

2018

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Brown, Charles R. and Brown, Mary B., "Extreme group sizes in a colonial bird favored during a rare climatic event" (2018). *Papers in Natural Resources*. 828.

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Extreme group sizes in a colonial bird favored during a rare climatic event

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Citation: Brown, C. R., and M. B. Brown. 2018. Extreme group sizes in a colonial bird favored during a rare climatic event. *Ecosphere* 9(9):e02428. 10.1002/ecs2.2428

Abstract. What maintains stasis in animal group-size distributions is an unresolved problem in behavioral ecology. One potential driver could be rare climatic events that favor certain group sizes in ways that do not occur in normal conditions. We investigated mortality among colonially nesting cliff swallows (*Petrochelidon pyrrhonota*) during a rare climatic event in western Nebraska in 1996 that led to the starvation of thousands of adult birds. Colonies at the extreme end of the size distribution exhibited less size reduction (higher adult survival) than those of intermediate size. That this event resulted in disruptive selection on colony size was suggested by an underrepresentation of locally produced yearling birds that recruited into colonies of intermediate size the following year. There was no evidence that the colony-size-related mortality could be explained by differential sorting of birds among colonies based on body size or differing patterns of selection on morphology. The selection on colony size was likely driven by lower competition for food in the smallest colonies and better quality foraging habitat associated with the largest colonies, with these advantages enhanced in severe weather. Selection on colony size during rare climatic events can reinforce or oppose selection occurring during other times of the annual cycle. Whether such selection results in long-term change in the colony-size distribution may depend on the frequency and severity of these climatic events.

Key words: cliff swallow; climatic events; coloniality; colony size; disruptive selection; natural selection; *Petrochelidon pyrrhonota*; social behavior.

Received 3 August 2018; accepted 16 August 2018. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Animals breeding in groups of different sizes can experience very different ecological and social environments (Alexander 1974, Wittenberger and Hunt 1985, Brown and Brown 2001). Studies on various taxa have identified a number of positive and negative effects on fitness directly attributable to colony size (Hoogland and Sherman 1976, Hoogland 1979, Brown and Brown 1996, Avilés and Tufiño 1998). An unresolved question, however, is what maintains variation in the size of colonies (and animal groups more generally) when some sizes confer higher fitness

than others do, at least in the short term (Pulliam and Caraco 1984, Williams et al. 2003, Brown 2016). With colony-size preferences known to be heritable (Brown and Brown 2000a, Møller 2002, Serrano and Tella 2007), why selection does not remove individuals occupying the less successful colony sizes remains paradoxical. Various hypotheses have been proposed, including that individuals do not have total control over their group size (Sibly 1983, Zemel and Lubin 1995), that incomplete estimates of individual fitness lead us to concluding that some colony sizes are best when they actually are not (Minias et al. 2015, Brown 2016), and that selection fluctuates

spatiotemporally such that different-sized colonies are favored at different times or places (Jones and Riechert 2008, Brown et al. 2016) due to changes in food, predators, parasites, or other environmental conditions.

Temporally fluctuating selection (Siepielski et al. 2009, Bell 2010) can theoretically maintain variability in a trait as long as fitness associated with the trait regularly changes. Fluctuating selection is a promising hypothesis to explain variation in group size. For example, in colonial cliff swallows (*Petrochelidon pyrrhonota*), annual survival selection on colony size was found to vary in direction and form in different years, with larger colonies advantageous for survival in some years, intermediate-sized colonies best in other years, and smaller colonies favored in still others (Brown et al. 2016). These fluctuations correlated with broad-scale climatic patterns in the birds' breeding and wintering areas, such as extent of seasonal drought.

Another documented driver of fluctuating selection is the occurrence of rare climatic events (Gibbs and Grant 1987, Grant and Grant 2002). These can result in unusually intense episodic selection (Grant et al. 2017) and have led to rapid evolution of morphological traits in particular (Bumpus 1899, Grant and Grant 1993, Brown and Brown 1998, 2011). In some cases, animals' behavior can also respond to the unusual conditions created by rare climatic events (Brown and Brown 2000b, Wingfield et al. 2017), although whether social behavior undergoes intense episodic selection and whether such selection results in long-term changes in behavior is not known.

