

Current Biology

Climate fluctuations influence variation in group size in a cooperative bird

Highlights

- Greater anis nest in communal groups containing two or three pairs
- Individual fitness benefits of group size are partly dependent on climate
- The strength and direction of selection on group size were inconsistent across years
- Fluctuating selection may therefore contribute to observed variation in group size

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In brief

A long-term study of a cooperatively breeding bird, the greater ani, reveals that small group sizes are favored in dry years, whereas larger groups are favored in wet years. Riehl and Smart find that variation in climate altered the costs and benefits of sociality, suggesting that fluctuating selection contributes to variation in group size.

Report

Climate fluctuations influence variation in group size in a cooperative bird

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<https://doi.org/10.1016/j.cub.2022.07.057>

SUMMARY

Variation in group size is ubiquitous in social animals, but explaining the range of group sizes seen in nature remains challenging.^{1–3} Group-living species occur most frequently in climatically unpredictable environments, such that the costs and benefits of sociality may change from year to year.^{4–6} It is, therefore, possible that variation in climate may help to maintain a range of group sizes, but this hypothesis is rarely tested empirically.^{7,8} Here, we examine selection on breeding group size in the greater ani (*Crotophaga major*), a tropical bird that nests in cooperative groups containing multiple co-breeders and non-breeding helpers.⁹ We found that larger groups experience lower nest predation (due to cooperative nest defense) but suffer higher nestling starvation (due to intra-clutch competition). Long-term data revealed that the relative magnitude of these costs and benefits depends on climate, with frequent changes across years in the strength and direction of selection on group size. In wet years, individual reproductive success was higher in large groups than in small groups, whereas the opposite was true in dry years. This was partly a consequence of competition among nestlings in large clutches, which suffered significantly higher mortality in dry years than in wet years. Averaged over the 13-year study period, annual reproductive success was approximately equal for females in small and large groups. These results suggest that temporal changes in the direction of selection may help explain the persistence of a range of group sizes and that a full understanding of the selective pressures shaping sociality requires long-term fitness data.

RESULTS

Groups of social animals vary widely in size, and this variation affects many aspects of individual fitness. Although theory predicts that individuals should achieve their highest fitness in groups of intermediate sizes^{10,11} (and this is supported by the majority of empirical studies^{12–16}), most populations exhibit a range of group sizes, including some that are apparently disadvantageous relative to others (e.g., Shields and Crook,¹⁷ Packer et al.,¹⁸ Crofoot and Gilby,¹⁹ and Guindre-Parker and Rubenstein²⁰). Explaining the distributions of group sizes observed in nature, therefore, remains a central challenge in social evolution.^{1–3} The best-supported hypothesis to explain variation in group size posits that per capita fitness is indeed highest in intermediate-sized groups but that observed group sizes should often deviate from the optimum due to constraints or conflicts of interest between group members.^{21–23} However, an alternative hypothesis is that no single group size is ideal; rather, the fitness consequences of group size might vary with environmental conditions, such that fluctuations in resources maintain a range of group sizes.^{7,24} This hypothesis predicts that the relationship between group size and individual fitness should depend at least partly on immediate environmental conditions, but that over longer time scales, individuals should experience roughly equal fitness returns across a range of group sizes. In

this paper, we test this hypothesis in a cooperatively breeding tropical bird, the greater ani (*Crotophaga major*). We used a long-term dataset to examine how climate affects the relationship between individual reproductive output and group size.

Greater anis are highly social birds that breed in communal groups containing two, three, or (rarely) four breeding pairs and up to two non-breeding helpers; total group size ranges from four to ten individuals.⁹ Each group constructs a single nest, and all group members contribute parental care indiscriminately to the mixed clutch of young.²⁵ Greater anis are long-lived (15–20 years), and groups are stable over time, with most nesting groups persisting for several years with little turnover in membership.²⁶ On average, adult breeders move between nesting groups once every 4.5 years; changes in group membership are more frequent following years in which groups fail to breed, particularly dry El Niño years.^{26,27} The number of non-breeding helpers in a given group is not consistent across years, since helpers typically remain for only 1 year before dispersing; however, the number of breeding pairs in the group is highly consistent across years, despite changes in group membership.²⁶

