VOL. 195, NO. 6 THE AMERICAN NATURALIST JUNE 2020

Survival Benefits of Group Living in a Fluctuating Environment

Sarah Guindre-Parker[1,2,*] **and Dustin R. Rubenstein**[2,3]

1. Department of Ecology, Evolution, and Organismal Biology, Kennesaw State University, Kennesaw, Georgia; 2. Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York; and Department of Ornithology, National Museums of Kenya, Nairobi, Kenya; 3. Center for Integrative Animal Behavior, Columbia University, New York, New York

Submitted July 3, 2019; Accepted November 22, 2019; Electronically published April 6, 2020

Online enhancements: supplemental PDF. *Dryad data:* https://doi.org/10.5061/dryad.stqjq2c05.

ABSTRACT: Group living is predicted to arise only when the fitness benefits outweigh the costs of sociality. Group-living species—including cooperatively breeding and family-living birds and mammals—occur most frequently in environments where climatic conditions fluctuate unpredictably from year to year. The fitness consequences of group living are thus expected to vary with changing environmental conditions, though few studies have examined this possibility. We examined whether living in large social groups improves adult survivorship in cooperatively breeding superb starlings (*Lamprotornis superbus*). We also tested the hypothesis that larger groups buffer against harsh conditions by increasing survivorship most under periods of low rainfall. We found that group size was positively correlated with adult survival but in a sex-specific manner: female survival increased with group size across all environmental conditions, whereas male survival increased with group size only in wet years. Together with previous work in this system, our results suggest that larger groups confer survival benefits by reducing predation, rather than by improving access to food or buffering against physiological stress. Although group living does not appear to buffer against harsh conditions in adult starlings living in a fluctuating environment, living in larger groups does confer a survival advantage.

Keywords: survival, Cox proportional hazards model, group size.

Introduction

Since social animals face automatic costs of group living but few automatic benefits (Alexander 1974; Kokko et al. 2001), sociality is expected to arise only when individuals gain fitness benefits that outweigh the costs (Alexander 1974). Group living has been shown to confer fitness benefits across diverse taxa, including spiders (Brown and Brown 2004; Bilde et al. 2007), birds (Brown et al. 2003), mammals (Clutton-Brock et al. 1999; Mosser and Packer 2009), and nonhuman primates (Brent et al. 2017; Alberts 2018). Although the benefits of group living are likely to be most important in species living in harsh and unpredictable environments (Shen et al. 2017), few studies have explored how the fitness benefits of grouping vary across fluctuating environmental conditions (but see Brown et al. 2016). Nevertheless, the global distribution of social animals, such as cooperatively breeding birds and mammals, is associated with harsh and unpredictable environmental conditions (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011; Lukas and Clutton-Brock 2017), which has been taken as evidence that alloparents (individuals other than parents who provision or defend the young) serve to buffer against environmental uncertainty (Jetz and Rubenstein 2011; Cornwallis et al. 2017). More recently, however, the incidence of family living in the absence of alloparental care was also shown to be associated with environmental fluctuations, suggesting that ecological conditions previously thought to be associated with alloparental care may also be associated with group living (Griesser et al. 2017*a*). Fluctuating environments are known to increase variation in the costs and benefits of group living, both among (Baglione et al. 2002; Kocher et al. 2014) and within (Brown et al. 2016) populations. Although environmental conditions can thus shape optimal group size (Markham et al. 2015; Brown et al. 2016), which itself may oscillate as environmental conditions change, the role of climatic fluctuations in shaping the fitness consequences of group living remains unclear.

Superb starlings (*Lamprotornis superbus*) are plural cooperative breeders that live in groups that can number more than 50 individuals (mean ± SE $= 22.2 \pm 0.65$ in this study). These social groups are comprised of both kin (individuals born within the group) and nonkin (immigrants) of both sexes that defend territories year-round (Rubenstein 2016). Immigrants play an important role in adding to group size, since annual fledging success can be extremely low and is unrelated to social group size (Rubenstein 2011, 2016). In contrast, after recruiting into a group and gaining a breeding position, superb starlings remain in their social group for their lifetime, which limits the impact of emigration on group

---

[*] Corresponding author; email: sguindre@kennesaw.edu.

ORCIDs: Guindre-Parker, https://orcid.org/0000-0002-6205-3752; Rubenstein, https://orcid.org/0000-0002-4999-3723.

Am. Nat. 2020. Vol. 195, pp. 1027–1036.
DOI: 10.1086/708496

size (beyond natal dispersal). Multiple pairs in each group will breed during each rainy season, and a minority of nonbreeding group members become alloparents at one of the active nests (mean percentage of a social group ± SE = 13% ± 0.7% in this study). The majority of nonbreeders forgo reproduction or alloparental care (hereafter, "nonbreeder/nonalloparents"; mean percentage of a social group ± SE = 53% ± 1.7% in this data set). Therefore, superb starling social groups are considerably larger than required for alloparental care alone, and the number of alloparents at a nest is not correlated with social group size (Rubenstein 2006; Guindre-Parker and Rubenstein 2018*a*). The cumulative guarding and provisioning behavior performed at a nest enhances breeder reproductive success (Rubenstein 2007*b*; Guindre-Parker and Rubenstein 2018*a*), suggesting that nonbreeding/nonalloparent group members may provide direct benefits of group living independently of rearing young. Some cooperative breeders, such as the noisy miner (*Manorina melanocephala*), show a clear division of labor where some nonbreeders provision young, while others focus on predator defense and otherwise contribute little to offspring care (Arnold et al. 2005). Indeed, in a number of cooperatively breeding species, group living confers important benefits that occur independently of alloparental care, including more effective territory defense (Farabaugh et al. 1992), improved foraging success (Wright et al. 2001), reduced predator attacks while foraging (Gullett et al. 2012), reduced susceptibility to kleptoparasitism (Ridley and Raihani 2007), improved thermoregulation (du Plessis and Williams 1994; du Plessis et al. 1994), and reduced adult mortality and group extinction under harsh environmental conditions (Clutton-Brock et al. 1999). While the reproductive benefits of alloparental care are well documented for superb starlings (Guindre-Parker and Rubenstein 2018*a*, 2018*b*), the fitness consequences of living in some of the largest social groups known for a cooperatively breeding bird remain unknown.

