

Fluctuating survival selection explains variation in avian group size

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Most animal groups vary extensively in size. Because individuals in certain sizes of groups often have higher apparent fitness than those in other groups, why wide group size variation persists in most populations remains unexplained. We used a 30-y mark-recapture study of colonially breeding cliff swallows (*Petrochelidon pyrrhonota*) to show that the survival advantages of different colony sizes fluctuated among years. Colony size was under both stabilizing and directional selection in different years, and reversals in the sign of directional selection regularly occurred. Directional selection was predicted in part by drought conditions: birds in larger colonies tended to be favored in cooler and wetter years, and birds in smaller colonies in hotter and drier years. Oscillating selection on colony size likely reflected annual differences in food availability and the consequent importance of information transfer, and/or the level of ectoparasitism, with the net benefit of sociality varying under these different conditions. Averaged across years, there was no net directional change in selection on colony size. The wide range in cliff swallow group size is probably maintained by fluctuating survival selection and represents the first case, to our knowledge, in which fitness advantages of different group sizes regularly oscillate over time in a natural vertebrate population.

cliff swallow | coloniality | group size | natural selection | social behavior

Most social animals exhibit wide variation in group size (1–3), with the smallest and largest groups often differing in size by several orders of magnitude. Natural group size variation has proven useful in studying both the benefits of sociality and some of the costs, such as the spread of disease among groups (4–6). Surprisingly, in almost all species, some group sizes occur that are clearly disadvantageous relative to others (7, 8). Individuals in the less successful group sizes should be selected against (9), especially given known heritable preferences for group sizes (10–12), genetic differences among individuals in different-sized groups (13, 14), and behavioral specializations for particular group sizes (15, 16). What maintains size variation (and the associated variation in individual behavior) in the face of apparent group size-related fitness costs remains one of the most perplexing, but unresolved, problems in behavioral biology (17–19).

One mechanism that can maintain long-term stasis in trait distributions such as group size is temporally fluctuating selection, in which selection alternately favors traits in one direction and then the opposite direction (20–22). Although perhaps common in nature (23), only a relatively few studies have demonstrated statistically significant reversals in selection direction (24, 25), and whether fluctuating selection is a common evolutionary process remains unclear. In the case of group size, fluctuating selection could hypothetically generate a long-term stasis in group size distributions if the sign of directional and/or non-linear selection regularly reversed such that small groups were favored in some years, medium-sized groups were best in others, and large groups were advantageous in still other years.

Here, we use a 30-y field study of a colonially nesting songbird to investigate temporal differences in the form and direction of survival selection on group size, a genetically based trait in this

species (10). We use the results to infer relative advantages and disadvantages of particular group sizes in different years, and we find that reversals in the direction of selection can be predicted partially by annual variation in drought conditions. The results are the first, to our knowledge, to show formally that a fitness effect of different group sizes can fluctuate among years over a long timescale in a natural population.

The cliff swallow (*Petrochelidon pyrrhonota*) is a sparrow-sized bird found primarily in western North America. It attaches its gourd-shaped mud nests underneath overhanging ledges on the sides of steep cliffs and canyons, often in high density (26). Recently, cliff swallows in many areas have colonized artificial nesting sites such as highway bridges and culverts underneath roads or railroad tracks, where they nest as single pairs or (more often) in colonies of up to 6,000 nests in size (27). Our study site in western Nebraska (28) contains ~200 cliff swallow colony sites. Feeding exclusively on flying insects, cliff swallows breed typically from late April to late July before migrating to southern South America (primarily Argentina) for the winter (26).

We used long-term mark-recapture of banded birds to estimate annual survival probabilities of cliff swallows occupying nesting colonies of different sizes. During the 30 y of the study, more than 229,000 total individual swallows were marked, and those birds were captured more than 400,000 times at up to 40 colonies per year (Table S1). We examined annual survival selection in both first-year birds (from when first banded as nestlings to their first breeding season, with sexes combined, as nestlings

Significance

A characteristic feature of animal groups is extensive variation in size. Biologists have recognized that group size can often have profound effects on the fitness of individuals, and often certain group sizes afford greater short-term benefits than others. When individuals in some group sizes are less successful, what maintains pervasive variation in group sizes in nature remains a fundamental problem in behavioral biology. In colonial cliff swallows, survival advantages regularly fluctuate among group sizes over time. This study shows that changes in the direction and form of natural selection on colony size serve to maintain a wide range of group sizes and represents the first case, to our knowledge, in which the advantages and disadvantages of different group sizes regularly fluctuate in a natural vertebrate population.

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cannot be sexed) and ≥ 1 -y-old adults (from one breeding season to the next) of each sex. Colony size was the number of active cliff swallow nests in either the natal colony (for first-year birds) or breeding colony (28).

