

Resolving the Paradox of Environmental Quality and Sociality: The Ecological Causes and Consequences of Cooperative Breeding in Two Lineages of Birds

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ABSTRACT: Cooperatively breeding animals occur in virtually every ecosystem on earth. Comparative and biogeographic studies suggest that both benign and harsh—as well as stable and fluctuating—environments can favor the evolution of cooperative breeding behavior. The fact that cooperative societies occur in environments of such contrasting quality creates a paradox of environmental quality and sociality. The dual benefits framework—which leads to the prediction that the ecological consequences of sociality (e.g., range size) vary depending on the benefits that individuals of each species receive by forming social groups—offers a potential resolution to this paradox. Here we use a case study of two avian lineages, starlings (*Sturnidae*) and hornbills (*Bucerotidae*), in which environmental unpredictability appears to have opposite effects on the evolution of cooperation to test the dual benefits framework. Consistent with previous work, harsh and unpredictable environments promote cooperative breeding behavior in starlings, which in turn leads to larger geographic ranges. However, cooperatively breeding hornbills occur in benign and stable environments, but sociality does not influence range size. Our study suggests that the paradox of environmental quality and sociality arises largely because cooperative breeding is an umbrella term encompassing social species that form groups for different reasons. We demonstrate that differentiating among the functional causes of social group formation is critical for developing a predictive framework for understanding the evolution of cooperative breeding behavior.

Keywords: cooperative breeding, dual benefits, ecological constraints, sociality, cooperation.

Introduction

From the seas to rift valley lakes, tropical savannas to boreal forests, cooperatively breeding animals occur in virtually every ecosystem on earth and are widely distributed across all continents with the exception of Antarctica (Jetz and Rubenstein 2011; Lukas and Clutton-Brock 2017). Yet comparative and biogeographic studies suggest that cooperative breeding behavior is favored in both benign (Avilés et al. 2007) and harsh environments (Soucy and Danforth 2002; Sun et al. 2014) as well as in stable (Ford et al. 1988; Gonzalez et al. 2013) and fluctuating environments (DuPlessis et al. 1995; Kaspari and Vargo 1995; Rubenstein and Lovette 2007; Jetz and Rubenstein 2011; Sheehan et al. 2015; Lukas and Clutton-Brock 2017). In stable or benign environments, low annual mortality and habitat saturation often facilitate the evolution of delayed dispersal and cooperative breeding behavior (Russell 1989; Arnold and Owens 1999; Hatchwell and Komdeur 2000). In contrast, in harsh and fluctuating environments, the low probability that solitary individuals breed successfully favors the evolution of cooperative breeding behavior (Emlen 1982; Rubenstein and Lovette 2007). These seemingly inconsistent biogeographic patterns that both benign and harsh—as well as stable and fluctuating—environments can favor the evolution of cooperative breeding behavior constitutes a paradox of environmental quality and sociality (Shen et al. 2017), which is best illustrated in two clades of birds, the African starlings (*Sturnidae*) and hornbills (*Bucerotidae*). Cooperatively breeding species of African starlings are found more commonly than noncooperative ones in unpredictable environments (Rubenstein and Lovette 2007), but the reverse pattern is observed in hornbills, as cooperatively breeding species occur more frequently in stable environments (Gonzalez et al. 2013).

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Resolving this paradox of environmental quality and sociality and determining why cooperative breeding behavior evolves in such different types of environments requires understanding the potential fitness benefits that individuals receive through the formation of cooperative social groups. The dual benefits framework for the formation of cooperatively breeding groups distinguishes between two primary categories of direct benefits: (1) resource defense benefits that derive from group-defended critical resources and (2) collective action benefits that result from social cooperation among group members (Shen et al. 2017). Since conspecifics tend to share similar niches, resource defense benefits often arise from intense intraspecific competition over breeding vacancies or critical resources where social group formation increases access to critical resources (Alexander 1974; Emlen 1982; Koenig et al. 1992; Shen et al. 2017). As a result of these resource defense benefits, cooperation should enhance an individual's ability to survive and reproduce in a saturated environment (e.g., where population density is high), something that typically occurs in benign and stable environments where survival is high and offspring tend to accumulate (McNamara and Dall 2011). In contrast, collective action benefits emerge from active coordination among group members that enhances the efficiency of group activities, such as foraging (Courchamp et al. 2002; Gusset and Macdonald 2010), provisioning (Emlen and Wrege 1991; Hatchwell 1999; Cornwallis et al. 2009), protecting young (Austad and Rabenold 1985), predator detection and deterrence (Rabenold 1984, 1985; Clutton-Brock et al. 1999; Rubenstein 2006), and energy conservation (Hatchwell et al. 2009; van Dijk et al. 2013). Collective action benefits are likely to be most important when local conditions are harsh and unpredictable because they may directly increase reproductive success in the face of environmental challenges. For example, the benefit of cooperatively provisioning young is often more pronounced when environmental conditions are poor (Emlen and Wrege 1991; Hatchwell 1999; Cornwallis et al. 2017), and the positive effect of active group defense of young is greater under high predation risk (Austad and Rabenold 1985). Thus, cooperation should facilitate coping with a variety of environmental challenges in groups that form because of collective action benefits.