Superb starlings live in a harsh environment (Rubenstein and Lovette 2007; Rubenstein 2016) where the intensity and duration of rainfall vary unpredictably within and among years. Variation in rainfall can even drive changes in social group size (Rubenstein 2011), where social groups tend to increase in size following periods of increased rainfall during the dry season (hereafter, "prebreeding period"; Rubenstein 2006, 2011), though spatial variation in group size is unrelated to food availability within each territory (i.e., grass cover and insect abundance; Rubenstein 2011). Here we examine whether adult survivorship varies with group size in seven social groups and whether fluctuations in environmental conditions (rainfall and territory grass cover) alter the relationship between group size and adult survival. Although the causes of mortality are poorly understood for adult superb starlings, predation, disease, starvation, and senescence are all possible culprits where sociality could buffer adults from these diverse causes of death. We predict that (i) adult superb starlings in larger groups will have higher survival and (ii) group size will predominantly buffer against harsh environmental conditions (e.g., those characterized by low rainfall or low territory grass cover) by having a disproportionately positive impact on survival under harsh conditions. Finally, we discuss the potential mechanisms through which group living confers survival benefits to adult superb starlings in light of current and previous research in this system. Ultimately, this study provides one of the few empirical tests in a cooperative breeder of whether grouping results in fitness benefits independent from those associated with alloparental care, as well as whether the relationship between group living and survivorship changes with fluctuations in environmental conditions.

Material and Methods

Study System

A population of superb starlings consisting of seven social groups was monitored continuously from 2001 to 2015 at the Mpala Research Centre, Laikipia, Kenya (0°17′N, 37°52′E). In our study population, superb starlings breed twice per year during the short (October–November) and long (March–June) rainy seasons, where zero to seven breeding pairs will reproduce in each group in each season (short rain: mean ± SE = 1.5 ± 0.11; long rain: mean ± SE = 2.3 ± 0.14). Individuals are uniquely marked with a numbered metal ring and a combination of four colored leg bands. Birds born within this population are banded as nestlings, while immigrants are captured and marked via routine trapping throughout the year (Rubenstein 2016). Although superb starling females have a tendency to disperse from their natal group (only 7% remain in their natal group; Rubenstein 2006), whereas males have a tendency to be the philopatric sex and remain on their natal territory (41% remain in their natal group; Rubenstein 2006), there is a great deal of variation in whether individuals of either sex will remain in their natal group or disperse. For example, females can remain on their natal territories their entire lives, though they almost never breed (Rubenstein 2006), and males frequently disperse and breed in a nonnatal social group, as approximately half of the males in our study population are immigrants (Rubenstein 2016).

In our study system, 49% of individuals were banded at the nest and are therefore of known age. Birds captured outside of the nest were aged according to their iris color (see supplementary materials 1; supplementary materials 1–3 are available online). We assumed that immigrants with a brown and white iris were 1 year of age, whereas those with a pure white iris were a minimum of 2 years of age (Sweijd and Craig 1991). Banded individuals in our population typically emigrate from their social group between 1 and 3 years of age, with 76% of immigrants dispersing by age 3 (Rubenstein 2006). It is possible for individuals to delay dispersal beyond this period, however, and it would be impossible to differentiate older immigrants from younger ones based on iris color. Thus, immigrant age represents a minimum age rather than a precise age.

We used focal nest observations performed during the long and short breeding seasons, as well as routine census observations and trapping data collected during the breeding and nonbreeding seasons, to identify the members of each social group. During the breeding season, we monitored breeding roles via focal behavioral observations at the nest (Guindre-Parker and Rubenstein 2018*a*): the social mother was identified as the individual performing nest incubation, the social father was defined as the male guarding the mother during incubation bouts, the alloparents provided nest guarding or offspring provisioning assistance, and the nonbreeding/nonalloparent group members did not engage in any way with nests or nestlings for the entirety of the breeding season. Although superb starling individuals adopt one role in a given breeding season, these roles are flexible from one breeding season to the next, as breeders and alloparents frequently take "breaks" where they become nonbreeding/nonalloparents in subsequent seasons. Thus, it is not possible to ascribe a single, consistent breeding role to an individual for its entire lifetime, and breeding roles change frequently from season to season (even for more dominant breeding individuals). Group size was calculated using a combination of all breeding and nonbreeding observations to determine the total number of individuals alive within the group in a given season, as calculated previously for this species (Pollack and Rubenstein 2015). Group size varied among social groups and among seasons, ranging from 7 to 57 individuals across all social groups (mean ± SE = 18.9 ± 0.5; fig. 1). Between 2001 and 2015, the largest social group had on average 29 members (ranging across seasons from 23 to 57 individuals), while the smallest social group had on average 14 members (ranging across seasons from 9 to 19 individuals; the social group with seven birds was on average the second-smallest group).

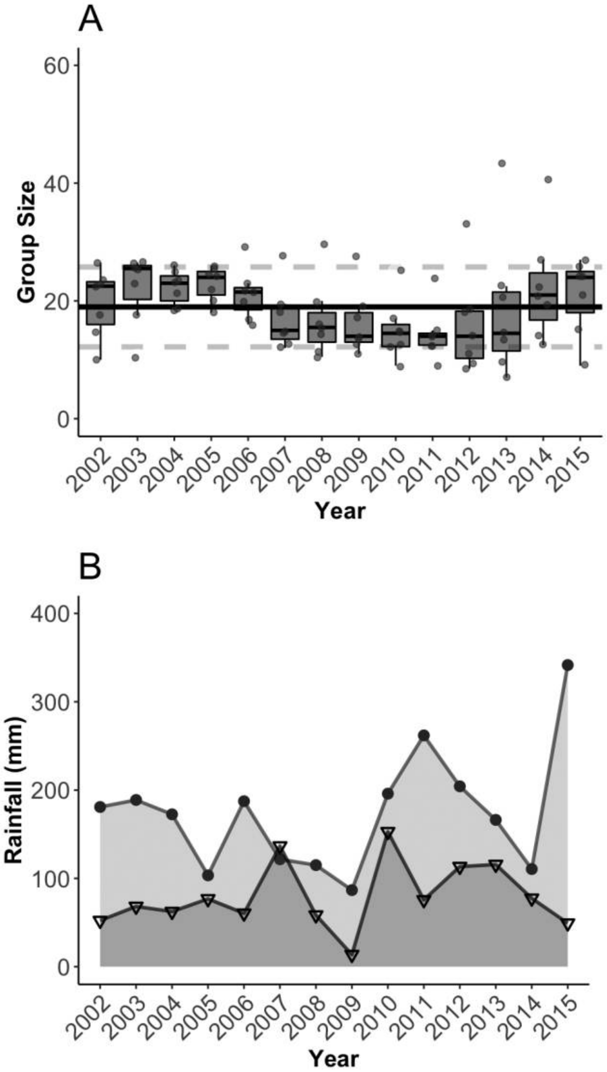

Figure 1: Seven groups of superb starlings that varied in size among social groups and seasons were studied from 2002 to 2015. *A*, Boxplots depict the distribution of social group size averaged across the short and long rainy seasons for each group and each year, with the median (black line), first and third quartiles (box), and interquartile range (multiplied by 1.5; whiskers). Circles represent data points (jittered). The study-wide mean group size is indicated by a solid black horizontal line ±1 SD (dashed pale gray lines). *B*, Rainfall also varied across the years of our study; symbols depict mean annual breeding rainfall (circles) and prebreeding rainfall (triangles).