We used the mark–recapture data (Table S1) with Program MARK (29) to perform linear and quadratic regression of colony size on survival, with the resulting selection gradients (30) specifying the form and direction of selection (31). Linear selection gradients describe positive or negative directional selection, whereas quadratic ones were indicative of stabilizing (if negative) or disruptive (if positive) selection on colony size. The regression for first-year survival included the effect of hatching date, a major determinant of first-year survival in many birds (32). Analyses for adults used multistate models (33) with two states, in which (for computational reasons) survival was estimated for each focal colony size as one state and all other colony sizes as a second state. To determine whether any annual changes in selection were related to seasonal weather conditions, perhaps through effects on parasite populations or food supply, we examined relationships between selection gradients and drought indices for the birds' 3-mo (May–July) breeding period in Nebraska and for the 3 mo (November–January) they are resident in Argentina. Earlier work showed that these birds are sensitive to drought conditions that influence breeding time and that the effect of colony size on breeding time varies with the extent of summer drought (34). The wintering range in northeastern Argentina also exhibits high annual variability in the degree of drought (35).

Results and Discussion

For first-year birds, the 95% confidence interval of the directional (linear) survival selection gradient on colony size did not overlap 0 in 11 of 17 y: the positive and negative selection coefficients (Fig. 1A) showed that both large and small colonies, respectively, were favored in different years (Fig. 2A and B). Years with coefficient confidence intervals overlapping 0 represented cases of no detectable selection. Across all 17 y, the mean selection coefficient for first-year survival did not differ significantly from 0 ($t_{16} = 0.15$; $P = 0.88$), indicating no net long-term advantage associated with either larger or smaller natal colonies.

Among adults of both sexes, directional selection coefficients ($n = 24$) also fluctuated in sign, with confidence intervals of 10 for males and 9 for females not overlapping 0 (Fig. 1B). Annual survival in some years was higher for adults occupying smaller colonies and in other years for those using larger colonies (Fig. 2C and D). Across 24 y, the mean directional selection coefficient for breeding adults did not differ significantly from 0 for either males ($t_{23} = 1.40$; $P = 0.17$) or females ($t_{23} = 0.37$; $P = 0.71$), indicating, as for first-year birds, no net long-term survival advantage for birds of particular colony sizes. Year-specific gradients on colony size did not covary for first-year birds and adults (Fig. S1), indicating that selection likely operated on both life history stages independently.

We found evidence of nonlinear (variance) selection on colony size for one or both sexes of adult birds in 14 y in which coefficient confidence intervals did not overlap 0 (Fig. 1C). That 12 of the 14 variance gradients were negative indicates that the nonlinear selection was primarily stabilizing, with intermediate-size colonies favored (Fig. 2E). In 1 y, however, survival selection for both sexes was disruptive and favored birds occupying the two extremes of the colony size distribution (Fig. 2F). Some years showed evidence of both directional and stabilizing selection, whereas others had one or the other (Fig. 1B and C).

For first-year birds, there was no indication of significant nonlinear selection on colony size in any year. A first-year survival model with a quadratic term for colony size was a much poorer fit than the one without a quadratic term (*Estimating*

Figure 1 consists of three vertically stacked scatter plots (A, B, and C) showing selection gradients on colony size over time. The x-axis for all plots represents years from 1982 to 2010. Panel A: 'Directional selection gradient (\pm SE) on colony size' for first-year survival. Data points are black circles with error bars. Asterisks are present for years 1982, 1984, 1986, 1988, 1990, 1992, 1994, 1998, 2000, 2002, 2006, and 2008. Panel B: 'Directional selection gradient (\pm SE) on colony size' for adult survival. Data points are blue circles (males) and red circles (females) with error bars. Asterisks are present for years 1988, 1990, 1992, 1994, 1996, 1998, 2000, 2002, 2004, 2006, 2008, and 2010. Panel C: 'Variance selection gradient (\pm SE) on colony size' for adult survival. Data points are blue circles (males) and red circles (females) with error bars. Asterisks are present for years 1988, 1990, 1992, 1994, 1996, 1998, 2000, 2002, 2004, 2006, 2008, and 2010.

Fig. 1. Annual standardized directional (linear) selection gradients (± 1 SE) on colony size in cliff swallows for (A) first-year survival (nestling to first breeding season) of both sexes combined and (B) adult survival (breeding season to breeding season) of males (blue circles) and females (red circles), and standardized variance (quadratic) selection gradients (± 1 SE) on colony size for (C) survival of adult males (blue circles) and adult females (red circles). Years in which 95% confidence intervals did not overlap 0 are shown with an overlaid asterisk. Colony size refers to natal colony size in A and breeding colony size in B and C.