It is possible that the reason starlings and hornbills show contrasting patterns between sociality and environmental predictability is because social species in each taxon form groups for different reasons. Long-term data from cooperatively breeding superb starlings (*Lamprotornis superbus*) suggest that cooperative breeding behavior in this species can promote flexibility in offspring care behavior such that helpers can aid in both nest guarding and offspring provisioning—two behaviors that provide collective action benefits—which could mitigate variability in the cost of raising young under different environmental conditions (Ruben-

stein 2011, 2016; Guindre-Parker and Rubenstein 2018a, 2018b). This hypothesis is consistent with results from a comparative study of African starlings showing that cooperatively breeding species occur more commonly in fluctuating environments where interannual variation rainfall is high and unpredictable (Rubenstein and Lovette 2007).

In contrast to these multiple studies suggesting that starlings derive collective action benefits from cooperation, several lines of evidence suggest that resource defense benefits are likely to be the primary reason that cooperative breeding behavior has evolved in hornbills (Leighton 1986; Gonzalez et al. 2013). First, most hornbill species nest in cavities, which are valuable resources defended by a group (Kemp 2001), and cooperative breeding behavior and territoriality co-occur in hornbills (Gonzalez et al. 2013). Second, the relatively high survival rates and longevity of hornbills reduce the availability of breeding vacancies. Finally, hornbills are relatively large in size and able to feed their nestlings with small vertebrates, which are less susceptible than insects to population fluctuations during dry years and are less sensitive to climate variation (Gonzalez et al. 2013). Thus, sociality in starlings appears to be the result of collective action benefits associated with unpredictable environments, whereas sociality in hornbills appears to be the result of resource defense benefits associated with habitat saturation in stable environments.

Despite this clear distinction underlying why cooperatively breeding groups form, an idea that dates back at least 40 years (Alexander 1974; Emlen 1982; Koenig et al. 1992), it remains empirically challenging to directly distinguish between different types of grouping benefits at the interspecific level using comparative analyses with large numbers of relatively poorly studied species where the fitness benefits of group living have not been assessed. One potential way to investigate the dual benefits framework at the interspecific level and to help resolve the paradox of environmental quality and sociality is to test predictions regarding the ecological consequences of cooperation on traits like niche breadth (Shen et al. 2017). Since collective action benefits help organisms cope with environmental challenges or interspecific competition, cooperation should enable individuals to overcome a variety of environmental challenges and, in doing so, expand their ecological niche in the face of competitor species (Sun et al. 2014; Shen et al. 2017). In contrast, resource defense benefits are mainly derived from competing with conspecifics rather than with other species, so cooperation should have little impact on the niche breadth of social species that form groups for this reason.

These alternative hypotheses regarding grouping benefits and niche breadth evolution bridge the two seemingly distinct fields of social evolution and biogeography. Indeed, few studies have explicitly investigated the relationships among social variation and niche breadth. However, an ex-

perimental study of cooperatively breeding burying beetles (*Nicrophorus nepalensis*) that manipulated group size and environmental conditions found that cooperation is necessary for beetles to expand their thermal niche as well as to outcompete competitor species for access to critical resources (Sun et al. 2014). Moreover, a comparative study in birds demonstrated that cooperative breeding behavior may facilitate the colonization of harsh environments (Cornwallis et al. 2017). However, a comparative study in sponge-dwelling snapping shrimps (genus *Synalpheus*) found that sociality is constrained by sponge host breadth and evolves only in species that are host generalists (Brooks et al. 2017). Thus, although there is little consensus on how sociality influences niche breadth in different taxa, the dual benefits framework produces testable predictions to help explore this critical issue.