At our field site in Panama, El Niño episodes are associated with above-average temperatures, low annual rainfall, and long dry seasons, whereas La Niña years exhibit the opposite conditions.²⁸ Our study period (2007–2019) encompassed two El Niño episodes, two La Niña episodes, and 7 years of weak to

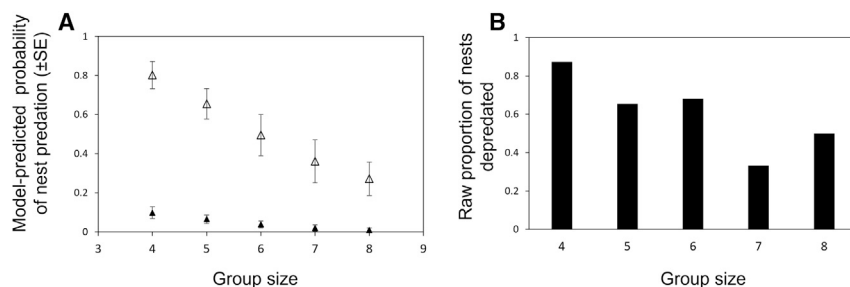


Figure 1. Nest predation as a function of communal group size in greater anis

(A) Model-predicted probabilities of nest predation as a function of group size, separated by nest-site type to illustrate the interaction between group size and nest-site type (shoreline nests, open triangles; emergent nests, solid triangles).

(B) Raw data showing the proportion of nests depredated as a function of group size, for shoreline nests only.

See also [Data S1C](#) and [S1D](#).

moderate ENSO conditions as defined by NOAA.²⁹ We used a multivariate modeling approach to ask how several candidate predictors (including climate, group size, and interactions between climate and group size) affected nest predation risk, nestling survival, and overall individual reproductive output, and we used linear regression of group size on individual reproductive output to estimate directional selection coefficients for two aspects of group size (the number of breeding pairs and the number of non-breeding helpers) for each year of the study.^{7,30}

We found that the distribution of group sizes was stable across years and did not vary with climate, despite variation in annual precipitation ([Figure S1](#)). Breeding group size averaged 4.6 individuals over the 13-year study period (\pm SE = 0.04; range = 4–8, n = 516), with 81.6% of groups comprising two breeding pairs (n = 421 group-years) and 18.2% comprising three breeding pairs (n = 94 group-years, details of group composition in [Data S1A](#)). One group (0.19%) contained four breeding females and was excluded from analyses. Climate did not have a detectable effect on the distribution of group sizes: the Southern Oscillation Index (SOI) was not a significant predictor of total group size (z = 0.38, p = 0.71), the number of breeding pairs in a group (z = 0.35, p = 0.73), or helper presence (z = –1.23, p = 0.22; [Data S1B](#)).

Nest predation risk decreased sharply with group size, and this effect was also independent of climate ([Data S1C](#)). The risk of nest predation was highest for the smallest groups (those with four group members, model-predicted nest predation rate = 68.6% \pm SE = 4.2%) and decreased by approximately 15% with each additional group member (effect of group size on nest predation probability: β = –0.98, z = –4.33, p < 0.0001; model-predicted values, [Figure 1A](#); raw data, [Figure 1B](#)). These results were qualitatively similar when group size was coded as two separate predictors (the number of breeders and the number of helpers) or one (the total number of individuals), indicating that the presence of a helper in the group has approximately the same effect on nest predation as the presence of a breeder ([Data S1D](#)). The effect of group size on predation risk was much greater on nests built in risky shoreline sites (which are vulnerable to terrestrial predators; n = 408 of 521 nests, 78%) than on nests built in emergent vegetation (which are surrounded by water and largely immune to terrestrial predators; n = 113 of 521 nests, 22%). This resulted in a significant interaction between group size and nest-site type ([Figure 1A](#)).