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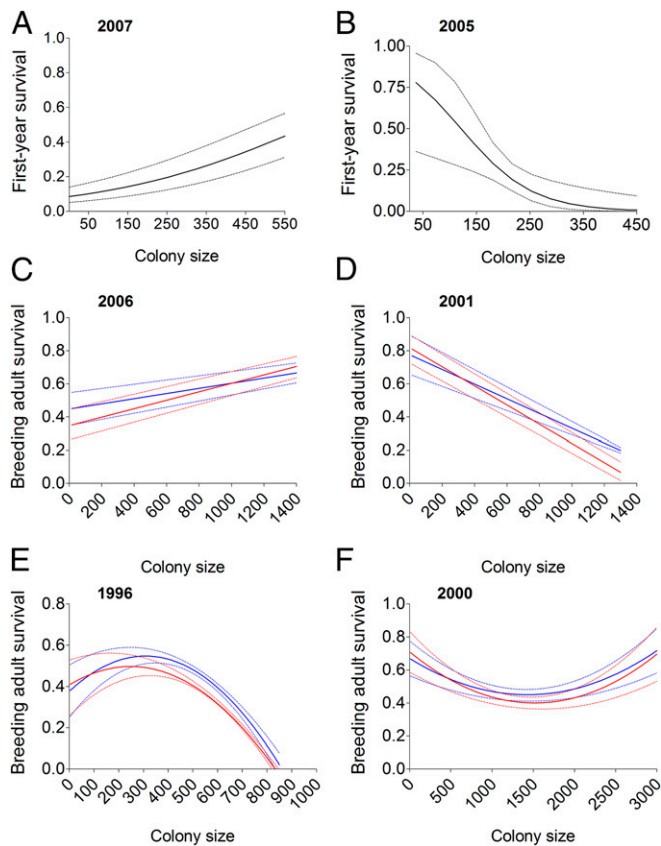


Fig. 2. Examples of variation in first-year (A and B) and adult (C–F) annual survival probabilities of cliff swallows in relation to natal or breeding colony size in years with significant positive (A and C) and negative (B and D) directional selection on colony size and in years with stabilizing (E) and disruptive (F) selection on colony size. The estimated survival function, solid line; 95% confidence interval, dotted lines; males (blue lines), females (red lines).

Selection), and the 95% confidence intervals for all of the estimable yearly quadratic coefficients overlapped 0.

For first-year birds, variation in the annual directional selection coefficients was significantly predicted by extent of drought in Argentina [multiple regression; β (\pm SE) = 5.8822 (\pm 1.0681); $t_{14} = 5.51$; $P < 0.0001$], but not by drought in Nebraska [$\beta = 0.1011$ (\pm 0.0638); $t_{14} = 1.58$; $P = 0.13$; model $r^2 = 0.69$]. Birds from larger natal colonies were favored in cooler and wetter years on the wintering range, whereas those from smaller colonies did better in hotter and drier years (Fig. 3A). For breeding adult males, annual variation in the directional selection coefficient was significantly predicted by extent of drought in Nebraska [$\beta = 0.0059$ (\pm 0.0026); $t_{21} = 2.28$; $P = 0.033$], but not by drought in Argentina [$\beta = 0.0207$ (\pm 0.0265); $t_{21} = 0.78$; $P = 0.44$; model $r^2 = 0.20$]. As was the case for first-year birds during winter, adult males from larger colonies were favored in cooler and wetter years during the breeding season, whereas the reverse held for birds from smaller colonies (Fig. 3B). Drought in neither Nebraska nor Argentina significantly predicted annual variation in the directional selection coefficient for adult females ($P \geq 0.49$; model $r^2 = 0.04$). Variance selection coefficients were not significantly predicted by drought in either Nebraska or Argentina for either adult males ($P \geq 0.12$; model $r^2 = 0.12$) or adult females ($P \geq 0.63$; model $r^2 = 0.01$).

Cliff swallows living in different-sized colonies experience different costs and benefits of sociality; for example, the cost of ectoparasitism by blood-feeding swallow bugs (*Oeciacus vicarius*) increases in larger colonies, along with the benefit of greater

foraging efficiency by virtue of information exchange among residents (28). Survival integrates these (and other) costs and benefits, and our analyses here suggest that the net effect of them varies among years and partially correlates with drought conditions. In cool and wet breeding seasons when flying insects are less abundant (low-resource years), adult cliff swallows from larger colonies (with more foraging information available) probably find more food than do birds from smaller colonies (28). In contrast, in drier years, flying insects are more readily available everywhere (high-resource years), and thus there is less benefit to having foraging information. In wet years, ectoparasite numbers in general are reduced because cooler weather slows the bugs' development. However, dry years accelerate ectoparasite development and magnify the parasites' effects, which are especially severe for birds in large colonies (28, 36). For these reasons, breeders occupying smaller colonies should be in better condition than birds