Previous comparative phylogenetic analyses examining environmental conditions and social evolution in starlings (Rubenstein and Lovette 2007) and hornbills (Gonzalez et al. 2013) produced contrasting results. Here we build on those studies to explore how cooperative breeding behavior—together with environmental and other biotic factors—shapes geographic range sizes (a proxy for niche breadth since wider niche breadth generally predicts larger geographical range size; Gaston 2003; Slatyer et al. 2013) in taxa that appear to form social groups for different reasons. On the basis of the dual benefits framework (Shen et al. 2017), we predict that cooperatively breeding species of starlings (which appear to form groups because of collective action benefits) will have larger geographical ranges (i.e., wider niche breadths) than noncooperative species. In contrast, we do not expect that cooperative breeding behavior will be related to range size (or niche breadth) in hornbills because hornbills are likely to cooperate because of resource defense benefits. Ultimately, by comparing the ecological consequences of cooperative breeding behavior in two groups of highly social birds, this study will help to resolve the paradox of environmental quality and sociality and determine why cooperation evolves in such different types of environments and groups of organisms.

Methods

Phylogenies and Traits

We used previously published phylogenies, one of starlings—which included all 45 Sturnidae species of African origin endemic to mainland Africa and its satellite islands (Rubenstein and Lovette 2007; Maia et al. 2016)—and one of hornbills—which included 61 species distributed in tropical forests and savannahs of Asia and Africa (Gonzalez et al. 2013). The social system of each species was classified as cooperative or noncooperative and was determined through the use of published accounts for both starlings (Craig and Feare 1999; Fry

et al. 2000; Rubenstein and Lovette 2007) and hornbills (Cockburn 2006; Jetz and Rubenstein 2011; Gonzalez et al. 2013). Since body mass seemed to partially affect the relationship between climate and social behavior and differentially influence the patterns in passerine and nonpasserine birds (Jetz and Rubenstein 2011), we included this variable in our models. The body mass (in grams) of each species was determined through the use of published accounts (Dunning 2008). The geographic range size of each species was estimated using digital bird species distribution maps of the world (BirdLife International and Handbook of the Birds of the World 2016). Since the four subspecies of *Tockus erythrorhynchus* were treated as different species (*Tockus erythrorhynchus*, *Tockus kempfi*, *Tockus ruahae*, and *Tockus rufirostris*) by Gonzalez et al. (2013), we treat the four subspecies as separate species based on subspecies borders described by Kemp and Kirwan (2017).

Climatic Data

We extracted climatic data from the distribution ranges of each species using the Climatic Research Unit Timeseries (CRU TS) database v3.24 (Harris et al. 2014). Climatic variables included (1) mean annual temperature (°C), (2) diurnal temperature range (DTR; °C), (3) seasonal temperature range (STR; °C), (4) mean annual precipitation (MAP; mm), (5) within-year variation in precipitation (mm), and (6) among-year variation in precipitation (mm). We calculated the mean values of each climatic variable across all 55 × 55-km grid cells within the geographic distribution range of each species. The climatic variables used here are similar to those used in the previous studies of these taxa with the updated CRU database (Rubenstein and Lovette 2007; Gonzalez et al. 2013), except that we added DTR and STR into the analysis because recent studies have shown that temperature variability is crucial in shaping species' range sizes (Chan et al. 2016; Ficetola et al. 2017). STR was log transformed before any analysis since it was strongly right skewed. Since DTR, MAP, and among-year variation in precipitation were highly correlated, we performed a principal component analysis (PCA) to generate the first principal component (PC1), which explained 79.1% of the variation and can be considered a proxy of environmental harshness (sensu Botero et al. 2014; Cornwallis et al. 2017; table A1; tables A1–A5 are available online).

Comparative Analyses

We first assessed whether climatic variables and body mass predicted the occurrence of cooperative breeding behavior in each taxon using phylogenetic generalized linear models (GLMs) implemented in the R package phylolm (Ho and Ané 2014), which is appropriate for analyses with binary response variables (Ives and Garland 2010). We also assessed

whether the occurrence of cooperative breeding behavior, body mass, and climatic variables predicted range sizes of species in each taxon using phylogenetic generalized least squares models (PGLSs) implemented in the R package nlme (Pinheiro et al. 2017). In each PGLS model, we estimated phylogenetic signal with Blomberg's K (Blomberg et al. 2003) using maximum likelihood to correct for potential bias caused by phylogenetic nonindependence. In each phylogenetic GLM or PGLS model, independent variables were standardized before analysis. For each of the analyses, we first tested a full model with all predictors and then obtained the best-fitting model from all possible combinations of the predictors using a corrected Akaike information criterion (AICc; Hurvich and Tsai 1989). We also present a summary of all models with $\Delta\text{AICc} < 2$ and then conducted model averaging over these models (Burnham and Anderson 2002) using the R package AICcmodavg (Mazerolle 2016). We also used ANOVA and pairwise comparisons to compare the degree of environment harshness occupied by cooperatively and noncooperatively breeding starlings and hornbills.