Environmental Conditions

Environmental conditions fluctuate across years (i.e., rainfall) and territories (i.e., grass cover). Both rainfall and grass cover shape the availability of insects, which are the preferred source of food delivered to nestlings and consumed by adults (Feare and Craig 1998; Rubenstein 2006). As a result, environmental conditions are known to impact superb starling behavior during breeding (Guindre-Parker and Rubenstein 2018*a*) and are similarly likely to impact survival. In addition, prebreeding rainfall during the dry season may also play a role in shaping fitness in superb starlings, since it is during this period that breeding roles are determined (Rubenstein 2007*a*) and when the majority of dispersal takes place (Rubenstein 2016). Variation in rainfall may influence multiple potential sources of mortality for adult superb starlings at our study site, including access to food, prevalence of parasites and pathogens (Titcomb et al. 2017; Weinstein et al. 2017), and predator abundance (including potential adult starling predators, such as snakes and birds of prey; McCauley et al. 2006; Byrom et al. 2014).

We measured rainfall during each year using a centralized automated Hydrological Services TB3 Tipping Bucket Rain Gauge located within 15 km of each social group (Caylor et al. 2017). We calculated breeding rainfall in the long (March–June) and short (October–November) rain breeding seasons, as well as prebreeding rainfall during the dry season immediately preceding the long (December–February) and short (July–September) rains. Prebreeding rainfall ranged from 6.1 to 193.1 mm (mean ± SE = 80.6 ± 9.3 mm), while breeding rainfall ranged from 7.8 to 370.2 mm (mean ± SE = 167.9 ± 21.9 mm; fig. 1). Territory quality was defined by grass cover—an index of insect availability—calculated as the long-term average of the percentage of dropped pins that touched vegetation from monthly vegetation transects performed between 2008 and 2015 (for detailed methods, see Rubenstein 2007*c*). Mean territory grass cover ranged from 60% to 73% (mean ± SE = 68% ± 2.0%) among the seven territories.

Survival Models

We used time-varying Cox proportional hazards regression models to determine whether group size or environmental conditions shaped survival independently in males and females (Fox et al. 2006; Saino et al. 2011; Wolfe et al. 2016), since this approach can handle both time-dependent and time-independent predictors and does not require the specification of a probability distribution for survival times (Fox and Weisberg 2002). Both male and female superb starlings can delay dispersal, which typically occurs by 3 years of age and as a single emigration event in their lifetime (Rubenstein 2016). Individuals do not emigrate once they gain a breeding position, whether they joined their social group via immigration or birth (Rubenstein 2016). As a result—for birds that have bred at least once in our population—we can avoid confounding disappearance due to death with emigration from the social group. We performed our analyses on a subset of birds that had bred at least once in their social group ($n = 61$ for males, $n = 69$ for females), although they were not always breeding in every season and nearly all individuals in this subset performed all breeding roles at some point over their life span. We monitored individual presence and breeding role as described above during two seasons per year (long season and short season—see "Environmental Conditions"). We assumed that individuals that had not been observed for five continuous seasons were no longer alive—their death was recorded as the end of the season when they were last observed (sensu Pollack and Rubenstein 2015). Our results were robust to this assumption, as they did not change after performing a sensitivity analysis where we extended the length of subsequent breeding seasons required before assuming that an individual had died (e.g., six or seven seasons; see supplementary materials 2). Since we had no sense of the age of adults that were present at the beginning of our banding efforts in 2001, we excluded these individuals from survival analyses (although they were included in group size estimates)—this represented 29% of adult males and 18% of adult females that have bred at least once in our study population. Therefore, the only censoring in our analyses occurred when individuals were still alive at the end of the study period.

We built separate proportional hazards models for males and females—while the sexes are similar in morphology and dominance hierarchies (Rubenstein 2016), they do exhibit differences in physiology (Pikus et al. 2018), patterns of DNA methylation (Rubenstein et al. 2015), and behavior (Guindre-Parker and Rubenstein 2018*a*), all of which could influence survivorship differently. Importantly, running a model with the sexes combined produced qualitatively similar results, showing a survival benefit in larger groups (data not shown). Each model included the following predictor variables: prebreeding rainfall, breeding rainfall, territory grass cover, and social group size. In addition, we included interactions between group size and each of the three environmental predictors. All variables in our models were continuous and standardized using z-scores before analysis. While some of the predictor variables can covary through time in this system, they were not linearly related to one another in the data set and could therefore be included in the same model (all variance inflation factor < 2, excluding interaction terms; Fox and Monette 1992). Importantly, we used two cluster terms in every Cox proportional hazards model to account for the nonindependence of observations collected from the same individual across seasons (ID) or for multiple individuals sampled in each social group (group ID). These cluster terms offer an alternative to using a mixed modeling approach (i.e., with random effects) to account for the fact that observations from the same identifier are likely correlated (Wang 2014). Proportional hazards models were performed using the survival package (ver. 2.40-1) in R version 3.2.4 (R Development Core Team 2016). We checked that our data set did not violate the proportional hazards assumption using the cox.zph function in the survival package. Data sets and code are deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.stqjq2c05; Guindre-Parker and Rubenstein 2019).