Although the risk of nest predation decreased with group size, the costs of intra-group competition increased as a function of the number of breeding pairs. This was a consequence of increased communal brood size and decreased nestling survival in groups with more breeding females. First, although the total

number of eggs in the communal clutch was higher for three-pair groups than for two-pair groups (three-pair groups: total clutch size = 9.07 \pm 0.43 eggs; two-pair groups: total clutch size = 7.45 \pm 0.10 eggs; z = 5.05, p < 0.0001; [Data S1E](#)), the number of eggs contributed by each female was lower in three-pair groups (three-pair group: individual clutch size = 3.02 \pm 0.14 eggs; two-pair group: individual clutch size = 3.73 \pm 0.05 eggs; z = –5.14, p < 0.0001; [Figure 2A](#); [Data S1F](#)). Climate had no detectable effect on either communal or individual clutch size (p = 0.73 and p = 0.66, respectively). Second, excluding depredated nestlings, nestling survival was significantly lower for nestlings in three-pair clutches than for nestlings in two-pair clutches (83% \pm 3% in three-pair groups, 92% \pm 1% in two-pair groups). This was due to increased starvation in large broods, particularly in dry years: survival rates for nestlings in two-pair groups were unaffected by climate (β = –0.23, z = –0.23, p = 0.82; [Figure 2B](#); [Data S1G](#)), but survival rates for nestlings in three-pair groups increased significantly with SOI values (β = 2.46, z = 2.88, p = 0.004; [Figure 2B](#); [Data S1G](#)).

Over the 13-year study period, individual reproductive output was approximately equal in groups with two and three breeding pairs (two-pair: mean = 0.60 \pm SE = 0.06 offspring fledged per attempt, n = 442 female-years; three-pair: mean = 0.71 \pm SE = 0.09 offspring fledged per attempt; n = 183 female-years; p = 0.87; [Figure 3A](#)). However, these averages masked a significant interaction between climate and group size. Individual reproductive output in two-pair groups was not significantly affected by climate: the number of offspring fledged per female remained constant despite annual variation in the SOI (β = –0.02, z = –0.17, p = 0.86; [Data S1H](#)). By contrast, reproductive success in three-pair groups increased significantly with SOI (β = 0.49, z = 3.70, p < 0.001; [Data S1H](#)). Individual reproductive output in three-pair groups was more than 4 times higher in the two wettest years of the study period (mean = 1.42 \pm 0.18 offspring fledged) than in the two driest years (mean = 0.30 \pm 0.12 offspring fledged). As a result, there was a significant interaction between group size and climate: compared with two-pair groups, females in three-pair groups had relatively lower reproductive output in dry years and relatively higher reproductive output in wet years ([Figure 3B](#); [Data S1I](#)).

Analysis of individual reproductive success for 11 years revealed that the strength and direction of selection on the number of breeders in groups changed frequently ([Figure 4A](#)). For 3 years (2008, 2012, and 2013), the number of breeding pairs was under positive selection with respect to reproductive output: the directional selection coefficients were positive and 95% confidence intervals did not overlap zero, indicating that females in three-pair

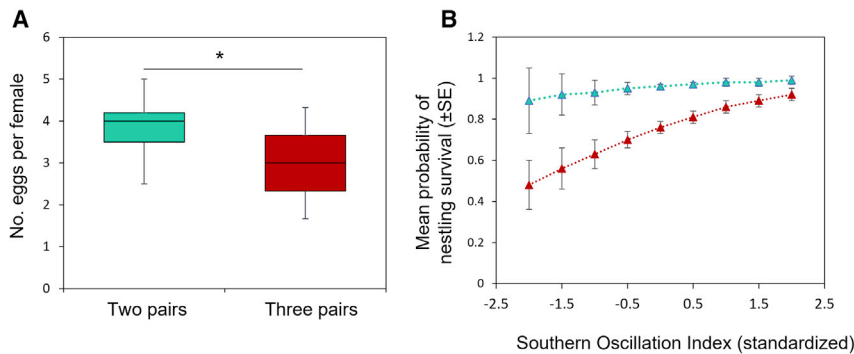


Figure 2. Costs of competition for breeding adults in greater ani groups

(A) Per capita clutch size (number of eggs contributed to the incubated clutch). Boxes represent medians and interquartile range, whiskers represent observed minima and maxima, and the asterisk indicates statistical significance at $p < 0.001$.