We further explored the directionality of the relationships among species' range sizes, cooperative breeding behavior, body mass, and the climatic variables that we identified as important in the GLM or PGLS analyses using phylogenetic confirmatory path analysis (Hardenberg and Gonzalez-Voyer 2013). Only predictors in the GLM or PGLS models with minimum AICc values were kept in the analyses. We first built hypothetical causal models, which were directed cyclic graphs for the relationships among the variables of interest, based on the results from the phylogenetic GLM and PGLS analyses. Next, we used the d -separation method to test the validity of each hypothetical model. The model of interest was then converted to a set of conditional independencies, which allowed us to further test the significance of each existing and missing link among variables via phylogenetic GLM or PGLS (Hardenberg and Gonzalez-Voyer 2013). Finally, we calculated Fisher's C -statistics and the C -statistic information criterion (CICc) on the basis of the significance of missing links for each model. All data analyses were conducted using R 3.2.3 (R Development Core Team 2015). Data have been deposited in the Dryad Digital Repository (<https://dx.doi.org/10.5061/dryad.nk3560s>; Lin et al. 2019).

Results

Environmental and Life-History Correlates of Cooperative Breeding

Consistent with previous studies of starlings (Rubenstein and Lovette 2007) and hornbills (Gonzalez et al. 2013), we found that (1) cooperative breeding behavior in starlings occurred more frequently in harsh and unpredictable environments (phylogenetic GLM, best model, $P = .008$; fig. 1*a*, 1*b*; ta-

ble A2, pt. C), where mean annual rainfall was lower (fig. A1*a*, A1*b*; figs. A1–A3 are available online), among-year variation in rainfall was higher (fig. A2*a*, A2*b*), and DTR was higher (fig. A3*a*, A3*b*), but that (2) cooperative breeding behavior in hornbills occurred in more benign and predictable environments (phylogenetic GLM, best model, $P = .010$; fig. 1*c*, 1*d*; table A3, pt. C), where mean annual rainfall was higher (fig. A1*c*, A1*d*), among-year variation in rainfall was lower (fig. A2*c*, A2*d*), and DTR was lower (fig. A3*c*, A3*d*). Furthermore, results of the model averaging method were almost identical to the best model results (table A2, pt. D; table A3, pt. D). Thus, cooperatively breeding starlings and hornbills had nearly nonoverlapping environmental niches (ANOVA, interaction social system \times bird family, $P < .001$; pairwise comparison between cooperatively breeding starlings and hornbills, $P < .001$), whereas noncooperatively breeding starlings and hornbills shared similar environmental niches (pairwise comparison between noncooperatively breeding starlings and hornbills, $P = .42$; fig. 2). In addition, body mass did not influence cooperative breeding behavior in either hornbills or starlings (tables A2, A3).

Ecological Consequences of Cooperative Breeding

After confirming the ecological and life-history correlates of cooperative breeding behavior in these two avian groups, we explored the ecological consequences of cooperative breeding behavior by comparing species' range sizes in cooperative and noncooperative breeders of each taxon (fig. 3). Interestingly, we found that cooperatively breeding starlings occupied larger ranges than noncooperatively breeding species (PGLS, best model, $P = .003$; fig. 3*a*; table A4, pt. C) but that only mean annual temperature (PGLS, best model, $P = .003$) positively influenced range size in starlings (fig. 4*a*; table A4, pt. C). In contrast, range size did not differ between cooperative and noncooperative species of hornbills (PGLS, full model, $P = .676$; fig. 3*b*; table A5, pt. A), but climatic factors (STR and within-year variation in precipitation, PGLS, best model, $P = .001$ and 0.003 , respectively; fig. 4*b*, 4*c*; table A5, pt. C) and body mass (PGLS, best model, $P = .034$; table A5, pt. C) positively influenced range size of cooperative and noncooperative species alike. Furthermore, model averaging only slightly changed the above results (table A4, pt. D; table A5, pt. D) such that the influence of body mass on range size in hornbills became marginally significant ($P = .058$; table A5, pt. D).

Possible Causal Relationships between Social System and Range Size of Species

By using phylogenetic path analysis, we further confirmed that cooperative breeding behavior in starlings influenced range size, not the other way around (fig. 5*a*; table A4). In