We display our results as survival curves prepared using the survminer package (ver. 0.4.3) in R, which displays the survival probability as a function of age (years). Although all predictor variables in our survival models are treated as continuous, in our figures we illustrate the impact of group

Table 1: Results of Cox proportional hazards regression models for female ($n = 69$ individuals) and male ($n = 61$ individuals) superb starlings from seven social groups monitored across 28 seasons

	Estimate ± SE	*Z*	*P*	Hazard ratio (95% CI)
A. Females:				
Prebreeding rain	.02 ± .27	.08	.94	1.02 (.65–1.59)
Breeding rain	−.24 ± .24	−1.21	.23	.78 (.53–1.16)
Grass cover	.58 ± .43	1.77	.08	1.79 (.94–3.41)
Group size	−.96 ± .46	−2.22	.03	.38 (.16–.89)
Prebreeding rain × group size	−.33 ± .35	−1.09	.28	.72 (.39–1.31)
Breeding rain × group size	.22 ± .31	.75	.45	1.24 (.70–2.20)
Grass cover × group size	.12 ± .51	.26	.80	1.12 (.46–2.72)
B. Males:				
Prebreeding rain	−.54 ± .34	−1.74	.08	.58 (.32–1.07)
Breeding rain	−.36 ± .33	−1.27	.20	.70 (.40–1.21)
Grass cover	−.27 ± .26	−1.01	.28	.76 (.46–1.25)
Group size	−.84 ± .40	−2.59	<.001	.43 (.23–.82)
Prebreeding rain × group size	−1.21 ± .41	−3.30	<.001	.29 (.15–.61)
Breeding rain × group size	−.34 ± .40	−1.00	.32	.71 (.36–1.38)
Grass cover × group size	−.65 ± .35	−2.27	.02	.52 (.30–.91)

Note: For each continuous predictor, we present the coefficient estimate and standard error, *Z* statistic, *P* value, and hazard ratio with 95% confidence intervals (CIs). A negative estimate or a hazard ratio of <1 indicates that a predictor is positively correlated with survival, while a positive estimate or hazard ratio of >1 indicates a negative correlation.

size (or rainfall, grass cover, etc.) on survivorship by categorizing these predictors. To illustrate the impact of group size on survivorship, we created three survival curves for individuals from above average group sizes (where the social group is greater than mean group size + 1 SD), average group sizes (where the social group is within 1 SD of the mean), and below average group sizes (where the social group is smaller than mean group size − 1 SD).

Results

We found that female survival was unrelated to prebreeding rainfall, breeding rainfall, or territory grass cover (table 1). However, female survival increased significantly in larger social groups (fig. 2), where a greater proportion of females were alive after 12 years in larger than in smaller social groups. Finally, there was no significant interaction between group size and any of the three environmental variables included in our model (table 1), suggesting that fluctuating environmental conditions did not influence the positive association between female survival and group size.

Similarly, we found that male survival was unrelated to prebreeding rainfall, breeding rainfall, or territory grass cover (table 1). Male survival was also positively correlated with group size, and there were significant interactions between prebreeding rainfall and group size as well as between grass cover and group size. Briefly, male survival increased with group size, but only (i) in breeding seasons following periods of average or above average prebreeding rainfall (fig. 3) and (ii) on territories with average or above average grass cover (see supplementary materials 3). Thus, male survival was unrelated to social group size when rainfall was below the long-term average, although survivorship

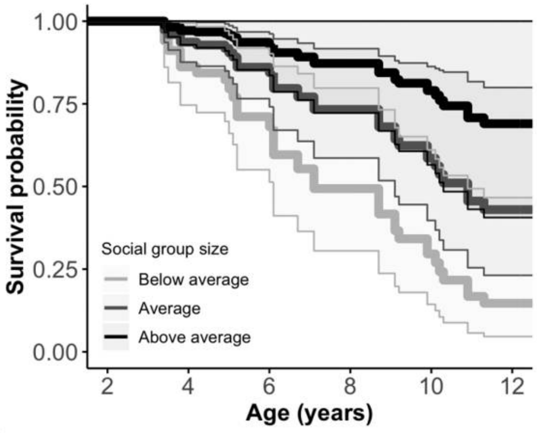

Figure 2: Female superb starling survival increased with group size ($n = 69$). Our survival model included group size as a continuous variable, but here we display survivorship curves for individuals in three categories of social groups: survival curves have different shading for group sizes that are above average (i.e., 1 SD above mean group size), (ii) average (i.e., within 1 SD of mean group size), or (iii) below average (i.e., 1 SD below mean group size). Thick survival curves represent survival model predictions with other model parameters set to their mean values. Thin lines represent 95% confidence intervals.

increased in larger groups under average and above average environmental conditions.

Discussion

We investigated whether adult survival in cooperatively breeding superb starlings varied with social group size and whether larger social groups buffered against the potentially negative impact of harsh environmental conditions. First, we found that neither prebreeding rainfall nor breeding rainfall nor grass cover was correlated to adult survivorship, which demonstrates that adult survival does not covary with abiotic environmental conditions. Instead, our results showed that adult survival covaried with the social environment, where survivorship in both males and females was positively related to group size. However, environmental conditions altered this correlation differently in the sexes, as female survival increased with social group size across all environmental conditions but male survival was highest in social groups of above average size and in periods of average or above average prebreeding rainfall. Our results provide evidence that although the fitness benefits of group living fluctuate little with environmental conditions, they do so in a sex-specific manner and in the opposite direction as we predicted. That is, large social groups do not exclusively increase survival under harsh conditions for either sex and instead increase survivorship (i) equally under all environmental conditions in females and (ii) most under benign conditions in males. Our primary finding that larger social groups confer survival benefits to adult members is consistent with evidence from a number of group-living species, including meerkats (Clutton-Brock et al. 1999) and cliff swallows (Brown et al. 2016). However, our results also contrast with several social species where group size did not alter adult survivorship, including velvety free-tailed bats (*Molossus molossus*; Gager et al. 2016), Siberian jays

