Evolution of Social Organization: Phylogenetic Analyses of Ecology and Sexual Selection in Weavers

Zitan Song (宋紫檀),[1,2] András Liker,[3] Yang Liu (刘阳),[1,2,*] and Tamás Székely[1,2,4,5]

1. State Key Laboratory of Biocontrol, School of Life Sciences/School of Ecology, Sun Yat-sen University, Guangzhou, Guangdong 510275, China;   2. Milner Center for Evolution, Department of Biology and Biochemistry, University of Bath, Bath BA1 7AY, United Kingdom;
3. MTA-PE Evolutionary Ecology Research Group, University of Pannonia, H-8201 Veszprém, Pf. 158, Hungary;   4. Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, China;   5. Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Hungary

ABSTRACT: Crook published a landmark study on the social organization of weavers (or weaverbirds, family Ploceidae) that contributed to the emergence of sociobiology, behavioral ecology, and phylogenetic comparative methods. By comparing ecology, spatial distribution, and mating systems, Crook suggested that the spatial distribution of food resources and breeding habitats influence weaver aggregation during both the nonbreeding season (flocking vs. solitary foraging) and the breeding season (colonial vs. solitary breeding), and the latter in turn impacts mating systems and sexual selection. Although Crook's study stimulated much follow-up research, his conclusions have not been scrutinized using phylogenetically controlled analyses. We revisited Crook's hypotheses using modern phylogenetic comparative methods on an extended data set of 107 weaver species. We showed that both diet and habitat type are associated with spatial distribution and that the latter predicts mating system, consistent with Crook's propositions. The best-supported phylogenetic path model also supported Crook's arguments and uncovered a direct relationship between nonbreeding distribution and mating system. Taken together, our phylogenetically corrected analyses confirm Crook's conjectures on the roles of ecology in social organizations of weavers; however, our analyses also uncovered an association between nonbreeding distributions and mating systems, which was not envisaged by Crook.

Keywords: sexual selection, social behavior, pair bonding, parental care, coloniality, sexual size dimorphism.

Introduction

Studies of behavioral ecology (or sociobiology) are proliferating, and over the past 50 years, these studies have mainly progressed in evolutionary biology and organismal biology (Wilson 1975; Davies et al. 2012; Rubenstein and Alcock 2019). One of the core research methods in behavioral ecology is phylogenetic comparative analyses, which are powerful evolutionary tools that have been facilitated by new statistical approaches, advanced molecular phylogenies, and a wealth of new data on ecology, behavior, and life histories of organisms (Felsenstein 2004; Futuyma and Kirkpatrick 2017). One of the seminal studies that facilitated the emergence of behavioral ecology and the use of comparative analyses for testing evolutionary hypotheses was Crook's (1964) study on the ecology and social behavior of small passerine birds, the weavers. This study is well cited (437 citations in Google Scholar, accessed October 9, 2021), and it is a classic example of a comparative approach in major organismal evolution textbooks (Davies et al. 2012).

Crook (1964) noticed the diversity of social organization in weaver birds (family: Ploceidae; order: Passeriformes) and sought to understand this diversity in terms of their ecology. He argued that in forests, food items (insects) are cryptic, easily disturbed, and widely distributed (fig. 1), and solitary foraging is an adaptation to exploit the food sources therein. Alternatively, in the savanna, food items (seeds) are locally abundant, and thus foraging in groups can enhance locating food patches. Moreover, in the savanna, safe nesting sites are limited; therefore, weavers breed in colonies, with males competing for nesting sites and the winners attracting several females. Because of abundant food sources in the savanna, females can feed an entire brood alone (i.e., without the help of a male), which allows males to seek additional mating opportunities and attain multiple females. Thus,