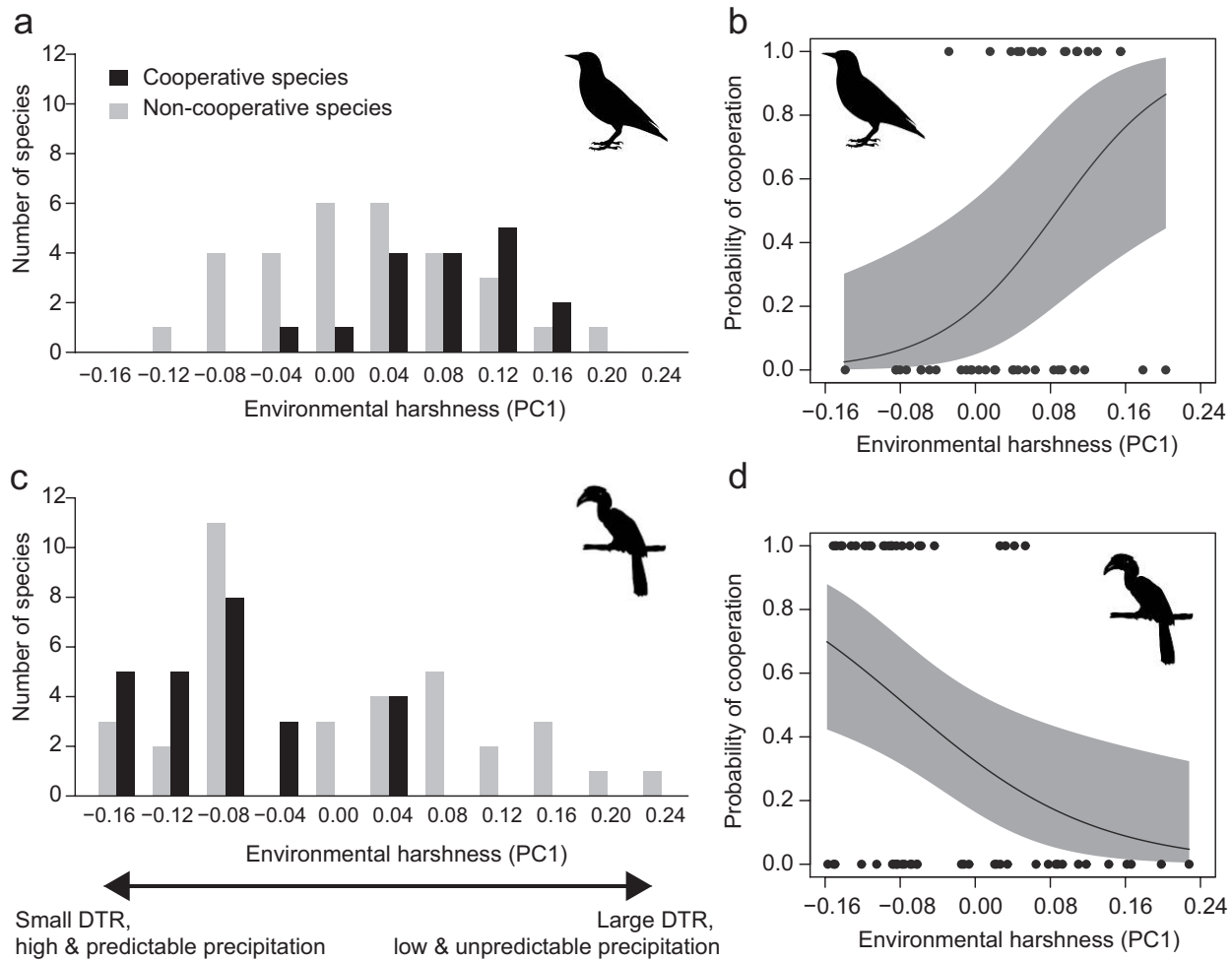


Figure 1: Frequency distributions of social systems (i.e., cooperative and noncooperative species) in relation to environmental principal component 1 (PC1; environmental harshness) in starlings (cooperative: $n = 17$; noncooperative: $n = 30$; *a*) and hornbills (cooperative: $n = 25$; noncooperative: $n = 35$; *b*). Environmental PC1 includes diurnal temperature range (DTR), mean annual precipitation, and among-year variation in precipitation, which were highly correlated variables. The probability of being a cooperatively breeding species in relation to environmental PC1 is shown for starlings ($n = 47$; *b*) and hornbills ($n = 60$; *d*). Shaded areas in *b* and *d* represent 95% confidence intervals.

contrast, environmental factors and life-history traits (body mass)—but not social system—influenced range size in hornbills (fig. 5*b*; table A5).