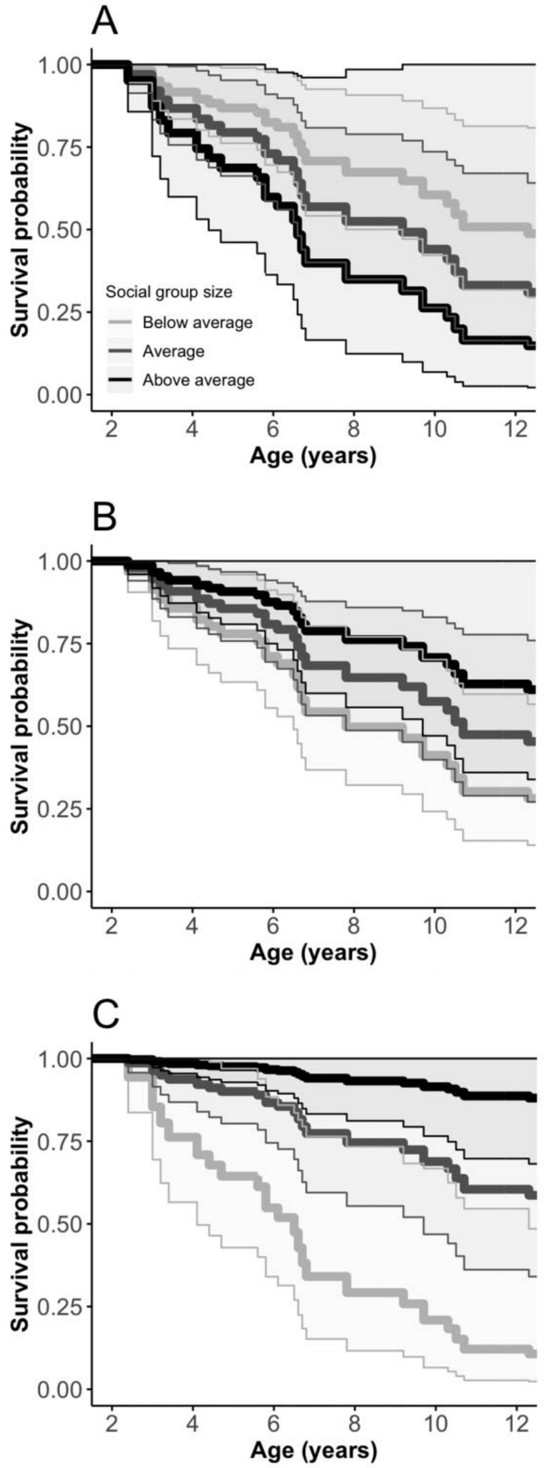

Figure 3: Male superb starling survival was correlated with an interaction between the group size and prebreeding rainfall ($n = 61$). Our survival models included group size and rainfall as continuous variables, but here we categorize these two variables to illustrate our results. When prebreeding rainfall was below average (i.e., 1 SD below mean rainfall; *A*), group size did not increase male survival. However, when prebreeding rainfall was average (within 1 SD of mean rainfall; *B*) or above average (i.e., 1 SD above mean rainfall; *C*), group size increased male survival. Thick survival curves represent survival model predictions with other parameters set to their mean values. Survival curves have different shading for group sizes that are above average (i.e., 1 SD above mean group size), (ii) average (i.e., within 1 SD of mean group size), or (iii) below average (i.e., 1 SD below mean group size). Thin lines represent 95% confidence intervals. We note that these confidence intervals are quite wide, likely because of the reduced sample sizes that result from categorizing group size and rainfall (vs. the continuous measures used in the analyses). Although this could limit our ability to detect differences in survivorship between categories of social group sizes when rainfall is below average, we note that the survivorship curve for the above-average-sized groups is well below that of the average and below average groups, suggesting that group size is unlikely to improve survival under low rainfall conditions despite a large confidence interval.

(*Perisoreus infaustus*; Griesser et al. 2017*b*), and rhesus macaques (*Macaca mulatta*; Brent et al. 2017).

Our study suggests that fluctuating environmental conditions may not play as important a role in shaping the fitness consequences of group living as has been found in other systems, including colonial cliff swallows (Brown et al. 2016). Instead, fluctuating environmental conditions may be more important for shaping the fitness consequences of alloparental care in cooperatively breeding species, as was previously argued (Jetz and Rubenstein 2011; Cornwallis et al. 2017), than for group living (Griesser et al. 2017*a*). One possibility for why males experience greater benefits of group living in benign environments rather than harsh ones is that social conflict and aggressive interactions increase in drier years and decrease under conditions of high rainfall in superb starlings (Rubenstein 2007*a*). These increased costs from social conflict in harsher years could mask the fitness benefits of group living in superb starling males, but not in females. The sexes could respond differently to social conflict, where females may be more likely to resolve conflicts using threats and males using aggression, as observed in other cooperatively breeding species (Cant and Young 2013; Nelson-Flower et al. 2018). In support of this idea in superb starlings, males tend to be dominant to females at feeding platforms (Rubenstein 2006), and males have higher testosterone than females outside of the offspring provisioning period (Pikus et al. 2018). Identifying the mechanisms that shape social conflict and reproductive skew—social or reproductive incentives, incomplete control, or self-inhibition (Reeve et al. 1993; Johnstone and Cant 1999; Hamilton 2004)—in group-living species will be necessary to reconcile any sex-specific differences in the fitness consequences of group living.

The potential mechanisms underlying the patterns of female and male survivorship with social group size can be inferred from both this study and previous work in this system. In general, group living may confer three primary types of fitness benefits: improved access to foraging, improved health or condition, or reduced predation risk (Krause and Ruxton 2002). The first potential benefit of group living (improved access to foraging) is unlikely to be the mechanism explaining the relationship between survival and group size in superb starlings because we found that environmental conditions that shape the availability of insects—including rainfall and territory grass cover—were not correlated with survival in either males or females. In other words, periods of low insect availability did not result in reduced survivorship for superb starlings. Similarly, larger superb starling groups do not have improved access to food since (i) individuals frequently forage beyond territory boundaries, (ii) group size is unrelated to territory quality, and (iii) territorial fights or takeovers have never occurred in this population (Rubenstein 2011). This is in contrast to some other cooperatively breeding species where larger groups have access to more food or improved foraging efficiency (Wright et al. 2001; Sichilima et al. 2008). Similarly, the second potential benefit of group living (improved health or condition) is also unlikely to explain the positive relationship between social group size and survivorship in superb starlings. Instead, previous theoretical and empirical work in this system has demonstrated that allostatic load (i.e., corticosterone hormone) is elevated for individuals in the largest social groups (Rubenstein and Shen 2009). This suggests that life in the largest social groups may actually represent a social stressor, from both expending and receiving aggression over within-group social conflict. Similarly, group members in cliff swallows and yellow baboons (*Papio cynocephalus*) have increased glucocorticoid hormones as colony size increases (Raouf et al. 2006; Markham et al. 2015). In contrast, larger social group sizes are linked to improved physiological indexes of condition in some species, including reduced oxidative stress in alpine marmots (*Marmota marmota*; Lardy et al. 2016), reduced water loss in banded geckos (*Coleonyx variegatus*; Lancaster et al. 2006), and reduced costs of thermoregulation in Mashona mole rats (*Fukomys darlingi*; Wiedenová et al. 2018) and sociable weavers (*Philetairus socius*; Paquet et al. 2016). The third potential benefit of group living (reduced predation risk) is the most likely explanation for why individual superb starlings in larger social groups have improved survivorship, though we did not measure predation risk directly. Indeed, the number of individuals responding to a predator model was greater in large relative to small superb starling social groups (Rubenstein 2006). More than one-third of individuals responding to the predator models—including a nest predator only and a nest and adult predator—were neither breeders nor alloparents guarding or provisioning nestlings (Rubenstein 2006), demonstrating that all group members, regardless of their breeding role, play an important part in mobbing predators (Rubenstein 2016). Nonbreeding individuals also refrained from mobbing predator models until a critical mass of five or six individuals was present, suggesting that larger social groups might increase the likelihood that this threshold is met or that it is met more rapidly (Rubenstein 2006). This explanation for our finding that group size is positively related to adult survivorship would be consistent with research from other cooperative breeders that live in large social groups and benefit from reduced predation risk, including meerkats (Clutton-Brock et al. 1999), chestnut-crowned babblers (Gullett et al. 2012), and cichlids (*Neolamprologus pulcher*; Jungwirth et al. 2015). Together, results from correlative observations, predator model experiments, and physiological studies in this system most strongly support the possibility that social group size leads to more efficient predator mobbing, the most likely mechanism through which adult superb starlings in larger social groups benefit from improved survivorship.