(B) Model-predicted values for survival probability of nestlings in communal broods as a function of the Southern Oscillation Index, separated by group size (controlling for helper presence and nest-site type). Groups containing two breeding pairs are shown in teal and three breeding pairs are shown in red. See also [Data S1F](#) and [S1G](#).

groups produced significantly more offspring than those in two-pair groups. These years represented 3 of the wettest 4 years in the dataset. For the remaining 8 years, coefficient confidence intervals overlapped zero (indicating no detectable selection on group size). However, the sign of the coefficients was negative in 5 years, including the 3 driest years in the dataset (2015, 2016, and 2019; all were El Niño years). Therefore, although we did not detect statistically significant selection for smaller groups in dry years, the signs of annual selection gradients were generally positive in wet years (with high SOI values) and negative in dry years (with low SOI values), consistent with the interaction between climate and group size described above. By contrast, the effect of helpers on reproductive output was more consistently positive, regardless of climate ([Figure 4B](#)). Selection coefficients on helper numbers were positive in 10 of 11 years (all years except 2019) and were statistically significant in 6 of those years, indicating positive selection on helper presence.

DISCUSSION

Previous studies have shown that temporal changes in the direction of selection can maintain variability in several morphological,^{31–33} behavioral,^{24,34–36} and life history³⁷ traits, but this hypothesis has rarely been invoked to explain variation in group-level properties such as the size of the social group.^{7,38} In this study, we found that the changing costs of intra-group competition under differing climatic conditions resulted in inconsistent individual fitness payoffs to membership in different-sized groups in the greater ani. Under cool and wet La Niña conditions, females in three-pair groups had considerably higher individual reproductive output (relative to females in two-pair groups), but the opposite

was true in hot and dry years. Across the 13-year study period, average reproductive output was approximately equal in groups with two and three breeding pairs, suggesting little difference in lifetime fitness returns between the two strategies. These results support the hypothesis that variation in group size (or, more accurately, the individual decisions that lead to group size) may be partly maintained by directional selection whose sign varies with environmental conditions that change over time.

The range of group sizes observed in this population of greater ani is narrow, limited to just two or three breeding pairs and non-breeding helpers. This distribution is undoubtedly shaped by stabilizing selection since pairs have never been observed to breed alone (apparently due to the high risk of predation) and groups with more than three laying females are extremely rare (apparently due to the high costs of competition among reproductive females⁹). This distribution of group sizes is nevertheless remarkable, precisely because of the strong constraints limiting group size in communal breeders. Communal laying in birds is typically interpreted as a best-of-a-bad-job strategy since hatching and fledging success (and individual reproductive output) usually decrease with clutch size.^{39,40} By contrast, helpers typically impose much lower costs than co-breeders do (for example, by consuming resources on the territory rather than by contributing to clutch size) and often have a net positive or neutral effect on the reproductive output of breeders (reviewed in [Koenig and Dickinson⁴¹](#)). Our results in greater ani are consistent with this pattern: although both breeders and helpers reduced the risk of nest predation, the presence of additional breeders was costly in resource-poor years. Although there was little difference in nestling survival between large and small clutches in cooler, wetter years, nestlings in large clutches

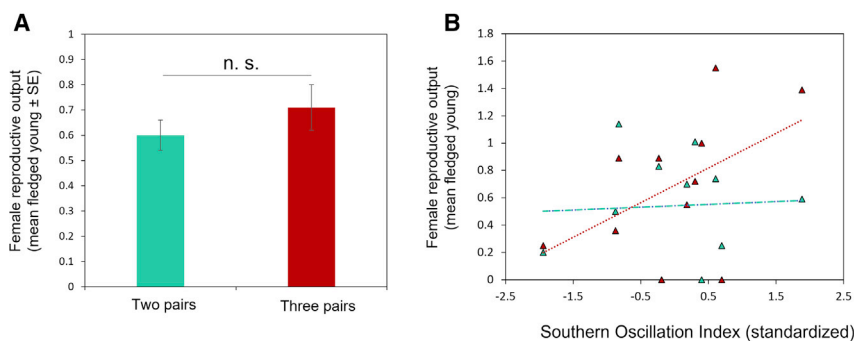


Figure 3. Individual reproductive output for females in greater ani groups

(A) Mean (\pm SE) number of nestlings fledged per female across the 13-year study period.