* Corresponding author; email: liuy353@mail.sysu.edu.cn.
   ORCIDs: Song, https://orcid.org/0000-0001-9739-0233; Liker, https://orcid.org/0000-0001-8545-4869; Liu, https://orcid.org/0000-0003-4580-5518; Székely, https://orcid.org/0000-0003-2093-0056.
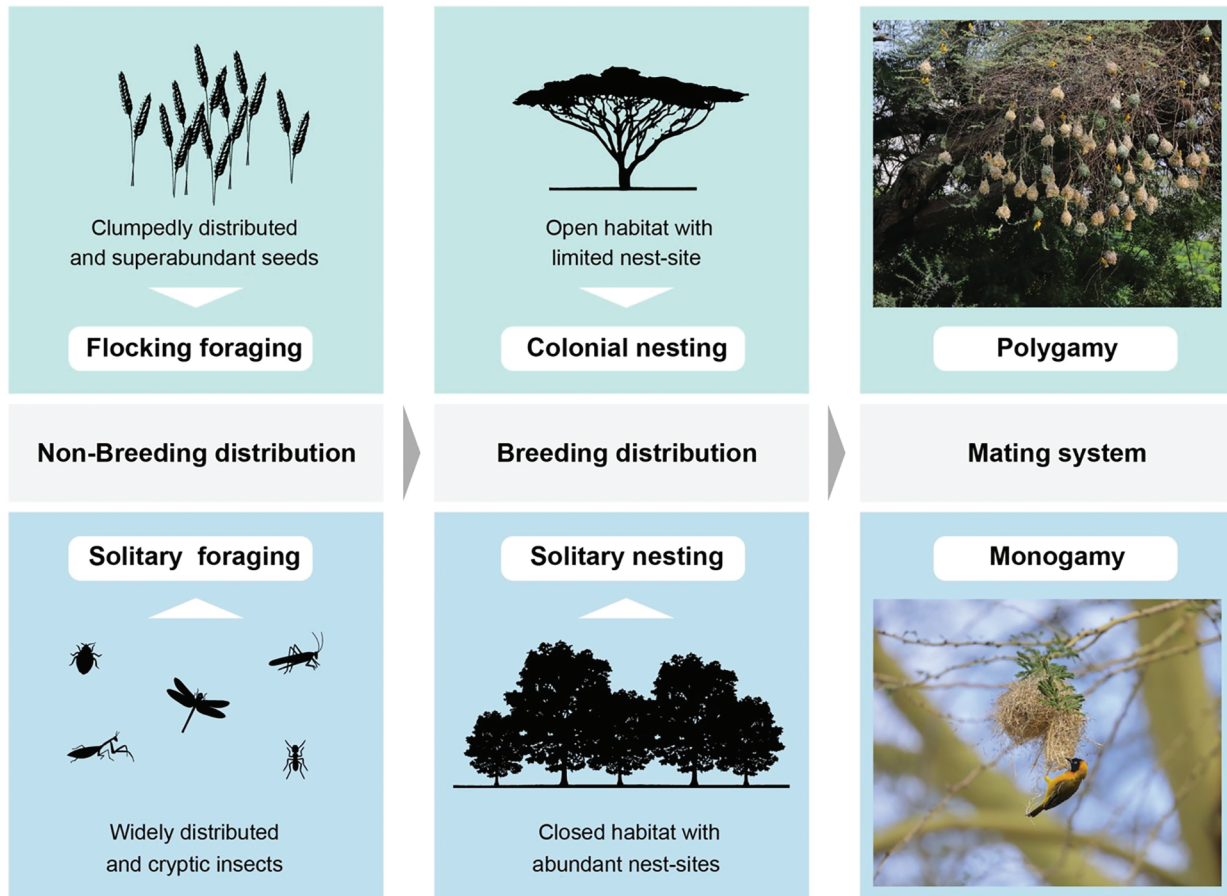
Figure 1: Social organization in relation to diet and habitat in weavers based on Crook (1964).

Crook (1964) thought that abundant food and limited nesting sites should favor polygamy (and, indirectly, sexual plumage dimorphism) in open habitats, whereas dispersed food in forest should favor monogamous pair bonds and weak sexual selection, since dispersed resources requires spaced-out breeding territories.

Crook's (1964) work was pathbreaking for two reasons. First, he noticed that across species, ecology (i.e., habitat and diet) tends to correlate with social organization during both the nonbreeding season and the breeding season. Second, he laid the foundation for comparative analyses by proposing nonindependent transitions between ecology, dispersal, and breeding system; then using 70 weaver species, he tested his hypothesized scenario (Davies et al. 2012). Although evolutionary biologists have been classifying social organization ever since Darwin (1871), Crook proposed a specific hypothesis regarding how different aspects of social organizations relate to each other and, importantly, how social organization is shaped by ecology.

However, Crook's study had limitations: First, he did not use statistics to test the propositions; his conclusions were drawn by categorizing species according to their ecological variables and social traits. Second, he did not consider that congeneric species may have similar suites of behavioral traits as the result of shared ancestry, which may violate the assumptions of comparative tests because species that share a phylogenetic history are not independent data points (Felsenstein 1985; Harvey and Pagel 1991). Although phylogenetic methods have progressed immensely in the past two decades (Freckleton et al. 2002; Nunn 2011; Davies et al. 2012), no study has evaluated Crook's hypotheses using a modern phylogenetic approach. Although more recent studies on breeding systems are providing new insights into the complexities of social life of many organisms, for instance, in relation to mate availability, sexual dimorphism, and genetic and social mating systems (Reynolds 1987; Fairbairn et al. 2007; Székely et al. 2010), Crook's original hypothesis about the roles of ecology in social organization in weavers

has remained influential—although as yet—untested using modern comparative approaches.