In 1996, a 6-d period of unusually cool and wet weather in late May led to the starvation of thousands of cliff swallows at our long-term study site in western Nebraska. The population was reduced by about 53% during this event, which led to intense natural selection on cliff swallow morphology and established trajectories on body dimensions that persisted for at least 10 yr following the event (Brown and Brown 1998, 2011). Here, we examine whether mortality varied among birds living in colonies of different sizes and whether the colony-size distribution of the survivors' offspring changed after the selection event in ways consistent with selection on colony size. The results offer insight into the factors that may generate group-size variation

and the potential importance of rare climatic events, which are too unpredictable to be studied systematically but that are predicted to increase with global climate change (Bailey and van de Pol 2016, Kingsolver and Buckley 2017).

METHODS

Study site and weather event

Our work was done in western Nebraska along the North and South Platte rivers, centered at the Cedar Point Biological Station (41.2097° N, 101.6480° W), and including portions of Keith, Garden, Lincoln, Deuel, and Morrill counties (Brown and Brown 1996). In this area, cliff swallows nest primarily underneath bridges over highways or rivers and inside concrete culverts under roads or railroad tracks. Cliff swallows are migratory, arriving in our study area beginning in late April, and most depart by late July for their wintering range in southern South America. The birds form breeding colonies that consist of from 2 to 6000 nests (mean \pm SE, 404 ± 13 , $n = 2318$), with some individuals nesting solitarily. Colony size at any given site can vary enormously across years, but the colony-size distribution in the study area has shown no long-term directional shifts across 30 yr of study (Brown et al. 2013). Cliff swallows show variable levels of both natal and breeding philopatry, typically 10–70% depending on colony size, parasite load, and other factors (Brown and Brown 2000a, Brown et al. 2017).

Being exclusively aerial insectivores, cliff swallows are sensitive to periods of cool and wet weather in late spring that temporarily reduces the abundance of flying insects. Starvation can result if such weather extends for ≥ 4 d (Brown and Brown 1998). On 24–29 May 1996, a weather event led to the death of thousands of cliff swallows in western Nebraska, with the population size in the study area requiring five years to recover to that of the years immediately before the kill (Brown et al. 2013). Based on climatic records, we could identify only two weather events of that likely severity between 1875 and the present (Brown and Brown 1998, Brown et al. 2018).

Field methods

We estimated cliff swallow colony sizes at 19 sites prior to the weather event, primarily from

16 to 22 May 1996. We visited these sites during sunny weather at a time when most residents would have been present. Colony size (number of active nests) was determined by counting nests where cliff swallow activity was occurring or by estimating the number of birds present at sites where not all nests were visible. Our survival analysis was restricted to the 19 sites where we gathered colony-size data for other reasons prior to the weather event. When the cold weather ended and the surviving birds resumed normal activity around nests, we returned to these sites in sunny weather (on 31 May–7 June) and estimated colony sizes using the same criteria used before the event.

We searched for birds that died at all accessible sites in the study area on 29–30 May, saving all salvageable specimens that were later prepared as study skins. We salvaged birds at some sites in addition to the 19 where we had estimated colony sizes. Body metrics (wing length, middle tail length, tarsus length, bill width, and bill length) were measured for all salvaged specimens (before skinning) and for surviving birds caught in mist nets in the 9 d following the weather event, as described in Brown and Brown (1998). In this study, we present only geometric mean body size, which integrates all measurements for each bird. Following Via and Shaw (1996), we used the mean of the log-transformed k original variables, $[\sum \ln(X_i)]/k$, where X_i is the value of the i th variable for a given observation. Additional information on measurements that comprised body size is given in Brown and Brown (1998).