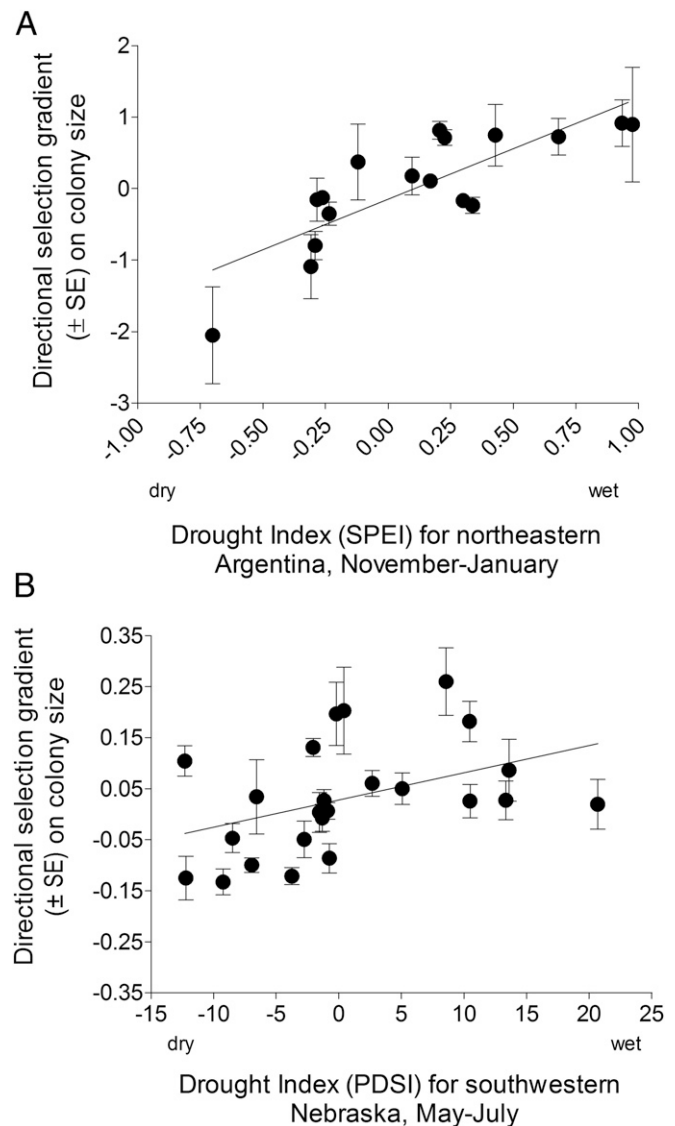


Fig. 3. Annual standardized directional selection gradients (\pm 1 SE) on colony size in cliff swallows for (A) first-year survival (both sexes combined) in relation to drought severity on the Argentine wintering grounds, as measured by the SPEI, and for (B) breeding adult male survival in relation to drought severity on the Nebraska breeding grounds, as measured by the modified PDSI. Lines indicate best-fit least-squares regression based on data for all years. Colony size refers to natal colony size in A and breeding colony size in B.

in larger colonies at the end of the season in drier years, and the reverse would apply in wetter years. Our analyses, at least for breeding males, were consistent with survival selection favoring birds from large colonies in low-resource, low-parasite years and birds from small colonies in high-resource, high-parasite years. The trend for breeding females, although not significant, was in the same direction.

Our data further show effects of natal colony size that are manifested on the wintering grounds. Perhaps one reason why first-year birds from larger natal colonies survive better than birds from smaller natal colonies during low-resource winters (i.e., winters that are cool and wet) is because large-colony birds are inherently more social, and their greater degree of sociality can afford more information-related benefits when food is scarce in winter (37). That same sociality might be less advantageous when food is abundant, and possibly more costly if different prey (e.g., fewer swarming insects) are exploited in drier winters. Taking advantage of social information in foraging is likely to be more important during a bird's first winter when it is relatively inexperienced, and possibly for this reason, survival selection varied with winter drought for first-year birds, but not for adults.

Some group-living species apparently anticipate seasonal weather conditions in advance, and adjust their group sizes accordingly (38). However, cliff swallows do not seem to do this (27), perhaps both because colony size preferences are heritable (and thus somewhat fixed) for individuals (10), and because they cannot predict whether the season will be a low-resource or a high-resource year at the time of settlement.