Discussion

Our study provides empirical evidence that the varying relationships between sociality and environmental predictability in cooperatively breeding taxa may at least be partially explained by the different reasons that social groups form and how these grouping benefits are likely to influence species' range sizes. We show that only social species that form groups because of collective action benefits—such as starlings that live in harsh and unpredictable environments

where having helpers increases reproductive success (Rubenstein and Lovette 2007; Rubenstein 2011, 2016) and survival (S. Guindre-Parker and D. R. Rubenstein, unpublished data)—have larger geographic range sizes than nonsocial species. In contrast, cooperation does not influence range size in hornbills. In sharp contrast to starlings, cooperatively breeding hornbills tend to occur in benign and stable environments where the resource defense benefit of overcoming intraspecific competition is likely to be the key ecological driver for the evolution of their social behavior. Therefore, our results suggest that the paradox of environmental quality and sociality arises largely because cooperative breeding is an umbrella term encompassing social species that form groups for very different reasons. The dual benefit framework articulates

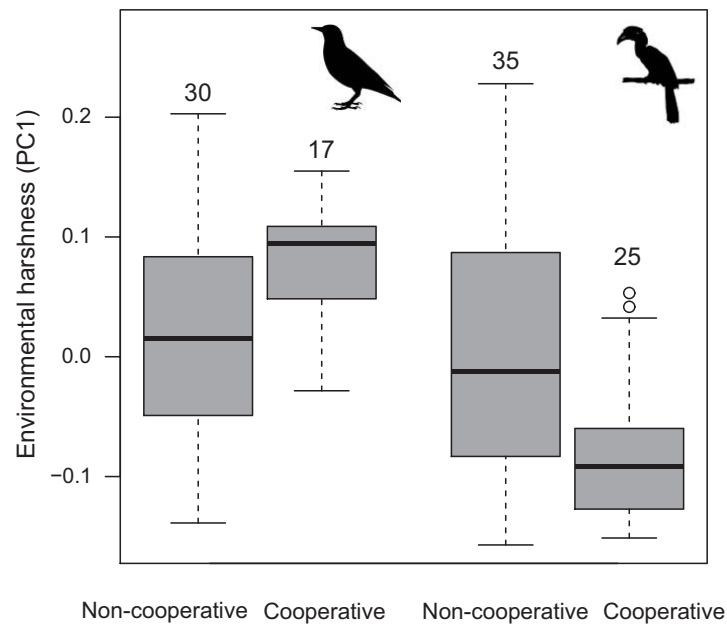


Figure 2: Comparison of climate niche (principal component 1 [PC1]) between cooperatively breeding and noncooperatively breeding starlings and hornbills. Each box shows the lower and upper quartile values. Thick line indicates the median value, whereas dashed lines indicate lower and upper extremes. Circles indicate outliers. Numbers represent sample sizes.

two primary categories of direct benefits that promote the formation of cooperatively breeding groups, and differentiating between the reasons that cooperative groups forms—such as resource defense versus collective action benefits—is crucial to achieving a predictive framework for understanding the relationship between cooperative breeding behavior and the environment.

Our results also help to clarify a recent hypothesis arguing that instead of harsh environments favoring cooperation, cooperative breeding in birds may actually facilitate the colonization of harsh environments (Cornwallis et al. 2017). Cornwallis et al. (2017) demonstrated that the evolutionary origins of cooperative breeding behavior in birds occurred in benign and stable environments. However, it is

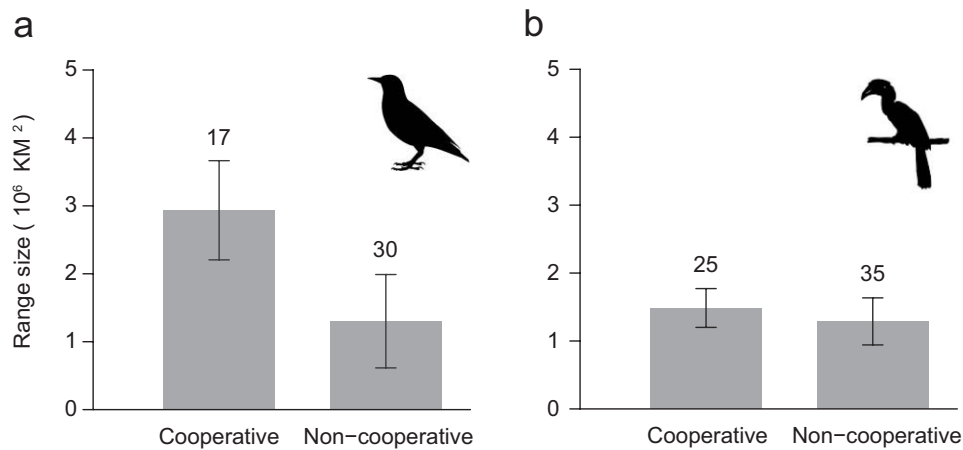


Figure 3: Comparison of geographic range size of cooperatively and noncooperatively breeding species of starlings (a) and hornbills (b). Bars represent means and error bars represent standard errors estimated by phylogenetic generalized least squares models. Numbers represent sample sizes.