(B) Mean number of nestlings fledged per female as a function of the Southern Oscillation Index, separated by group size. Both panels show raw data (not corrected for helper presence or nest-site type). Groups containing two breeding pairs are shown in teal, and three breeding pairs are shown in red. See also [Data S1H](#) and [S1I](#).

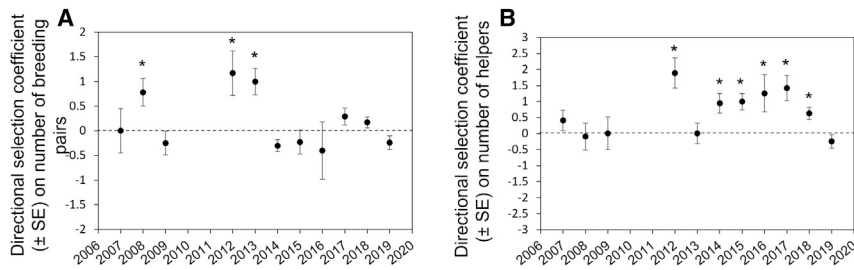


Figure 4. Annual standardized directional (linear) selection coefficients (± 1 SE) on group size

(A) Selection coefficients on the number of breeding pairs.

(B) Selection coefficients on the number of helpers. Years in which 95% confidence intervals did not overlap 0 are indicated with an asterisk above the value, and all are with respect to individual female reproductive output. See also [Figure S1](#).

(produced by three laying females) suffered significantly higher mortality in hot and dry years. Nestlings in small clutches (produced by two laying females) experienced only minor effects of climate.

At the proximate level, the primary benefit of social nesting in greater anis (decreased risk of nest predation) appears to be largely independent of climate, whereas the primary cost (increased competition among nestlings) is not. Groups with more breeding pairs produce larger communal clutches, which leads to greater competition among nestlings and increased mortality from causes unrelated to predation, primarily nestling starvation.⁴² Intra-clutch competition in large clutches may be exacerbated by prey scarcity in dry years for which adult caregivers may be unable to fully compensate. Insect abundance in tropical forests is seasonally correlated with rainfall and soil moisture^{43–45} and is hypothesized to correlate with rainfall and temperature on annual and supra-annual timescales (e.g., Lister and Garcia⁴⁶ and Lamarre⁴⁷). Our results, therefore, contribute to a growing body of evidence that food resources for insectivorous birds can be limited under El Niño conditions^{48–50} (though see Nishikawa et al.⁵¹).

Although communal nesting behavior (and other forms of sociality) must have a heritable component to evolve by natural selection, group size itself is not a genetic trait, and individuals in social groups typically show some degree of plasticity in the size of the social group they choose to join.^{52,53} In theory, if the direction of selection on group size were consistent rather than fluctuating—for example, if a large group size always resulted in the highest fitness payoffs to group members—this would favor reduced flexibility in individual preference and a narrower range of group sizes observed in the wild (selection would favor individuals who join large groups, and most groups observed should be large). However, if the fitness benefits to individuals of joining groups of different sizes vary across years (i.e., if selection on group size is not consistently in the same direction, as in this study), this could favor either increased individual flexibility in group size preference or a stable but broader distribution of group sizes. We found the latter to be true of our study population: although individual anis occasionally switched between groups of different sizes across years, group composition remained fairly constant, and the distribution of group sizes was independent of climate. This may be because breeding groups form several months before reproducing (so it may be difficult to predict breeding conditions at the time that changes in group membership occur) or because stability in group membership is associated with several fitness benefits, including increased reproductive synchrony,²⁶ a higher probability of breeding,²⁷ and longer tenure on territories.⁵⁴ The advantages of social

stability may explain why individuals typically remain in the same group for several years²⁶ and why group sizes do not track yearly changes in weather conditions.

