown et al. 1995; Brown and Brown 1996, 1999, 2004). Whereas previous work has mostly focused on determining how individuals sort among groups based on age, hormonal ability to handle stress, or parasite resistance (Brown and Brown 1996; Brown et al. 2005, 2014), this study suggests that individuals might also sort based on life-history strategy.

The two colonies with the lowest adult survival estimates and highest mean brood sizes were also the two sites that were the least perennially occupied of the 10 cliff swallow colony sites in this study (Brown, unpubl. data). Some colony sites are used by birds annually, whereas others are occupied in only some years (Brown et al. 2013a). Sites that are attractive to cliff swallows only occasionally (perhaps owing to temporary local abundance of food; Brown et al. 2002) might draw birds predisposed to invest more than average in fecundity. Consistent life-history differences were found in another colonial bird, the sociable weaver (*Philetairus socius*), in which individuals occupying different sized colonies invested unequally in egg size and immune defense (Spottiswoode 2007) and showed differences in adult survival (Brown et al. 2003).

Another possibility is that ecological differences among sites (e.g., in parasite load or local food availability; Brown and Brown 1996) simply allow cliff swallows at some colonies to be more successful (have greater brood sizes). When they are more successful, adult survival may be impaired strictly as a costly consequence of raising larger broods. However, unless birds predictably choose colonies solely based on a site's ecological potential for individual fecundity, this scenario seems less likely given that birds exhibited the same survival (and thus presumably the same fecundity) over their lifetimes as their parental cohort. In sociable weavers, experiments that manipulated colony resources showed that individuals did not exhibit plastic responses to local conditions, suggesting sorting among groups based on individuals' inherent life-history predispositions (Spottiswoode 2009). Regardless of mechanism, the observed trade-off between survival and fecundity suggests that fitness is not necessarily lower for birds (and their offspring) occupying the sites with lower adult survival.

Colony size and fluctuating selection

Could the patterns of survival detected here be related to systematic differences among birds in their choice of colony size? The extent to which breeding-colony size affects adult cliff swallow survival is unknown, although formal analyses of the effect of colony size on breeder survival are underway using a larger (non-experimental) data set. This same cross-fostering study illustrated earlier that cliff swallows have heritable colony-size preferences during their first breeding season (Brown and Brown 2000), such that individuals irrespective of where reared return to breed in colonies matching their birth colony size. If these preferences are retained throughout their lives, the results here on adult survival could reflect perennial sorting of individuals based on colony size and survival being affected by colony size in predictable ways.

However, we have found that the strong colony-size preferences shown by birds in their first year break down over time, with individuals increasingly less likely to use colony sizes similar to those of their birth as they get older (Roche et al. 2011), instead perhaps relying more on experience with a particular site (Brown et al. 2008). Thus, without permanent sorting of individuals among colony sizes, it seems unlikely that breeding-colony size alone can account for the strong parent–offspring resemblance in adult survival seen in this study. This result is all the more striking *because* both the parental and offspring cohorts

were distributed among many different colony sizes in the years during which adult survival was measured (Roche et al. 2011). Furthermore, if differences in survival are predictably linked to particular colony sizes without a survival–fecundity trade-off, the group sizes with lower survival should not persist over the long term. In cliff swallows, the colony-size distribution has remained largely unchanged over 30 years (Brown et al. 2013a), suggesting no directional selection on certain group sizes brought about by systematic survival-related costs or benefits associated with colony size.

Spatiotemporal fluctuations in selection pressures (Siepielski et al. 2009; Bell 2010; Tarwater and Beissinger 2013) are another mechanism that can maintain additive genetic variance in fitness-related traits. In cliff swallows, extreme climatic differences among years (Brown and Brown 2014) may mediate survival variation among individuals (Brown et al. 2013b), with some individuals better able to cope with the challenges inherent in hot and dry seasons (e.g., more blood-sucking ectoparasites) and others with those of cold and wet summers (e.g., increased risk of starvation). Climatically driven oscillation in selection pressures could maintain some level of additive genetic variation for survival ability, perhaps expressed in part through temporal shifts in morphological attributes related to foraging (Brown et al. 2013b).

The parent–offspring resemblance in adult survival probabilities in cliff swallows—and especially the maintenance of apparent heritable variation in survival across sites as part of a survival–fecundity trade-off—is consistent with the hypothesis that colonies represent nonrandom sorting of individuals among groups (Brown and Brown 1996, 2001; Spottiswoode 2007). These differences in survival illustrate that birds in different colonies have varying expected lifespans. The results are another component in our attempt for cliff swallows to understand the adaptive significance of coloniality and its complex interconnected web of selection pressures and evolutionary responses that often vary in space and time (Wittenberger and Hunt 1985).

Conflict of interest The authors declare that they have no conflicts of interest.

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