Although temporally fluctuating selection on morphology is known for some species (20, 39), this sort of selection has rarely been shown for behavioral traits (40). Fluctuating survival selection has not previously been applied to explain group size variation, likely in part because the majority of datasets are insufficient in temporal and spatial scope to detect the full extent of annual variability in selection. Our results were possible only because we had 30 y of survival data. A more typical-length study (3–4 y), depending on when conducted, could have concluded there was not an effect of colony size (e.g., adults in 1992–1996), that the effect was typically negative (e.g., adults in 1997–2003), or that it was usually positive (e.g., adults in 2005–2008; Fig. 1*B*). With longevity being the major determinant of fitness in small songbirds such as cliff swallows (41, 42), the regular reversals in survival selection based on colony size could help explain why groups of different sizes persist over the long term.

Materials and Methods

Study Site. We studied cliff swallows near the Cedar Point Biological Station (41°13' N, 101°39' W) in southwestern Nebraska along the North and South Platte rivers, with the study area including portions of Keith, Deuel, Garden, Lincoln, and Morrill counties. In this area, the birds nest mostly on the sides of bridges and in box-shaped road culverts (27). Colonies were defined as birds from groups of nests that interacted at least occasionally in defense against predators or by sharing information on the whereabouts of food. Typically, all of the nests on a given bridge or road culvert constituted a colony (28), with most colonies separated from the next nearest one by 1–10 km. Colony size varied widely; in our study area, it ranged from 2 to 6,000 nests (mean \pm SE: 404 ± 13 ; $n = 2,318$ colonies), with some birds nesting solitarily. The distribution of colony sizes in the population showed some annual variability, but there was no long-term change in the colony size distribution over the course of 30 y (27).

Animal use was approved by a series of Institutional Animal Care and Use Committees of Yale University and the University of Tulsa (most recently, under protocol TU-0020).

Field Methods. Colony size in all cases refers to the maximum number of active nests at a site, with an active nest defined as one in which one or more eggs were laid. Colony sizes were determined by direct counts of all active nests (from inspecting nest contents) or by estimation based both on nest counts of portions of a colony site and on the number of birds present at a site (28).

First-year survival estimates relied on nestling cliff swallows that were banded with uniquely numbered U.S. Geological Survey bands, typically at 10 d of age (43). Among the nestlings involved in a cross-fostering study in 1997 and 1998 (10, 44), only those that were both born and reared in their natal nest in their natal colony (i.e., not transferred between colonies) were included in these analyses. The total number of nestlings, the number of colonies from which these nestlings came, and the size range of those colonies each year are shown in Table S1. At sites in which some nests were fumigated to remove ectoparasites (28), only nestlings from nests that were not fumigated were included.

We monitored the survival of cliff swallows each year through 2013 via systematic mist-netting at 12–40 colony sites per season (45, 46) (Table S1). 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 (45–47), and over the summer, we typically captured 10–60% of the residents at a colony.

Survival of birds banded as nestlings to the next (their first) breeding season was considered first-year survival and only estimated for birds incapable of flight when first banded. The subsequent survival (to later years) of these birds and for all birds first caught and banded as adults was considered adult (breeding) survival. The total number of adults newly banded, the total number of breeding colonies sampled, the size range of those colonies, and the total number of net captures each year are shown in Table S1. Many adults once banded were caught at different colonies in multiple years (up to 12 y, the oldest age of a cliff swallow recorded in the study area), and thus figured into annual adult survival estimates each year of their life.

Estimating Annual Survival. As in any mark–recapture study of an open population (48), our survival analyses measured local apparent survival only; permanent emigration from the study area was confounded with mortality. We make the assumption here that colony size did not influence permanent emigration in ways that would lead to biased survival estimates for individuals from different parts of the colony size distribution.

Capture histories, indicating in what years each bird was first banded and later recaptured and the size of its natal and/or breeding colonies, were constructed for all individuals. These capture histories were used in program MARK (29) to generate maximum likelihood Cormack–Jolly–Seber recaptures-only annual survival estimates. For first-year survival, the variable of interest (natal colony size) was fixed for each individual, as each bird could have only one colony size in which it was born. Thus, we used a single-state survival analysis in which natal colony size was modeled as a continuous covariate. Because hatching date has a major influence on a cliff swallow's probability of surviving its first year (49), we also included banding date (an approximate index of when in the season an individual hatched) as a continuous linear covariate. We were specifically interested in yearly differences in how natal colony size affected first-year survival, and thus we used a time-dependent survival model in which first-year survival was estimated separately for each year, with colony size and banding date as continuous linear individual covariates. Other potential covariates of survival (e.g., brood size, parasite load, body mass), although known for some individuals, were not used in these analyses because they were not measured for birds in all years.