Here, we revisit Crook's hypotheses using phylogenetically controlled analyses of 107 weaver species to quantify associations between ecology, social behavior, and life history. Specifically, we aim to answer the following questions (see table I and diagram I in Crook 1964): (i) do diet and habitat influence spatial distribution during the nonbreeding season (i.e., flocking behavior), (ii) does the nonbreeding distribution (i.e., flocking behavior) predict spatial distribution during breeding (i.e., coloniality), and (iii) does the degree of coloniality predict mating system and sexual dimorphism? In addition, we used phylogenetic path analysis (Santos and Cannatella 2011; von Hardenberg and Gonzalez-Voyer 2013) to uncover the potentially complex relationships between ecological variables and social behaviors by fitting a priori–defined path models to the data.

Material and Methods

Data Collection

We used primary research articles, reference books, and online resources to check and augment data on all 107 weaver species (Craig 2010) to increase the sample sizes used by Crook. The scoring of variables followed Crook's definitions. We extracted the ecological, behavior, and body size data from the *Handbook of the Birds of the World* (Craig 2010), relevant reference books (Cramp and Simmons 1988; Frith 2004; Dunning 2007), and published articles (retrieved from an extensive search of scientific names of weaver species in Google Scholar). The variable definitions, raw data, and associated references are compiled in tables S1 and S2 and uploaded in the Dryad Digital Repository (https://doi.org/10.5061/dryad.7wm37pvq4; Song 2022).

We used habitat type and diet type to represent nesting site and food resources, respectively, following Crook's definitions (tables S1, S2). Habitat type was classified as closed (i.e., dense evergreen forests), open (i.e., sparsely vegetated savanna or grasslands), or mixed (i.e., including both closed habitat and open habitat). Diet type was classified as insectivorous, omnivorous, or granivorous.

We used three variables to represent social organization: (1) breeding distribution, (2) nonbreeding distribution, and (3) mating system (Bennett and Owens 2002; Liker et al. 2013). Following Crook (1964), we scored breeding distribution using three levels: solitary (i.e., spaced-out territorial nesting), colony (i.e., nests are in dense colonies), and mixed (i.e., the species exhibit intermediate nesting distribution). For nonbreeding distribution, "solitary" refers to solitary foraging, "mixed" refers to foraging in small family parties or small mixed-species groups, and "flocking" refers to foraging in large groups. The social mating system was classi-

fied as monogamy or polygamy, with the latter including both simultaneous polygyny and lek mating systems (for a similar scoring system, see Liker et al. 2013).

Breeding plumage was classified as permanent or changing, with the latter referring to species that molt eclipse plumage into nuptial plumage during the breeding season. Sexual size dimorphism was calculated as $\log_{10}$(male body size) $-$ $\log_{10}$(female body size), and body size was included using three different measures: body mass, wing length, and tarsus length.

To ensure scoring consistency, two observers scored the descriptions of habitat type, diet type, coloniality, and grouping behavior of 107 species using the original data sources. Using the rpt function in the rptR package (Stoffel et al. 2017), we calculated the repeatability between observers. For all variables, we found high repeatability: habitat type ($R = 0.880$), diet type ($R = 0.881$), breeding distribution ($R = 0.902$), and nonbreeding distribution ($R = 0.991$).

Statistical Analyses

To control for phylogenetic uncertainty, we ran each analysis using 200 phylogenetic trees extracted from https://www.birdtree.org: 100 of these phylogenies used the Hackett backbone and 100 used the Ericson backbone (Jetz et al. 2012). These phylogenetic trees were generated using available genetic information (41 species) and taxonomic information compiled in a Bayesian framework when genetic data were lacking (75 species). Each analysis was performed 200 times using one tree from 200 phylogenetic trees in each run, and the mean and 95% confidence interval of statistical parameters for these 200 repetitions were calculated.

We conducted all analyses using phylogenetically adjusted statistics. We modeled breeding distribution, nonbreeding distribution, and mating system as functions of resource distribution and additional covariates using phylogenetic generalized least squares (PGLS; Martins and Hansen 1997; Freckleton et al. 2002). We first tested the effects of resource distribution on nonbreeding distribution by fitting PGLS models ($n = 98$). We then fitted PGLS models with resource distribution and nonbreeding distribution as independent variables to test their effects on breeding distribution ($n = 93$). PGLS are suitable for analyzing ordinal variables as long as they are organized along a continuum and represent discretized versions of actual (biologically) continuous variables (Graber 2013; Symonds and Blomberg 2014). PGLS are widely used in phylogenetic studies of discrete ordinal variables (Liker et al. 2013; Remeš et al. 2015; Adams et al. 2019; Iglesias-Carrasco et al. 2019; Lifjeld et al. 2019).

