Fluctuating survival selection explains variation in avian group size

Charles R. Brown  
*Department of Biological Sciences, University of Tulsa, charles-brown@utulsa.edu*

Mary Bomberger Brown  
*University of Nebraska-Lincoln, mbrown9@unl.edu*

Erin A. Roche  
*USGS Northern Prairie Wildlife Research Center, Jamestown, ND, eroche@usgs.gov*

Valerie A. O'Brien  
*University of Tulsa*

Catherine E. Page  
*University of Tulsa*

Follow this and additional works at: [http://digitalcommons.unl.edu/natrespapers](http://digitalcommons.unl.edu/natrespapers)

Part of the [Natural Resources and Conservation Commons](http://digitalcommons.unl.edu/natrespapers), [Natural Resources Management and Policy Commons](http://digitalcommons.unl.edu/natrespapers), [Ornithology Commons](http://digitalcommons.unl.edu/natrespapers), and the [Other Environmental Sciences Commons](http://digitalcommons.unl.edu/natrespapers)

[http://digitalcommons.unl.edu/natrespapers/536](http://digitalcommons.unl.edu/natrespapers/536)

This Article is brought to you for free and open access by the Natural Resources, School of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Natural Resources by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.
Fluctuating survival selection explains variation in avian group size

Charles R. Browna,1, Mary Bomberger Browna,2, Erin A. Rochea,3, Valerie A. O’Brien4,5, and Catherine E. Pagea* 

*Department of Biological Sciences, University of Tulsa, Tulsa, OK 74104

Edited by Joan E. Strassmann, Washington University in St. Louis, St. Louis, MO, and approved March 28, 2016 (received for review January 6, 2016)

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
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. 2 A and B). 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. 2 C 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 the 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. 2F). 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

![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.](image-url)
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; $\beta$ (±SE) = 5.8822 (±1.0681); $t_{14} = 5.51; P < 0.0001], but not by drought in Nebraska [$\beta = 0.1011$ (±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 [$\beta = 0.0059$ (±0.0026); $t_{21} = 2.28; P = 0.033$], but not by drought in Argentina [$\beta = 0.0207$ (±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
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 nesting 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 sociability 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 conducting, 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. 1B).

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 ± SE: 404 ± 13; n = 2,318 colonies), with some birds nesting solitarily. The distribution of colony sizes in the population showed variation, likely in part because the majority of datasets are in-

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 number of nestlings and adults from each colony 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 (24). We used Cormack-Jolly-Seber (CJS) mark–recapture analyses to estimate 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, parent body mass, and body mass changes)—although known for some individual years—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 (QAICc) 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 c-hat test (c = 1.54), and adjusted parameter variances in MARK accordingly. Graphic representation of first-year survival (Fig. 2A 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 ≥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 classes 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 colony size ≥50 nests and an “other” state that represented an observation of a cliff swallow at any 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 selected all subsequent estimates of survival, detection, and movement, using the dataset-specific estimates of over-dispersion 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 [(age + sex + year) × (state)]

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 colony size ≥50 nests and an “other” state that represented an observation of a cliff swallow at any 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 selected all subsequent estimates of survival, detection, and movement, using the dataset-specific estimates of over-dispersion 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 [(age + sex + year) × (state)]


Fig. S1. Annual survival selection gradient (±1 SE) on colony size for breeding adult cliff swallows in relation to the selection gradient (±1 SE) in the same year for first-year birds. Adult males are shown by closed circles (●), and females by open circles (○). There was no significant correlation between the first-year selection gradient and that for adult males ($r_s = -0.13; P = 0.67; n = 13$ y) or that for adult females ($r_s = -0.20; P = 0.50; n = 13$) in the same year. Only years for which selection coefficients for both age groups were available could be included.
Fig. S2. Region of primarily northeastern Argentina (denoted in white) where cliff swallows apparently concentrate in winter (26) that was used for calculating the SPEI for the 3-mo period, November–January, each year to describe drought conditions experienced by the birds on their wintering range.
Table S1. Measures of capture–recapture effort and parameters of colonies monitored