In comparing how colony sizes chosen by cliff swallows changed as a result of the severe weather event, we used only known yearling birds that had been banded in the study area (as nestlings or juveniles) in the previous summer. Using only locally banded birds helped us avoid pollution of the data set by the many immigrant birds that occurred in the study area and that may not have been exposed to the 1996 selection event. This also ensured that our comparison was only among individuals at the same life stage. Restricting our analysis to yearlings was especially important because colony choice among older birds may be influenced by experience at a site (Brown et al. 2008), whereas that for yearlings is more strongly heritable (Brown and Brown 2000a, Roche et al. 2011).

We compared the colony-size distributions of yearlings in 1997, the year after the selection event, to that of yearlings in 1995, the year before the selection event. Birds in both years were primarily ones caught as juveniles at a single colony site that attracted thousands of transient adults and locally fledged juveniles from throughout the study area and from multiple colonies of different sizes (Brown 1998). We netted at this site throughout most of July in both 1994 and 1996. Settlement of yearlings in 1995 and 1997 was monitored through a large-scale mark–recapture effort (Brown and Brown 2004, Roche et al. 2013, Brown et al. 2016) in which we visited 36 and 24 colonies and had 17,553 and 12,793 total cliff swallow captures in 1995 and 1997, respectively. Because yearlings banded in 1994 and 1996 came from the same subset of local colonies and were searched for the next year in the same way (sensu Brown and Brown 2004, Brown et al. 2016), this analysis was intended as a relative comparison of juvenile recruitment in the year immediately preceding the weather event (1995) and in the year immediately after it (1997). Sites studied in 1995 and 1997 included the same ones at which mortality was estimated in 1996, except in cases where the site was unused (no active nests) in 1995 or 1997, or in which we had no data from 1996.

Statistical analyses

Linear and quadratic regressions were performed with SAS (SAS Institute 2004). In analyzing extent of survival at colonies of different sizes, we used AIC (Akaike information criterion) to assess whether linear or quadratic models fit the data better. For analyses of whether body size could be predicted by an interaction between colony size and survival status (alive or dead), we used colony site as a random effect in a mixed model (Proc MIXED in SAS) to account for potential non-independence among birds at a given site. Selection differentials and their significance were calculated from formulas in Endler (1986:171–172), using the combined population of survivors and non-survivors as that before selection and the survivors only as that after selection (Brown and Brown 1998).

RESULTS

The smallest cliff swallow colony for which we had survival estimates was 75 nests and the