Preliminary analyses showed that recapture probability (48) for the nestling dataset was best modeled as separate by year, and, within each year, separate for the first-year age interval versus all others. For example, a model with year-dependent recapture but without an age difference had a Quasi-Akaike Information Criterion (QAIC_c) value 20.1 greater than an equivalent model with a first-year age difference in recapture. A similar model structure was used for survival, as we were specifically interested in yearly differences in first-year survival, and first-year survival is known to be different from that of the older age classes in cliff swallows (28, 49). First-year survival and associated effects of natal colony size could not be estimated separately for males and females because sex of nestlings at the time of banding cannot be determined in cliff swallows. We assessed the goodness of fit of a fully parameterized model for first-year survival, using the median \hat{c} -test ($\hat{c} = 1.54$), and adjusted parameter variances in MARK accordingly. Graphic representation of first-year survival (Fig. 2*A* and *B*) was plotted for the mean hatching date.

Single-state models could not be used for adult (breeding) survival, as the colony size an individual occupied often varied from year to year across its lifespan. Furthermore, adults were often not detected in a given year (but later re-encountered), and thus their colony size for the missing year or years were unknown. Therefore, we used a multistate survival model (33) in which annual survival to time $t + 1$ was estimated conditional on the breeding colony size an adult occupied in time t . We used seven different colony size

states, corresponding to colony sizes of 1–49 nests, 50–99 nests, 100–249 nests, 250–499 nests, 500–999 nests, 1,000–1,999 nests, and $\geq 2,000$ nests, and generated survival estimates for each state. These colony size categories were used in previous research (27, 28) and seem to be biologically justifiable, given, for example, the level of interaction among colony residents.

Because we were interested in estimating adult survival separately by year for 24 y, dividing colony sizes more finely into more states led to such a proliferation of survival, recapture, and transition parameters that such models were both unwieldy to run and often could not generate a given survival estimate because of sparseness of data for particular colony size/year combinations. Even running a model in which each of the seven colony size states each year was included proved unmanageable. Instead, for each of the seven colony-size groups, we created a two-state mark–recapture dataset. The two states consisted of a “focal” state that represented an observation of a cliff swallow at the colony size class of interest and an “other” state that represented an observation of a cliff swallow at any one of the other six colony size classes. For example, for the mark–recapture dataset in which the focal colony size class was a size of 1–49 nests, all captures of a cliff swallow at a colony of 1–49 nests were coded as a “1,” captures at all other colony sizes were coded as a “2,” and if a cliff swallow was not captured at all, this was coded as a “0.” We assessed the goodness of fit for each dataset, using program U-CARE (50), and corrected all subsequent estimates of survival, detection, and movement, using the dataset-specific estimates of overdispersion generated from U-CARE.

For each dataset, we built and ran a single multistate model. We modeled survival (S) by age (either first year caught as adult or after first year caught as adult), sex (male or female), colony size state, and year [$S(\text{age} + (\text{sex} \times \text{year} \times \text{state}))$]. We modeled detection (p) by sex, colony size state, and year [$p(\text{sex} + (\text{year} \times \text{state}))$]. Last, we modeled movement (ψ) by sex and state-to-state transition only [$\psi(\text{state} \times \text{sex})$]. Only models with this structure for movement were manageable enough to run. We interpreted the estimates generated by the single-model run for each mark–recapture dataset. We estimated adult survival in relation to breeding colony size for all years from 1987 to 2010, giving us at least 2 y of recapture for each yearly cohort.

Estimating Selection. For first-year survival estimates, both linear covariates (hatching date and natal colony size) were standardized within each year to yield a mean of 0 and a SD of 1. Within-year standardization was done because we were interested in year-specific effects on survival, and survival was estimated by year. This provided a standardized measure of selection (51). The β value obtained for natal colony size from program MARK represented the sign and magnitude of directional (linear) selection (the gradient) on colony size (30). The possibility of nonlinear selection on colony size was investigated by constructing a model identical to that used for estimating directional selection, but that also included a quadratic term (colony size squared) as an individual covariate. This model had a QAIC_c 170.6 greater than for the one without a quadratic term, indicating no evidence

for nonlinear (variance) selection on colony size for first-year birds. Some years did not have sufficient sample sizes to yield estimable parameters for either directional or nonlinear coefficients.

For breeding adults, we standardized colony size within each year, as done for nestlings (described earlier), and performed linear and quadratic regression of colony size on survival, using survival as estimated earlier and the colony sizes sampled in each year. This yielded yearly estimates of directional (β) and nonlinear (γ) selection. Quadratic (nonlinear) selection coefficients were doubled, as recommended by Stinchcombe et al. (52). Because we present standardized selection gradients, the strength of selection can be inferred directly from those coefficients.