To our knowledge, this is the first study to link climate fluctuations to the maintenance of group size variation in a cooperatively breeding species, although Brown et al.⁷ found similar dynamics in colony-nesting cliff swallows (*Petrochelidon pyrrhonota*). In that study, the relationship between colony size and adult survival varied across years and was partly dependent on climate, with adult survival being higher in large colonies in cooler and wetter years and higher in small colonies in hotter and drier years. Several studies of cooperative breeders have also found that the fitness effects of non-breeding helpers vary with climate, with helpers either having greater positive effects on breeder fitness in conditions of resource scarcity^{55–57} or imposing greater costs due to competition.⁵⁸ Taken together, these studies suggest that the costs and/or benefits of sociality can vary with climatically driven changes in resource abundance, altering the fitness consequences of group size and leading to variation in group size within populations. Given that cooperative breeding is most common in climatically unpredictable environments^{6,59} and that many cooperative species live in highly cohesive and relatively permanent social groups, it is possible that these dynamics play a more important role in maintaining group size variation in social animals than currently recognized.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2022.07.057>.

ACKNOWLEDGMENTS

We thank Meghan J. Strong for assistance with fieldwork, genetic analyses, and database management and Luke Carabbia, Amanda G. Savagian, and Maria G. Smith for field data collection. Funding for long-term data collection was provided to C.R. by the Smithsonian Tropical Research Institute, the Harvard Society of Fellows, the William F. Milton Fund at Harvard University, the Department of Ecology and Evolutionary Biology at Princeton University, the Program in Latin American Studies at Princeton University, the Grand Challenges Program of the High Meadows Environmental Institute at Princeton University, and the National Science Foundation (IOS-1755279 and IOS-184543). Funding to Z.F.S. was provided by the High Meadows Environmental Institute's Environmental Internship Program and the Smith-Newton Scholars Program. We thank Charles R. Brown, B. Rosemary Grant, Peter R. Grant, and Damien R. Farine for their insightful comments on earlier drafts of this manuscript.

AUTHOR CONTRIBUTIONS

Conceptualization, Z.F.S. and C.R.; project leader and study coordination, C.R.; formal analysis, C.R. and Z.F.S.; writing – original draft, C.R.; writing – review & editing, C.R. and Z.F.S.; visualization, C.R.; project administration, C.R.; funding acquisition, C.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: March 25, 2022

Revised: May 25, 2022

Accepted: July 21, 2022

Published: August 22, 2022

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Greater Ani <i>Crotophaga major</i>	Wild	N/A
Deposited data		
Climate fluctuations maintain variation in group size in a cooperative bird	This paper	https://figshare.com/articles/dataset/Riehl_and_Smart_Current_Biology_Data_for_Figshare_xlsx/20334870
Software and algorithms		
Stata 14	StataCorp. 2015. <i>Stata</i> Statistical Software: Release 14 College Station, TX: StataCorp LP.	https://www.stata.com/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for data should be directed to the lead contact, Christina Riehl (criehl@princeton.edu).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Field data have been deposited at [Figshare.com](https://figshare.com) and are publicly available as of the date of publication. Links are listed in the [key resources table](#).
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study site and species

We studied wild greater anis (*Crotophaga major*) in the Barro Colorado Nature Monument, Panama (9.1521° N, 79.8465° W), from 2007-2019.

METHOD DETAILS

Study population

The Barro Colorado Nature Monument in central Panama experiences a distinct dry season from December through May; the rainy season extends from mid-May through November.⁶⁰ Anis breed in the middle of the rainy season (June-Sept) with peak nesting activity in July and August.⁶¹ Nesting groups consist of two (~79% of groups), three (~19%), or, rarely, four (<2%) unrelated breeding pairs, which are socially monogamous and typically genetically monogamous (~90% of nestlings are produced by pairs that share a social pair-bond⁶²). Approximately 20% of breeding groups are assisted by 1-2 unpaired, non-reproductive “helpers,” which may be unrelated immigrants or non-dispersed offspring from a previous brood. Each breeding female contributes approximately equal numbers of eggs to the single communal nest, and all group members (both breeders and helpers) participate in nest defense, provisioning, and other forms of parental care to the mixed clutch.⁹