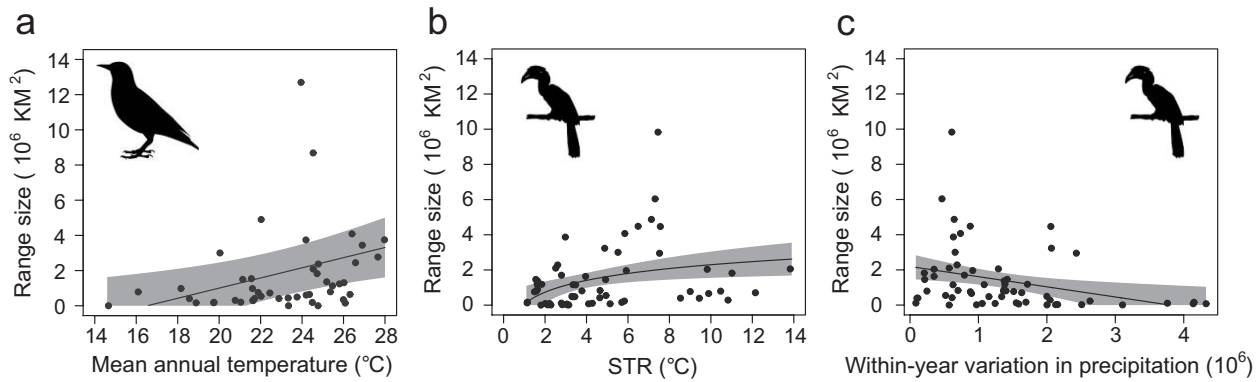


Figure 4: Geographic range size in relation to mean annual temperature in starlings ($n = 47$; *a*), seasonal temperature range (STR) in hornbills ($n = 60$; *b*), and within-year rainfall variation in hornbills ($n = 60$; *c*). Shaded areas represent 95% confidence intervals.

important to distinguish between the selective process (evolutionary history) and the product of selection (adaptation; Reeve and Sherman 1993). That is, despite higher evolutionary transition rates from solitary to cooperative breeding behavior in benign environments, cooperative breeding can still be an adaptation to harsh environments and have fitness advantages there, as has been observed in starlings and many other avian species living in similar environments (Emlen 1990; Covas et al. 2008; Rubenstein 2016; Russell 2016).

Therefore, we propose expanding the hypothesis from Cornwallis et al. (2017) to include the dual benefits framework to generate a mechanism for the patterns observed across birds in this and other studies. That is, cooperative breeding could have initially evolved for resource defense benefits (e.g., accessing and defending critical resources) as an adaptation to intraspecific competition in benign and stable environments where densities are high. For example, those family-living bird species—in which offspring delay dispersal and stay with their parents but do not perform helping behaviors—likely form groups for this reason (Griesser et al. 2017). However, after group formation, organisms are more likely to evolve more complex cooperative behaviors (e.g., cooperative provisioning, foraging, and predator defense) that require highly specialized systems of communication or coordination. These adaptations would then enable social species to colonize harsher environments and gain collective action benefits, which would in turn lead to a wider niche breadth and greater geographic range size. This proposed route of social evolution—from resource defense to collective action benefits—has also been described in several other studies (Allee 1938; Alexander 1974; Emlen 1991). In summary, instead of arguing that harsh environments do not favor cooperation, our study demonstrates that both harsh and benign environments can favor cooperative breeding but for different reasons. Moreover, these different forms of coop-

eration will result in distinct ecological consequences, such as variation in range sizes and ecological niche breadths.

The dual benefits framework argues that inter- versus intraspecific competition influences the formation of social groups in different ways (Shen et al. 2017). Niche theory claims that interspecific competition often limits a species' realized niche breadth (Hutchinson 1957; Van Valen 1965; Bolnick et al. 2010), whereas intraspecific competition often expands it (Bolnick 2001). However, little is known about how intraspecific cooperation influences the evolution of niche breadth (Wilson 1990, 2012; Sun et al. 2014; Shen et al. 2017). Our phylogenetic path analysis confirms that high environmental fluctuation favors cooperation, which in turn leads to larger range sizes in starlings. In contrast, although environmental stability favors cooperation in hornbills, likely for coping with intraspecific competition over critical resources, no apparent ecological consequences of cooperation on range size were observed. Cases like this where sociality does not confer ecological benefits have been observed in other taxa, including in many invertebrates. For example, sociality is considered to be an evolutionary dead-end strategy in many social spider species (Agnarsson et al. 2006; Avilés and Purcell 2012). We suspect that these cases are likely to be examples where groups form because of resource defense benefits, where intense intraspecific competition leads to limited dispersal, inbreeding, and small subdivided populations. However, we also caution against inferring intraspecific competition benefits simply from a lack of a correlation between cooperation and niche breadth. Statistical methods like phylogenetic path analysis (this study) and evolutionary transition analysis (Brooks et al. 2017; Cornwallis et al. 2017) can help identify the ecological drivers of sociality, which may help researchers infer both the benefits and the ecological consequences of group formation. Therefore, the problem of a lack of direct evidence of grouping benefits in large-scale