Weather Data. We make the assumption that weather conditions in year t may affect the relationship between colony size and survival, as measured to year $t + 1$. In assessing how this relationship varied with year, we used drought as an integrative measure of temperature and rainfall to describe annual weather conditions important to cliff swallows (34). For the summer breeding season, we used the modified Palmer Drought Severity Index (PDSI), available from the National Oceanic and Atmospheric Administration for Climate Division 7 of Nebraska (corresponding to southwestern Nebraska) for the combined months of May to July each year (www.ncdc.noaa.gov/cag/). We used these months, as that was the inclusive period that most cliff swallows were present in the Nebraska study area, and the PDSI for that period has been shown to predict cliff swallow breeding phenology (34). However, because the PDSI was not available for the birds' wintering range, for analyses of winter conditions, we used the Standardized Precipitation-Evapotranspiration Index (SPEI), a drought measure (53) that is more readily available worldwide. Based on the region of primarily northeastern Argentina (Fig. S2), where most cliff swallows apparently winter (26), we used the utility available at sac.csic.es/spei/map/maps.html to produce the SPEI for this region for the combined months of November–January each year. This period corresponds to when cliff swallows are most likely present on the Argentine wintering range (26).

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- Brown CR, Stutchbury BJ, Walsh PD (1990) Choice of colony size in birds. *Trends Ecol Evol* 5(12):398–403.
- Avilés L (1997) Causes and consequences of cooperation and permanent-sociality in spiders. *The Evolution of Social Behavior in Insects and Arachnids*, eds Choe J, Crespi B (Cambridge Univ. Press, Cambridge, UK), pp 476–498.
- Majolo B, Vizioli AB, Schino G (2008) Costs and benefits of group-living in primates: Group size effects on behaviour and demography. *Anim Behav* 76(4):1235–1247.
- Hoogland JL, Sherman PW (1976) Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol Monogr* 46(1):33–58.
- Brennan A, et al. (2014) A multi-scale assessment of animal aggregation patterns to understand increasing pathogen seroprevalence. *Ecosphere* 5(10):1–25.
- Nunn CL, Jordán F, McCabe CM, Verdolin JL, Fewell JH (2015) Infectious disease and group size: More than just a numbers game. *Philos Trans R Soc Lond B Biol Sci* 370(1669): 20140111.
- Brown CR, Brown MB (2001) Avian coloniality: Progress and problems. *Current Ornithology*, ed Nolan V, Thompson CF (Kluwer Academic/Plenum Publishers, New York), pp 1–82.
- Markham AC, Seguiere LR, Alberts SC, Altmann J (2015) Optimal group size in a highly social mammal. *Proc Natl Acad Sci USA* 112(48):14882–14887.
- Magurran AE, Seghers BH, Shaw PW, Carvalho GR (1995) The behavioral diversity and evolution of guppy, *Poecilia reticulata*, populations in Trinidad. *Adv Stud Behav* 24: 155–202.
- Brown CR, Brown MB (2000) Heritable basis for choice of group size in a colonial bird. *Proc Natl Acad Sci USA* 97(26):14825–14830.
- Møller AP (2002) Parent-offspring resemblance in degree of sociality in a passerine bird. *Behav Ecol Sociobiol* 51(3):276–281.
- Serrano D, Tella JL (2007) The role of despotism and heritability in determining settlement patterns in the colonial lesser kestrel. *Am Nat* 169(2):E53–E67.
- Bacon PJ, Andersen-Harild P (1987) Colonial breeding in mute swans (*Cygnus olor*) associated with an allozyme of lactate dehydrogenase. *Biol J Linn Soc Lond* 30(3): 193–228.
- Krieger MJB, Ross KG (2002) Identification of a major gene regulating complex social behavior. *Science* 295(5553):328–332.
- Dardenne S, Ducatez S, Cote J, Poncin P, Stevens VM (2013) Neophobia and social tolerance are related to breeding group size in a semi-colonial bird. *Behav Ecol Sociobiol* 67(8):1317–1327.
- Pruitt JN, Iturralde G, Avilés L, Riechert SE (2011) Amazonian social spiders share similar within-colony behavioural variation and behavioural syndromes. *Anim Behav* 82(6):1449–1455.
- Pulliam HR, Caraco T (1984) Living in groups: Is there an optimal group size? *Behavioural Ecology*, eds Krebs JR, Davies NB (Sinauer, Sunderland, MA), pp 122–147.
- Safran RJ (2004) Adaptive site selection rules and variation in group size of barn swallows: Individual decisions predict population patterns. *Am Nat* 164(2):121–131.
- Griesser M, Ma Q, Webber S, Bowgen K, Sumpter DJT (2011) Understanding animal group-size distributions. *PLoS One* 6(8):e23438.
- Grant PR, Grant BR (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296(5568):707–711.
- Bell G (2010) Fluctuating selection: The perpetual renewal of adaptation in variable environments. *Philos Trans R Soc Lond B Biol Sci* 365(1537):87–97.
- Kingsolver JG, Diamond SE (2011) Phenotypic selection in natural populations: What limits directional selection? *Am Nat* 177(3):346–357.
- Siepielski AM, DiBattista JD, Carlson SM (2009) It's about time: The temporal dynamics of phenotypic selection in the wild. *Ecol Lett* 12(11):1261–1276.
- Kingsolver JG, Diamond SE, Siepielski AM, Carlson SM (2012) Synthetic analyses of phenotypic selection in natural populations: Lessons, limitations and future directions. *Evol Ecol* 26(5):1101–1118.
- Morrissey MB, Hadfield JD (2012) Directional selection in temporally replicated studies is remarkably consistent. *Evolution* 66(2):435–442.