The most common cause of reproductive failure is predation on eggs and nestlings, primarily by terrestrial predators (snakes, including *Spilotes pullatus* and *Phrynonax [Pseustes] poecilonotus*, and monkeys, *Cebus capucinus*), which account for ~80% of nestling mortality. Nests are built along the shores of lakes and rivers, typically in emergent vegetation or in shoreline vegetation overhanging the water; previous studies have found that nests in emergent vegetation are less likely to be depredated than are shoreline nests, presumably because it is more difficult for terrestrial predators to access them.^{61,63} In this data set, 78% of nests were located on the shoreline (n = 408/521) and the remaining 22% in emergent vegetation (n = 113/521). Intra-group competition accounts for the remaining ~20% of nestling mortality, and can take the form of either infanticide (in which breeding adults kill nestlings that are

unlikely to be theirs, presumably to benefit their own offspring) or starvation (resulting from direct competition among nestlings for food⁴²).

We located nests at the beginning of each breeding season (prior to egg-laying in most cases) and checked each nest every 1-3 days throughout the nesting period. The number of group members present and the number of eggs or nestlings in the nest was recorded at each visit. The number and identity of breeding females in the group were confirmed genetically from egg maternity (see below). Nestlings were genetically sampled via brachial venipuncture at 2-4 days old and given a unique combination of colored leg bands at 4-5 days old. Since ani nestlings are capable of leaving the nest at ~6 days (typically due to disturbance at the nest), we ceased regular nest checks at this age, and considered nestlings to have survived to fledging if they were still alive at this age. Communal clutch size was measured as the total number of eggs incubated in the communal nest, individual clutch size was measured as the number of eggs contributed to the incubated clutch by a female, brood size was measured as the number of nestlings that hatched in the communal nest, and individual reproductive output from each nest attempt was measured as the number of nestlings produced by a female that survived to day 6. For overall analyses of nest predation rate, nest survival was coded as a binary outcome (0 = no nestlings in the communal clutch survived to day 6; 1 = at least one nestling survived to day 6). We used raw predation rates instead of an exposure-controlled metric (i.e. Mayfield or logistic exposure estimate) because all nests in the data set were followed from the beginning of the laying period.

For each year of the study (2007-2019), we estimated the Southern Oscillation Index (SOI), which quantifies variation in the El Niño–Southern Oscillation and is measured as the standardized difference in pressure at sea level between Tahiti and Darwin, Australia.²⁹ Negative SOI values reflect El Niño-like conditions, whereas positive values reflect La Niña-like conditions. We calculated a “bioyear” SOI for each year, defined as the mean monthly SOI value from the preceding November until October of that year, to best reflect conditions during the pre-breeding and breeding season of the year of interest. Annual SOI values are highly correlated with several local climate variables in the Barro Colorado Nature Monument, including the length of the dry season, seasonal and annual rainfall, and the annual frequency of extreme high temperatures.⁵⁰ Because these climate variables represent a correlated suite of conditions that are best captured by the overall SOI value,²⁷ and because we were interested in understanding the general effect of climate variability rather than the effects of individual climate metrics, we use bioyear SOI as the sole climate predictor in our analyses.

We monitored ~50 nesting groups per year (>90% of all nesting attempts in the study area²⁷) most of which were followed for multiple consecutive years. In this data set, 20.0% of groups contained non-breeding helpers (18.0% of groups had one helper, $n = 93$; and 2.3% of groups had two helpers, $n = 12$). The likelihood of having a helper did not differ with the number of breeding pairs in the group (20.4% of two-pair groups and 18.1% of three-pair groups had helpers; Pearson $\chi^2_1 = 0.05$, $P = 0.82$). Total sample sizes across 13 years were 521 group-years, 265 female-years, and 722 nestlings; sample sizes for each analysis are given in the supplemental tables.