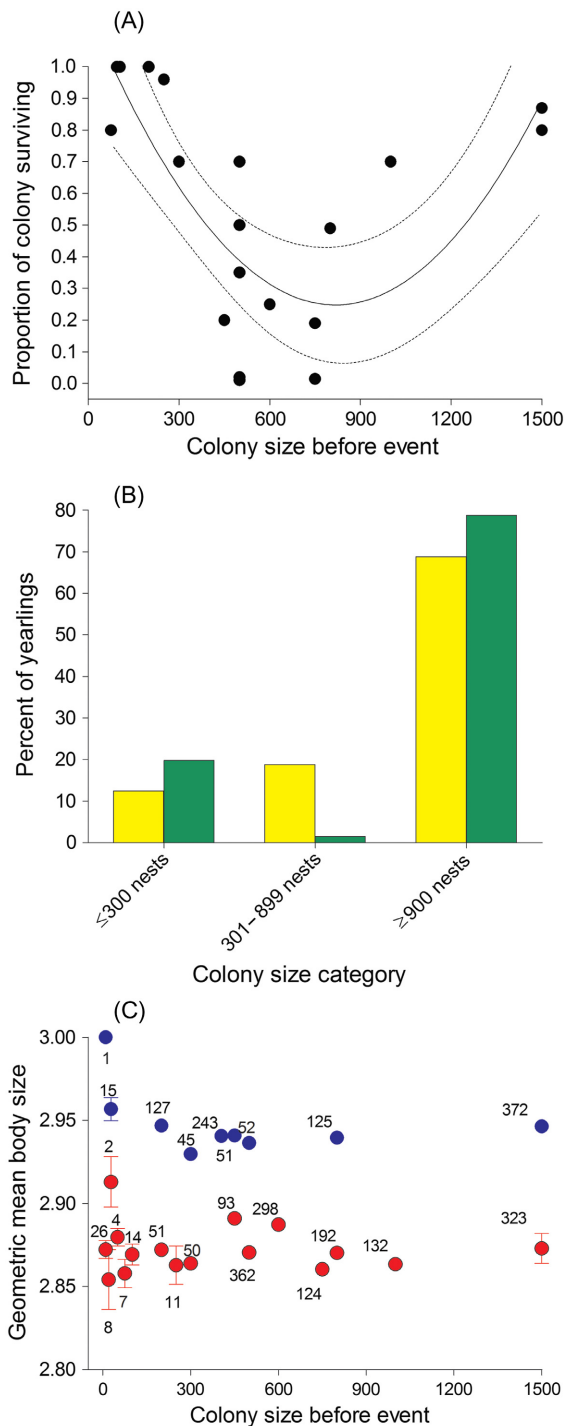


Fig. 1. (A) Proportion of a cliff swallow colony surviving a severe weather event in western Nebraska in relation to colony size (number of active nests) at the site immediately before the severe weather. Proportion was determined by dividing the colony size after the

largest was 1500 nests. The proportion of a colony's residents that survived the weather event showed a curvilinear pattern (Fig. 1A). Relatively small colonies of 75–300 nests in size (before the event) and relatively large ones ≥ 900 nests declined less in size than ones in the intermediate size range (301–899 nests; Fig. 1A). A quadratic model that contained a squared term for colony size (AIC = -51.54 , $r^2 = 0.604$) was a far better fit than one with only a linear term for colony size (AIC = -36.30 , $r^2 = 0.017$). The regression coefficient for the squared term was positive and significantly different from 0 ($t = 4.87$, $P = 0.0002$).

Given that there appeared to be three general classes of colony sizes among which survival differed (Fig. 1A), we assigned yearlings to the three groups based on their breeding colony of residency. The percentage distribution of yearlings among these colony-size classes in 1995 (before the event) differed significantly from that in 1997 (after the event; Fig. 1B). Yearlings were underrepresented in the intermediate colony-size class following the selection event, with similar percentages between years in the smallest and largest colonies (Fig. 1B). Yearlings settling in colonies < 75 nests in size were not tabulated for either year, because we had no quantitative data on extent of mortality at sites of that size.

Because individual survival during the weather event depended heavily on body size,

(Fig. 1. *Continued*)

event by that before the event. Curves show best-fit quadratic relationship \pm 95% confidence interval. (B) Percentage of yearling cliff swallows distributed among colony-size classes in the year before the selection event (yellow bars; $n = 394$ birds) vs. that in the year after the selection event (green bars; $n = 273$ birds). The distributions differed significantly ($\chi^2_2 = 49.2$, $P < 0.0001$). (C) Mean (\pm SE) cliff swallow geometric body size in relation to colony size before the severe weather for birds that survived (blue circles) and did not survive (red circles). Colony size explained little variation in body size for both survivors and non-survivors whether modeled as a linear or a quadratic relationship (r^2 from 0.00 to 0.02 on all). Sample size (number of birds measured) is shown for each colony.

with skeletally larger birds more likely to survive (Brown and Brown 1998), we examined whether body size varied among colony sizes in ways that might explain greater mortality in certain colonies. With colony site as a random effect, body size was best predicted by survival status (survivor, non-survivor; $F_{1, 2699} = 82.6$, $P < 0.0001$) and colony size ($F_{1, 2699} = 6.82$, $P = 0.009$), but there was no significant interaction between survival status and colony size ($F_{1, 2699} = 0.01$, $P = 0.92$). Thus, survivors were larger than non-survivors by about the same extent across all colony sizes (Fig. 1C).