26. Brown CR, Brown MB (1995) Cliff swallow (*Hirundo pyrrhonota*). *The Birds of North America*, ed Poole A, Gill F (Academy of Natural Sciences, Philadelphia, PA).
27. Brown CR, Brown MB, Roche EA (2013) Spatial and temporal unpredictability of colony size in cliff swallows across 30 years. *Ecol Monogr* 83(4):511–530.
28. Brown CR, Brown MB (1996) *Coloniality in the Cliff Swallow: The Effect of Group Size on Social Behavior* (Univ. Chicago Press, Chicago).
29. White GC, Burnham KP (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:5120–5138.
30. Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution* 37(6):1210–1226.
31. Brodie ED, III, Moore AJ, Janzen FJ (1995) Visualizing and quantifying natural selection. *Trends Ecol Evol* 10(8):313–318.
32. Verhulst S, Nilsson JA (2008) The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. *Philos Trans R Soc Lond B Biol Sci* 363(1490):399–410.
33. Lebreton JD, Nichols JD, Barker RJ, Pradel R, Spendlow JA (2009) Modeling individual animal histories with multistate capture-recapture models. *Adv Ecol Res* 41:87–173.
34. Brown CR, Brown MB (2014) Breeding time in a migratory songbird is predicted by drought severity and group size. *Ecology* 95(10):2736–2744.
35. Lovino M, García NO, Baethgen W (2014) Spatiotemporal analysis of extreme precipitation events in the northeast region of Argentina (NEA). *J. Hydro. Reg. Stud* 2: 140–158.
36. Brown CR, Brown MB, Rannala B (1995) Ectoparasites reduce long-term survival of their avian host. *Proc Biol Sci* 262(1365):313–319.
37. Brown CR, Brown MB, Shaffer ML (1991) Food-sharing signals among socially foraging cliff swallows. *Anim Behav* 42(4):551–564.
38. Thogmartin WE, McKann PC (2014) Large-scale climate variation modifies the winter grouping behavior of endangered Indiana bats. *J Mammal* 95:117–127.
39. Carlson SM, et al. (2007) Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*). *Ecol Lett* 10(6):512–521.
40. Le Coeur C, et al. (2015) Temporally fluctuating selection on a personality trait in a wild rodent population. *Behav Ecol* 26(5):1285–1291.
41. Clutton-Brock TH, ed (1988) *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Univ. Chicago Press, Chicago).
42. Newton I, ed (1989) *Lifetime Reproduction in Birds* (Academic Press, London).
43. Brown CR, Brown MB (1986) Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology* 67(5):1206–1218.
44. Brown CR, Roche EA, Brown MB (2015) Parent-offspring resemblance in colony-specific adult survival of cliff swallows. *Evol Ecol* 29(4):537–550.
45. Brown CR, Brown MB (2004) Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behav Ecol Sociobiol* 56(5):498–511.
46. Roche EA, Brown CR, Brown MB, Lear KM (2013) Recapture heterogeneity in cliff swallows: Increased exposure to mist nets leads to net avoidance. *PLoS One* 8(3): e58092.
47. Brown CR (1998) *Swallow Summer* (Univ. Nebraska Press, Lincoln).
48. Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecol Monogr* 62(1):67–118.
49. Brown CR, Roche EA, O'Brien VA (2015) Costs and benefits of late nesting in cliff swallows. *Oecologia* 177(2):413–421.
50. Choquet R, Lebreton JD, Gimenez O, Reboulet AM, Pradel R (2009) U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography* 32(6):1071–1074.
51. Endler JA (1986) *Natural Selection in the Wild* (Princeton Univ. Press, Princeton, NJ).
52. Stinchcombe JR, Agrawal AF, Hohenlohe PA, Arnold SJ, Blows MW (2008) Estimating nonlinear selection gradients using quadratic regression coefficients: Double or nothing? *Evolution* 62(9):2435–2440.
53. Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multiscalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index. *J Climatol* 23:1696–1718.