Genetic analyses

We identified females and quantified their reproductive output in each nesting attempt using both visual observations of color-banded birds (from 2007-2011; $n = 97$) and genetic identification of egg and nestling maternity (from 2007-2018; $n = 103$). Adults were captured in mist nets (2007-2011⁹) and nestlings were sampled in nests at 2-4 days of age. Blood samples (~30 μ L) were taken from adults and nestlings by brachial venipuncture and stored in lysis buffer for up to one year. Genomic DNA was extracted using several methods (Qiagen DNEasy Blood and Tissue kits for 2007-2010, Omega Bio-Tek EZNA Tissue kits for 2011-2017, and the automated Thermo Scientific KingFisher Flex Purification platform for 2018-2019) following the manufacturer’s protocols for avian blood or tissue.

Maternal genomic DNA was non-destructively sampled from freshly laid eggs by swabbing the surface of the egg with a Q-tip⁶⁴ and destructively sampled from eggshell membranes of unincubated eggs.⁶⁵ Both types of maternal DNA samples were extracted with Omega Bio-Tek EZNA Forensic DNA kits. Maternal identity was cross-validated using different sample types from the same individuals and nesting groups (detailed in Riehl and Strong⁶⁶). Samples were genotyped with 12 microsatellite markers developed for this species,⁶⁷ and egg and nestling maternity was assigned to females using the identity analysis function of Cervus 3.0.7, which identifies the same individual genotype from multiple samples.^{68,69} Nestling maternity was assigned in Cervus 3.0.7 using the parentage analysis function by testing the genotypes of all breeding female group members as candidate mothers. Two nestlings were excluded from analyses because maternity could not be assigned to any females in the breeding group. The measured typing error rate was 0.7% for blood and egg membrane samples and 2.5% for non-invasive swabs.⁶⁶ Genetic analyses are described in detail in Riehl and Strong.^{26,66} Genotypes could not be obtained for 99 of 722 nestlings (13.7%) because they died or were depredated before blood samples could be taken; however, these nestlings were still included in analyses of nestling survival because genetic identification of maternity was not required to estimate survival rates. We used genetic assignments of egg and nestling maternity to quantify individual female reproductive output for all years except 2019, in which we estimated average metrics by dividing communal clutch size and the total number of offspring fledged by the number of breeding females in the group and rounding to the nearest integer (genetic analyses for 2019 were delayed by the Covid-19 pandemic).

Hypothesis testing

We hypothesized that group size could affect individual reproductive output in several ways, any of which could interact with climate. We first asked whether the distribution of group sizes observed in the population (the number of breeding pairs in groups, and the presence and number of helpers) is itself dependent on climate, or whether this distribution is stable across years. We then

constructed models to identify factors predicting 1) nest predation risk; 2) individual clutch size; 3) the survival probability of nestlings, controlling for predation; and 4) total individual reproductive output (which should integrate predation risk, clutch size, and nestling survival). The goal of these models was to ask whether, and how, group size affects individual reproductive output (for example, positively, by reducing nest predation risk; or negatively, through intra-group competition), and whether these effects are dependent on climate. If variation in group size reflects suboptimal deviations from an ideal group size, we predicted that (1) the effect of group size on individual reproductive success should not depend on climate, and (2) individual fitness should be consistently higher in some group sizes than others. By contrast, if variation in climate is partly responsible for maintaining variation in group size, we predicted that (1) the effects of group size on individual fitness should vary with climate, and (2) no one group size should be optimal over the long term.

QUANTIFICATION AND STATISTICAL ANALYSIS

Mixed-effects logistic regression was used for binary response variables (nestling survival and nest predation). Mixed-effects linear regression was used for individual clutch size; mixed-effects negative binomial regression was used for individual reproductive output (number of offspring fledged) because data were skewed (many individuals had zero offspring) and the variance was higher than the mean. For analyses of nest predation risk, we used group-level data (since nest success or failure occurs at the level of the communal clutch). For individual clutch size, nestling survival probability, and individual reproductive output, we used individual-level data. We used total group size (the number of breeders and helpers) in some analyses, and number of breeding pairs (the number of females contributing eggs to the nest) in other analyses, depending on the response variable of interest; details are given in the [supplemental information](#). Models at the group level included the random effects of year and group identity to account for repeated measures from the same groups across years, and models involving individual female reproductive output included the random effect of female identity nested within group identity. Full models are given in [Data S1](#). Statistical analyses were performed in STATA 14.