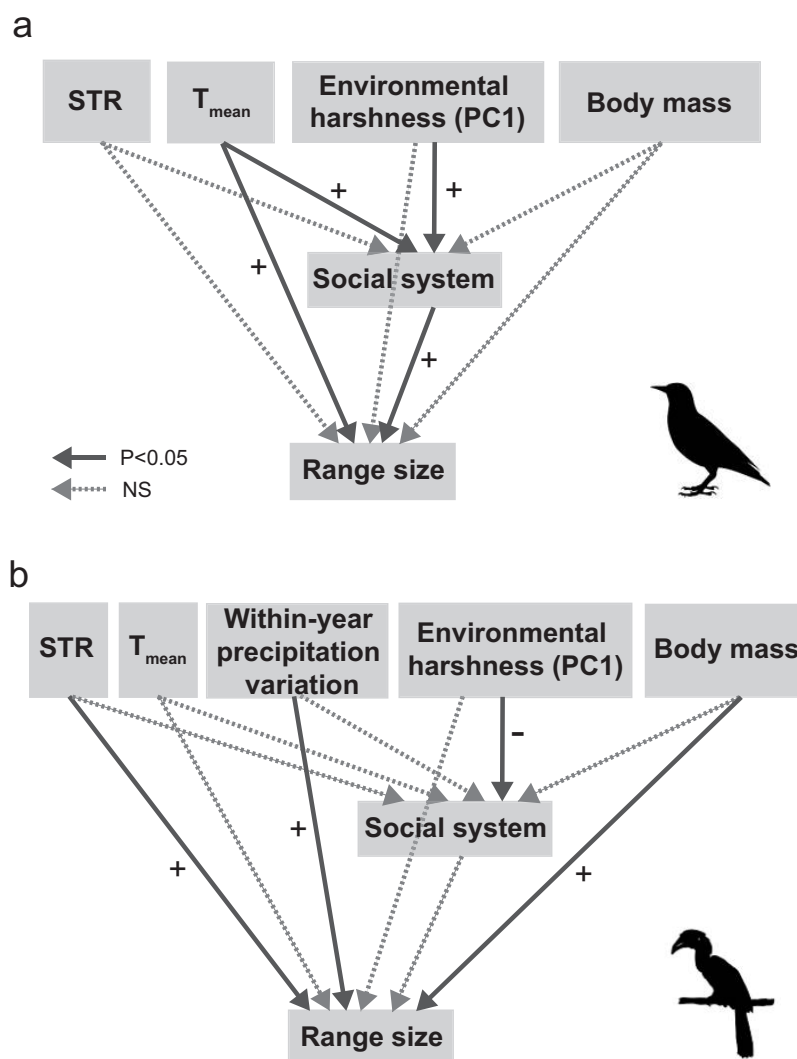


Figure 5: Relationships among climatic and life-history variables, social system (cooperative or noncooperative breeding), and range size of species as determined by phylogenetically controlled d -separation path analysis in starlings (*a*) and hornbills (*b*). Arrows indicate direct effects; solid lines represent statistically significant relationships, and dotted lines represent statistically nonsignificant (NS) relationships. Plus and minus signs represent positive and negative relationships, respectively. Only predictors in the generalized linear model or phylogenetic generalized least squares model with minimum corrected Akaike information criterion values were kept in the final model (see “Methods”). STR = seasonal temperature range.

comparative studies can be partially overcome. Nevertheless, further studies on grouping benefits in diverse taxa with different patterns of social organization will be crucial for understanding why sociality creates ecologically dominant species in terms of range size or abundance in some clades but not in others.

In conclusion, estimating range size has been shown to be essential for understanding niche breadth evolution and patterns of species distribution and richness (Gaston 2003; Slatyer et al. 2013; Chan et al. 2016). We applied the dual benefits framework for social evolution to two taxa known to exhibit

very different evolutionary relationships between climate variability and sociality and, in doing so, provide an empirical example supporting the prediction that different ecological benefits associated with sociality will drive different patterns of niche breadth evolution and range size expansion. This work helps resolve the paradox of environmental quality and sociality by demonstrating how different grouping benefits can influence feedback between social behavior and the environment. Ultimately, studying the ecological consequences of sociality will help us better understand the success, expansion, and failure of social organisms.

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