<table>
<thead>
<tr>
<th>Year</th>
<th>Natal colonies, n (size range)</th>
<th>Nestlings, n</th>
<th>Breeding colonies, n (size range)</th>
<th>Adults, n*</th>
<th>Total net captures, n*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1982</td>
<td>10 (1–1,600)</td>
<td>915</td>
<td>2 (600–2,000)</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>1983</td>
<td>6 (2–180)</td>
<td>637</td>
<td>2 (2–180)</td>
<td>418</td>
<td>448</td>
</tr>
<tr>
<td>1984</td>
<td>9 (1–345)</td>
<td>1,083</td>
<td>9 (1–345)</td>
<td>1,674</td>
<td>2,108</td>
</tr>
<tr>
<td>1985</td>
<td>1 (4)</td>
<td>1,512</td>
<td>1 (4)</td>
<td>937</td>
<td>1,402</td>
</tr>
<tr>
<td>1986</td>
<td>8 (1–140)</td>
<td>2,496</td>
<td>10 (10–1,100)</td>
<td>1,896</td>
<td>3,007</td>
</tr>
<tr>
<td>1987</td>
<td>4 (3–340)</td>
<td>2,022</td>
<td>14 (3–1,000)</td>
<td>2,162</td>
<td>4,055</td>
</tr>
<tr>
<td>1988</td>
<td>4 (6–54)</td>
<td>2,124</td>
<td>20 (12–3,500)</td>
<td>3,445</td>
<td>6,058</td>
</tr>
<tr>
<td>1989</td>
<td>3 (22–245)</td>
<td>240</td>
<td>23 (10–2,200)</td>
<td>4,521</td>
<td>9,518</td>
</tr>
<tr>
<td>1990</td>
<td>3 (86–190)</td>
<td>853</td>
<td>24 (18–3,000)</td>
<td>5,151</td>
<td>11,720</td>
</tr>
<tr>
<td>1991</td>
<td>5 (1–140)</td>
<td>890</td>
<td>35 (1–2,500)</td>
<td>7,808</td>
<td>17,901</td>
</tr>
<tr>
<td>1992</td>
<td>6 (1–380)</td>
<td>413</td>
<td>27 (3–3,000)</td>
<td>8,213</td>
<td>21,272</td>
</tr>
<tr>
<td>1993</td>
<td>6 (3–255)</td>
<td>508</td>
<td>40 (3–2,500)</td>
<td>7,752</td>
<td>19,831</td>
</tr>
<tr>
<td>1994</td>
<td>1 (19)</td>
<td>35</td>
<td>31 (19–2,300)</td>
<td>7,349</td>
<td>16,702</td>
</tr>
<tr>
<td>1995</td>
<td>0</td>
<td>0</td>
<td>36 (4–1,900)</td>
<td>7,330</td>
<td>17,553</td>
</tr>
<tr>
<td>1996</td>
<td>1 (450)</td>
<td>21</td>
<td>28 (3–850)</td>
<td>4,481</td>
<td>11,739</td>
</tr>
<tr>
<td>1997</td>
<td>4 (8–280)</td>
<td>1,563</td>
<td>24 (4–1,200)</td>
<td>4,370</td>
<td>12,793</td>
</tr>
<tr>
<td>1998</td>
<td>8 (1–1,200)</td>
<td>1,073</td>
<td>30 (10–1,400)</td>
<td>4,783</td>
<td>13,291</td>
</tr>
<tr>
<td>1999</td>
<td>1 (125)</td>
<td>29</td>
<td>25 (3–1,800)</td>
<td>5,926</td>
<td>17,006</td>
</tr>
<tr>
<td>2000</td>
<td>3 (130–1,150)</td>
<td>97</td>
<td>33 (10–3,000)</td>
<td>7,241</td>
<td>18,717</td>
</tr>
<tr>
<td>2001</td>
<td>3 (90–3,400)</td>
<td>111</td>
<td>30 (15–3,400)</td>
<td>6,223</td>
<td>16,401</td>
</tr>
<tr>
<td>2002</td>
<td>2 (525–3,600)</td>
<td>66</td>
<td>27 (95–3,600)</td>
<td>7,693</td>
<td>19,087</td>
</tr>
<tr>
<td>2003</td>
<td>4 (360–800)</td>
<td>124</td>
<td>27 (27–1,300)</td>
<td>7,316</td>
<td>20,309</td>
</tr>
<tr>
<td>2004</td>
<td>2 (145–500)</td>
<td>54</td>
<td>32 (3–3,000)</td>
<td>8,569</td>
<td>19,815</td>
</tr>
<tr>
<td>2005</td>
<td>4 (65–385)</td>
<td>343</td>
<td>24 (25–600)</td>
<td>5,636</td>
<td>16,308</td>
</tr>
<tr>
<td>2006</td>
<td>5 (195–700)</td>
<td>282</td>
<td>26 (16–1,800)</td>
<td>5,787</td>
<td>14,002</td>
</tr>
<tr>
<td>2007</td>
<td>14 (22–565)</td>
<td>472</td>
<td>34 (15–2,000)</td>
<td>5,936</td>
<td>12,862</td>
</tr>
<tr>
<td>2008</td>
<td>2 (2–1,800)</td>
<td>57</td>
<td>27 (2–1,800)</td>
<td>5,175</td>
<td>13,358</td>
</tr>
<tr>
<td>2009</td>
<td>30 (1–2,000)</td>
<td>7,112</td>
<td>30 (1–2,000)</td>
<td>7,112</td>
<td>16,457</td>
</tr>
<tr>
<td>2010</td>
<td>28 (8–790)</td>
<td>8,359</td>
<td>28 (8–790)</td>
<td>8,359</td>
<td>18,828</td>
</tr>
<tr>
<td>2011</td>
<td>23 (35–600)</td>
<td>6,913</td>
<td>23 (35–600)</td>
<td>6,913</td>
<td>16,487</td>
</tr>
<tr>
<td>2012</td>
<td>15 (20–1,545)</td>
<td>5,168</td>
<td>15 (20–1,545)</td>
<td>5,168</td>
<td>12,474</td>
</tr>
<tr>
<td>2013</td>
<td>12 (20–675)</td>
<td>2,264</td>
<td>12 (20–675)</td>
<td>2,264</td>
<td>6,361</td>
</tr>
</tbody>
</table>

Measures include total number of natal colonies, natal colony size range (number of active nests within a season), nestlings banded in those colonies, total number of breeding colonies, breeding colony size range (number of active nests within a season), adults newly banded, and total net captures for cliff swallows in the southwestern Nebraska study area each year. Colonies monitored and/or capture data were insufficient in some years for estimating survival of first-year (nestling) birds in relation to colony size. Breeding adult survival was estimated only for years with >10 breeding colonies monitored.

*Includes those at fumigated colonies, as some of these birds had been resident at a nonfumigated colony in a previous year or were found at a nonfumigated colony in a later year.