Although our results suggest that superb starlings gain a survival benefit of living in larger groups, it remains unclear what factors limit group size or maintain small groups in nature. One possibility is that small groups are in fact demographic sinks (Bateman et al. 2013)—where individuals have lower fitness—that accept immigrants more readily and provide more opportunities for independent breeding so that they do not collapse. Indeed, small social groups of pied babblers are more likely to accept immigrants than large ones (Ridley 2016). A second possibility is that while larger groups increase adult survival, smaller groups may increase other components of fitness (including inclusive fitness) or recruitment, as seen in Namibian social spiders (*Stegodyphus dumicola*; Bilde et al. 2007). Another factor that may cause small groups to persist despite the survival benefit of living in larger groups includes the low recruitment rate observed in superb starlings (Rubenstein 2016). The majority of reproductive attempts fail, which may lead to a limited pool of natal recruits. Finally, another possibility is that social conflict also increases as groups get larger, as has been shown in many cooperative breeders (Bilde et al. 2007; Kutsukake and Clutton-Brock 2008; Dantzer et al. 2017; Peña and Nöldeke 2018), including superb starlings (Rubenstein and Shen 2009; Pikus et al. 2018; but see Shen et al. 2014). While directional selection on group size in superb starlings could have favored the evolution of larger social groups that accept both male and female immigrant members, increasing social conflict (as measured by endocrine allostatic load; Rubenstein and Shen 2009) in larger groups may have contributed to the evolution of plural breeding in this species and put a limit on group size.

In conclusion, we found that adults gained a survival advantage of group living in cooperatively breeding superb starlings in addition to and independent of the reproductive benefits that breeders gain from having alloparents at the nest (Guindre-Parker and Rubenstein 2018*a*). Social group size is correlated with increased adult survival in superb starlings of both sexes, although environmental conditions influence this relationship in a sex-specific manner. That is, group size was unrelated to male survival in years of low prebreeding rainfall but increased survival under wet conditions, whereas group size was associated with increased female survival similarly across all environmental conditions. Fluctuating environmental conditions therefore played a limited role in changing the fitness consequences of group living in superb starlings. Future studies on the evolution of group living in cooperatively breeding species as well as other social mating or breeding systems will therefore need to examine how fluctuating environmental conditions shape the multiple potential benefits and/or costs of sociality.

Acknowledgments

We are grateful to W. Watetu, G. Manyaas, and J. Mosiany for their assistance in the field, as well as all other volunteers, students, and field assistants who have helped collect data since 2001. We thank G. Parker for assistance with statistical analyses, as well as three anonymous reviewers for their helpful feedback. We acknowledge Kenya's National Commission for Science, Technology, and Innovation; Kenya's National Environmental Management Authority; the Kenya Wildlife Service; and the Mpala Research Centre for enabling this work. We also thank our sources of funding: S.G.-P. was supported by the US National Science Foundation (IOS-1501257), the Natural Science and Engineering Research Council of Canada, the Animal Behaviour Society, and Columbia University. D.R.R. was supported by the US National Science Foundation (IOS-1121435, IOS-1257530, IOS-1439985).

Literature Cited

Alberts, S. C. 2018. Social influences on survival and reproduction: insights from a long-term study of wild baboons. Journal of Animal Ecology 88:1–20.

Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics 5:325–383.

Arnold, K. E., I. P. F. Owens, and A. W. Goldizen. 2005. Division of labour within cooperatively breeding groups. Behavior 142:1577–1590.

Baglione, V., J. M. Marcos, D. Canestrari, and J. Ekman. 2002. Direct fitness benefits of group living in a complex cooperative society of carrion crows, *Corvus corone corone*. Animal Behaviour 64:887–893.

Bateman, A. W., A. Ozgul, J. F. Nielsen, T. Coulson, and T. H. Clutton-Brock. 2013. Social structure mediates environmental effects on group size regulation in an obligate cooperative breeder, *Suricata suricatta*. Ecology 94:1–10.

Bilde, T., K. S. Coates, K. Birkhofer, T. Bird, A. A. Maklakov, Y. Lubin, and L. Avilés. 2007. Survival benefits select for group living in a social spider despite reproductive costs. Journal of Evolutionary Biology 20:2412–2426.

Brent, L. J. N., A. Ruiz-Lambides, and M. L. Platt. 2017. Family network size and survival across the lifespan of female macaques. Proceedings of the Royal Society B 284:20170515.

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

Brown, C. R., M. B. Brown, E. A. Roche, V. A. O'Brien, and C. E. Page. 2016. Fluctuating survival selection explains variation in avian group size. Proceedings of the National Academy of Sciences of the USA 113:201600218.

Brown, C. R., R. Covas, M. D. Anderson, and M. B. Brown. 2003. Multistate estimates of survival and movement in relation to colony size in the sociable weaver. Behavioral Ecology 14:463–471.