Quantitative measures of selection on body size for birds in four classes of colony sizes (including that for 1–74 nests, for which we had no quantitative colony-wide mortality estimates) showed that the form of natural selection was similar among colony sizes, but the apparent intensity of selection varied (Table 1). The directional selection differential was the lowest (although still highly significant) for birds in the largest colony-size class, while the variance differential was highest at those sites (Table 1).

DISCUSSION

While a variety of studies have shown that survival or reproductive success either systematically increases or decreases with colony size, or is highest at intermediate-sized colonies (Brunton 1999, Brown and Brown 2001, Williams et al.

2003), the results reported here are among a very few to show a strong advantage for individuals in the smallest and largest (the extreme) group sizes. With colony-size preference being heritable in cliff swallows (Brown and Brown 2000a), our results suggest that in certain situations disruptive selection can favor a bimodal distribution of colony sizes. The underrepresentation of yearling cliff swallows in the intermediate-sized colonies in the year following the selection event is consistent with residents of the two extreme colony-size classes having higher fitness in at least the short term.

The mechanisms generating the higher survival of cliff swallows in the smallest and largest colonies during severe weather are likely food-related. Swallow mortality during these events seems to be a direct result of starvation (lack of flying insects) and not exposure per se, given that birds often die inside their enclosed, relatively well-insulated mud nests. Cliff swallows in all colonies invested less in their offspring in 1996, likely because the adults were food-stressed that season (Brown and Brown 2004). These birds experience food competition, even when foraging is not restricted by bad weather, and competition increases in larger colonies (Brown and Brown 1996). However, the very largest colonies also tend to occur in areas with the most habitat complexity within their foraging ranges, and this complexity probably results in greater local insect abundance in general (Brown et al. 2002). Birds in the largest colonies also have the greatest opportunities for transfer of information about food locations (Brown and Brown 1996). With competition lowest in the smallest colonies, and habitat-driven food abundance and information transfer greatest in the largest colonies, the intermediate-sized colonies perhaps have the worst of both worlds in severe weather when food is unusually scarce. In such situations, heightened competition for a more limited food base and fewer opportunities for information transfer likely result in reduced survivorship of adults occupying the colonies of intermediate size.

Given the strong selection on morphological traits observed during this event (Brown and Brown 1998), the mortality differences among colony sizes could have partly reflected differences in how birds of particular morphology

Table 1. Mean (\bar{x}), variance (var), and sample size (n) for geometric mean body size of cliff swallows before and after a weather event, and directional (i) and variance (j) selection differentials, for birds in 4 colony-size classes.

Variable	10–74 nests	75–300 nests	301–899 nests	≥900 nests
\bar{x} (before)	2.8789	2.9097	2.8954	2.9045
\bar{x} (after)	2.9596	2.9424	2.9400	2.9464
var (before)	0.001670	0.002100	0.001761	0.01213
var (after)	0.0007879	0.0007463	0.0005661	0.0005504
n (before)	140	305	1540	827
n (after)	16	172	471	372
i^\dagger	1.9741	0.7150	1.0623	0.3805
j^\ddagger	–0.5282	–0.6447	–0.6784	–0.9546

† All significant at $P < 0.00001$.

‡ All significant, 10–74 nests at $P = 0.043$, all others at $P < 0.0001$.

distributed themselves among colony sizes. For example, if birds with smaller body sizes tended to preferentially settle in the intermediate-sized colonies, we might detect higher mortality there for this reason alone. However, the observed distribution of body sizes among colonies, and the patterns of selection on morphology documented, suggests this is not the case. There was no evidence that body size was appreciably smaller before the event in the intermediate-sized colonies (301–899 nests; Table 1), and survival and colony size did not statistically interact in predicting the observed body-size variation. For these reasons, social factors and food competition are more likely to explain our results (Fig. 1A) than colony-size-related differences in selection on morphology.