Byrom, A. E., M. E. Craft, S. M. Durant, A. J. K. Nkwabi, K. Metzger, K. Hampson, S. A. R. Mduma, et al. 2014. Episodic outbreaks of small mammals influence predator community dynamics in an east African savanna ecosystem. Oikos 123:1014–1024.

Cant, M. A., and A. J. Young. 2013. Resolving social conflict among females without overt aggression. Philosophical Transactions of the Royal Society B 368:20130076.

Caylor, K., J. Gitonga, and D. Martins. 2017. Mpala Research Center meteorological and hydrological dataset. Mpala Research Centre, Laikipia, Kenya.

Clutton-Brock, T. H., D. Gaynor, G. Mcilrath, A. Maccoll, R. Kansky, P. Chadwick, M. Manser, et al. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. Journal of Animal Ecology 68:672–683.

Cornwallis, C. K., C. A. Botero, D. R. Rubenstein, P. A. Downing, S. A. West, and A. S. Griffin. 2017. Cooperation facilitates the colonization of harsh environments. Nature Ecology and Evolution 1:1–26.

Dantzer, B., N. C. Bennett, and T. H. Clutton-Brock. 2017. Social conflict and costs of cooperation in meerkats are reflected in measures of stress hormones. Behavioral Ecology 28:1131–1141.

du Plessis, M. A., W. W. Weathers, and W. D. Koenig. 1994. Energetic benefits of communal roosting by acorn woodpeckers during the nonbreeding season. Condor 96:631–637.

du Plessis, M. A., and J. B. Williams. 1994. Communal cavity roosting in green woodhoopoes: consequences for energy expenditure and the seasonal pattern of mortality. Auk 111:292–299.

Farabaugh, S. M., E. D. Brown, and J. M. Hughes. 1992. Cooperative territorial defense in the Australian magpie, *Gymnorhina tibicen* (Passeriformes, Cracticidae), a group-living songbird. Ethology 92:283–292.

Feare, C., and A. Craig. 1998. Starlings and mynas. Helm, London.

Fox, G. A., B. E. Kendall, J. W. Fitzpatrick, and G. E. Woolfenden. 2006. Consequences of heterogeneity in survival probability in a population of Florida scrub-jays. Journal of Animal Ecology 75:921–927.

Fox, J., and G. Monette. 1992. Generalized collinearity diagnostics. Journal of the American Statistical Association 87:178–183.

Fox, J., and S. Weisberg. 2002. Cox proportional-hazards regression for survival data: an appendix to an R and S-PLUS companion to applied regression. Sage, Thousand Oaks, CA.

Gager, Y., O. Gimenez, M. T. O. Mara, and D. K. N. Dechmann. 2016. Group size, survival and surprisingly short lifespan in socially foraging bats. BMC Ecology 16:1–12.

Griesser, M., S. M. Drobniak, S. Nakagawa, and C. A. Botero. 2017*a*. Family living sets the stage for cooperative breeding and ecological resilience in birds. PLoS Biology 15:1–17.

Griesser, M., E. Mourocq, J. Barnaby, K. M. Bowgen, S. Eggers, K. Fletcher, R. Kozma, et al. 2017*b*. Experience buffers extrinsic mortality in a group-living bird species. Oikos 126:1258–1268.

Guindre-Parker, S., and D. R. Rubenstein. 2018*a*. Multiple benefits of alloparental care in a fluctuating environment. Royal Society Open Science 5:172406.

———. 2018*b*. The oxidative costs of parental care in cooperative and pair-breeding African starlings. Oecologia 188:53–63.

———. 2019. Data from: Survival benefits of group living in a fluctuating environment. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.stqjq2c05.

Hamilton, I. M. 2004. A commitment model of reproductive inhibition in cooperatively breeding groups. Behavioral Ecology 15:585–591.

Jetz, W., and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21:72–78.

Johnstone, R. A., and M. A. Cant. 1999. Reproductive skew and the threat of eviction: a new perspective. Proceedings of the Royal Society B 266:275–279.

Jungwirth, A., D. Josi, J. Walker, and M. Taborsky. 2015. Benefits of coloniality: communal defence saves anti-predator effort in cooperative breeders. Functional Ecology 29:1218–1224.

Kocher, S. D., L. Pellissier, C. Veller, J. Purcell, M. A. Nowak, M. Chapuisat, and N. E. Pierce. 2014. Transitions in social complexity along elevational gradients reveal a combined impact of season length and development time on social evolution. Proceedings of the Royal Society B 281:20140627.

Kokko, H., R. A. Johnstone, and T. H. Clutton-Brock. 2001. The evolution of cooperative breeding through group augmentation. Proceedings of the Royal Society B 268:187–196.

Krause, J., and G. D. Ruxton. 2002. Living in groups. Oxford University Press, Oxford.

Kutsukake, N., and T. H. Clutton-Brock. 2008. The number of subordinates moderates intrasexual competition among males in cooperatively breeding meerkats. Proceedings of the Royal Society B 275:209–216.

Lancaster, J., P. Wilson, and R. Espinoza. 2006. Physiological benefits as precursors of sociality: why banded geckos band. Animal Behaviour 72:199–207.

Lardy, S., B. Rey, K. Salin, Y. Voituron, and A. Cohas. 2016. Beneficial effects of group size on oxidative balance in a wild cooperative breeder. Behavioral Ecology 27:1820–1825.

Lukas, D., and T. Clutton-Brock. 2017. Climate and the distribution of cooperative breeding in mammals. Royal Society Open Science 4:160897.

Markham, A. C., L. R. Gesquiere, S. C. Alberts, and J. Altmann. 2015. Optimal group size in a highly social mammal. Proceedings of the National Academy of Sciences of the USA 112:14882–14887.

McCauley, D. J., F. Keesing, T. P. Young, B. F. Allan, and R. M. Pringle. 2006. Indirect effects of large herbivores on snakes in an African savanna. Ecology 87:2657–2663.

Mosser, A., and C. Packer. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Animal Behaviour 78:359–370.

Nelson-Flower, M. J., T. P. Flower, and A. R. Ridley. 2018. Sex differences in the drivers of reproductive skew in a cooperative breeder. Molecular Ecology 27:2435–2446.

Paquet, M., C. Doutrelant, M. Loubon, F. Theron, M. Rat, and R. Covas. 2016. Communal roosting, thermoregulatory benefits and breeding group size predictability in cooperatively breeding sociable weavers. Journal of Avian Biology 47:749–755.

Peña, J., and G. Nöldeke. 2018. Group size effects in social evolution. Journal of Theoretical Biology 457:211–220.

Pikus, A. E., S. Guindre-Parker, and D. R. Rubenstein. 2018. Testosterone, social status and parental care in a cooperatively breeding bird. Hormones and Behavior 97:85–93.

Pollack, L., and D. R. Rubenstein. 2015. The fitness consequences of kin-biased dispersal in a cooperatively breeding bird. Biology Letters 11:20150336.

Raouf, S. A., L. C. Smith, M. B. Brown, J. C. Wingfield, and C. R. Brown. 2006. Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows. Animal Behaviour 71:39–48.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Version 3.2.4. http://www.R-project.org.

Reeve, H. K., S. T. Emlen, and L. Keller. 1993. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? Behavioral Ecology 9:267–278.

Ridley, A. R. 2016. Southern pied babblers: the dynamics of conflict and cooperation in a group-living society. Pages 115–132 *in* W. D. Koenig and J. L. Dickinson, eds. Cooperative breeding in vertebrates: studies of ecology, evolution and behavior. Cambridge University Press, Cambridge.

Ridley, A. R., and N. J. Raihani. 2007. Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. Behavioral Ecology 18:324–330.

Rubenstein, D. R. 2006. The evolution of the social and mating system of the plural cooperatively breeding superb starling, *Lamprotornis superbus*. PhD diss. Cornell University, Ithaca, NY.

———. 2007*a*. Stress hormones and sociality: integrating social and environmental stressors. Proceedings of the Royal Society B 274:967–975.

———. 2007*b*. Temporal but not spatial environmental variation drives adaptive offspring sex allocation in a plural cooperative breeder. American Naturalist 170:155–165.

———. 2007*c*. Territory quality drives intraspecific patterns of extrapair paternity. Behavioral Ecology 18:1058–1064.

———. 2011. Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. Proceedings of the National Academy of Sciences of the USA 108:10816–10822.

———. 2016. Superb starlings: cooperation and conflict in an unpredictable environment. Pages 181–196 *in* W. D. Koenig and J. L. Dickinson, eds. Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior. Cambridge University Press, Cambridge.

Rubenstein, D. R., and I. J. Lovette. 2007. Temporal environmental variability drives the evolution of cooperative breeding in birds. Current Biology 17:1414–1419.

Rubenstein, D. R., and S.-F. Shen. 2009. Reproductive conflict and the costs of social status in cooperatively breeding vertebrates. American Naturalist 173:650–661.

Rubenstein, D. R., H. Skolnik, A. Berrio, F. A. Champagne, S. Phelps, and J. Solomon. 2015. Sex-specific fitness effects of unpredictable early life conditions are associated with DNA methylation in the avian glucocorticoid receptor. Molecular Ecology 25:1714–1728.

Saino, N., M. Caprioli, M. Romano, G. Boncoraglio, D. Rubolini, R. Ambrosini, A. Bonisoli-Alquati, et al. 2011. Antioxidant defenses predict long-term survival in a passerine bird. PLoS ONE 6:e19593.

Shen, S.-F., E. Akcay, and D. R. Rubenstein. 2014. Group size and social conflict in complex societies. American Naturalist 183:301–310.

Shen, S.-F., S. T. Emlen, W. D. Koenig, and D. R. Rubenstein. 2017. The ecology of cooperative breeding behaviour. Ecology Letters 20:708–720.

Sichilima, A. M., N. C. Bennett, C. G. Faulkes, and S. C. Le Comber. 2008. Evolution of African mole-rat sociality: burrow architecture, rainfall and foraging in colonies of the cooperatively breeding *Fukomys mechowii*. Journal of Zoology 10:276–282.

Sorato, E., P. R. Gullett, S. C. Grif, and A. F. Russell. 2012. Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. Animal Behaviour 84:823–834.

Sweijd, N., and A. J. F. K. Craig. 1991. Histological basis of age-related changes in iris color in the African pied starling (*Spreo bicolor*). Auk 108:53–59.

Titcomb, G., B. F. Allan, T. Ainsworth, L. Henson, T. Hedlund, R. M. Pringle, T. M. Palmer, et al. 2017. Interacting effects of wildlife loss and climate on ticks and tick-borne disease. Proceedings of the Royal Society B 284:20170475.

Wang, M. 2014. Generalized estimating equations in longitudinal data analysis: a review and recent developments. Advances in Statistics 2014:303728.

Weinstein, S., G. Titcomb, B. Agwanda, C. Riginos, and H. Young. 2017. Parasite responses to large mammal loss in an African savanna. Ecology 98:1839–1848.

Wiedenová, P., R. Šumbera, and J. Okrouhlík. 2018. Social thermoregulation and socio-physiological effect in the subterranean Mashona mole-rat (*Fukomys darlingi*). Journal of Thermal Biology 78:367–373.

Wolfe, M. L., E. M. Gese, P. Terletzky, D. C. Stoner, and L. M. Aubry. 2016. Evaluation of harvest indices for monitoring cougar survival and abundance. Journal of Wildlife Management 80:27–36.

Wright, J., E. Berg, S. R. De Kort, V. Khazin, and A. A. Maklakov. 2001. Safe selfish sentinels in a cooperative bird. Journal of Animal Ecology 70:1070–1079.

References Cited Only in the Online Enhancements

Bond, C. J. 1919. On certain factors concerned in the production of eye colour in birds. Journal of Genetics 9:69–81. doi:10.1007/BF02983518.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: application of the Andersen-Gill model to Yellowstone grizzly bears. Journal of Wildlife Management 68:966–978.

Lovette, I. J., and D. R. Rubenstein. 2007. A comprehensive molecular phylogeny of the starlings (Aves: Sturnidae) and mockingbirds (Aves: Mimidae): congruent mtDNA and nuclear trees for a cosmopolitan avian radiation. Molecular Phylogenetics and Evolution 44:1031–1056. doi:10.1016/j.ympev.2007.03.017.

Nogueira, D. M., and M. A. S. Alves. 2008. Iris colour as an indicator of age feature in female Brazilian tanagers (Passeriformes: Emberizidae) confirmed by a molecular sexing technique. Revista de Biología Tropical 56:1629–1633.

Scholten, C. J. 1999. Iris colour of Humboldt penguins *Spheniscus humboldti*. Marine Ornithology 27:191–194.

Associate Editor: Timothy A. Linksvayer
Editor: Daniel I. Bolnick