Although the rare climatic event likely led to disruptive selection on colony size in cliff swallows in 1996, there was no long-term change in the colony-size distribution in the population. Over 30 yr, the colony-size distribution has been relatively stable (Brown et al. 2013). This result could be, in part, because intermediate colony sizes themselves can confer advantages over small and large ones during more benign years without climatic events. Annual survival in cliff swallows is subject to fluctuating selection (in both direction and form) on colony size that varies among years depending on whether the birds experience hot and dry, or cool and wet, conditions on either the breeding or wintering grounds. For example, in the year of the event, 1996, there was no significant directional annual survival selection on colony size for adults, but in the following year directional selection favored smaller colonies for both males and females (Brown et al. 2016). First-year birds, on the other hand, that survived to fledge from the intermediate-sized colonies in 1996 had higher annual survival than those from the smallest and largest colonies (Brown et al. 2016). Thus, selection on colony size for young birds was opposite that observed for adults during the climatic event and opposite the pattern of recruitment seen in the year after the event.

The apparent contradiction between survival and recruitment for first-year birds from 1996 could be in part because different metrics were used for each: Annual survival was inferred using multiple years of recapture (*sensu*

Lebreton et al. 1992), whereas observed recruitment was based strictly on recapture percentages the first year. Also, the 1996 weather event may have selected for particularly high-quality juveniles from the intermediate-sized colonies who survived despite the costs of such sites that summer and thus had high survival subsequent to the weather event. The form and intensity of selection on colony size can apparently vary with life stage, time of year, and between years in cliff swallows, making it difficult to disentangle the long-term effect of any single selection event.

Our ability to detect long-term effects of rare climatic events such as this one is likely compromised by a highly open cliff swallow population in which many immigrant birds not exposed to a particular selection event settle in the study area each year. Nevertheless, that we could still detect the signature of disruptive selection on first-year birds in 1997 despite both the presence of immigrants and opposing selection on annual survival (due in part to conditions on the wintering grounds; Brown et al. 2016) from 1996 to 1997 attests to the potential magnitude of the disruptive selection in the 1996 climatic event.

Over a 24-yr period during which we measured annual survival of cliff swallows in relation to colony size, in only year (2000) did we find evidence of significant disruptive selection on colony size (Brown et al. 2016). In that case, the widest variation in survival probabilities among colony sizes was only about 0.24, compared to variation of 0.99 in birds' 6-d survival probabilities during the climatic event. Thus, short-term weather events have the potential to cause far stronger selection on colony size than do the broader scale conditions that these animals experience over a year and that are more commonly measured in annual survival studies in general. On the other hand, despite these events' short-term impact, they may not be sufficiently common to result in major changes to the colony-size distribution. Although we detected five unusual climatic events that resulted in cliff swallow mortality in our study area from 1982 to 2018 (Brown and Brown 1998, Brown et al. 2018), in only one of these (1996) was mortality widespread enough for us to measure effects of colony size. However, with unusual climatic events predicted to increase in frequency in the future (Bailey and van de Pol 2016, Kingsolver and Buckley 2017),

their effect on social behavior should be closely monitored.

ACKNOWLEDGMENTS

We thank Beth Chasnoff, Zina Deretsky, Leila Hatch, Sarah Huhta, Lorky Libaridian, Charlene Pate-naude, Gabriela Redwine, Kara Rodgers, Sarah Rosenberg, Annemarie Rundquist, and Zoe Williams for field assistance; the School of Biological Sciences of the University of Nebraska-Lincoln for use of the Cedar Point Biological Station; Duane Dunwoody, Dave and Deb Knight, and Loren Soper for access to land; the National Science Foundation (BSR-9015734, DEB-9613638, DEB-1453971, IOS-1556356) and the University of Tulsa for financial support; and Douglas Morris, Valerie O'Brien, and two anonymous reviewers for helpful comments on the manuscript.

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