We used phylogenetic logistic regression to test the effect of breeding distribution on the binary variables (i.e., mating

system, $n = 83$; breeding plumage, $n = 105$). The effect of breeding distribution on sexual size dimorphism (wing length, $n = 93$; tarsus length, $n = 88$; body mass, $n = 68$) was tested by fitting PGLS models. PGLS models for variables with normal or ordinal distributions were fitted using the pgls function in the R package caper (Orme et al. 2013), which implements generalized least squares models while accounting for phylogeny through maximum likelihood estimates of λ (Pagel 1999). Phylogenetic logistic regression models with binary response variables were fitted by the phyloglm function in the R package phylolm (Ho and Ané 2014).

We conducted phylogenetic path analyses (PPAs) to test hypothesized relationships between ecology and social organization. We followed Santos (2012) and used phylogenetic independent contrasts as input data that were entered into confirmatory path analysis. PPAs were run 200 times using independent contrasts calculated with the 200 different phylogenetic trees (see above). PPA is suitable for assessing direct and indirect relationships among candidate variables, and it allows testing alternative models of presumed relationships by estimating the path coefficients and overall model fit (Santos and Cannatella 2011). Because the number of potential relationships rapidly increased with the number of variables, we followed a two-step approach (Gonzalez-Voyer et al. 2016). First, we determined the associations between the five key variables (i.e., diet, habitat, nonbreeding distribution, breeding distribution, and mating system; $n = 75$) by assuming that each variable has only one path to each of the other variables (fig. S1). Following Crook (1964), we prespecified that resource distributions affected breeding distribution, mating system, and/or nonbreeding distribution (fig. S1; also see Jarman 1974; Emlen and Oring 1977). Second, using the best-supported model from the first set (i.e., the models with the lowest corrected Akaike information criterion [AICc] and highest R^2), we built a full path model that included all potential paths between key variables (fig. S2). Then from the full path model, the nonsignificant associations were eliminated, and the final best-supported path model (with the best model fit and lowest AICc) was retained.

The fit of a given path model to the data was estimated by Fisher's C statistic, which tests whether the minimum set of conditional independencies of a model is fulfilled by the data; thus, it provides an estimate of the goodness of fit of the model to the data (Shipley 2013). Additionally, we measured the model fit of individual models using four of the most widely used indexes: Tucker-Lewis index (TLI; Tucker and Lewis 1973), Bentler's comparative fit index (CFI; Bentler 1990), root mean square error of approximation (RMSEA; Browne and Cudeck 1992), and standardized root mean square residual (SRMR; Bentler 1995). TLI and CFI > 0.95, RMSEA < 0.06, and SRMR < 0.08 indicate acceptable/

good fit of models to the data (Hooper et al. 2008; West et al. 2012). Fisher's C statistic was tested by the piecewiseSEM package (Lefcheck 2016), and other fitted indexes were obtained using the lavaan package (Rosseel 2012). All statistical analyses were performed with R version 3.6.0 (R Development Core Team; http://cran.r-project.org/).

Results

Resource Distribution and Social Organization

Flocking during the nonbreeding season occurs in nearly all of the 98 weaver species (fig. 2A), and consistent with Crook's (1964) hypotheses, we found that both diet and habitat predict nonbreeding distribution (table 1): 78.13% of 32 species that live in open habitats (fig. 3A) and 92.31% of 26 species that have a granivorous diet (fig. 3B) live in flocks, whereas only 15.63% of 32 species from closed habitats and 11.43% of 35 species with insectivorous diet live in flocks (fig. 3A, 3B). Furthermore, nonbreeding distribution predicts breeding distribution (table 2), and species that forage in flocks are more likely to breed colonially than solitarily (table 2; fig. 3C).

Breeding Distribution, Sexual Dimorphism, and Mating System

Spatial distribution during breeding is related to mating system and sexual size dimorphism (table 3), since solitary nesting species are more likely to be monogamous (figs. 2B, 4A). We found consistent, albeit nonsignificant, patterns using tarsus length and body mass as indicators of body size (table 3). Furthermore, colonial species tend to have nuptial plumage (table 3; fig. 4B) and greater sexual size dimorphism than solitary nesters (table 3; fig. 4C).

Phylogenetic Path Analyses

From the first set of seven candidate models (including Crook's original hypothesis and six alternative scenarios; see table 4; fig. S1), the best-supported model was consistent with Crook's original hypothesis (table 4) that diet and habitat predict nonbreeding distribution, which in turn predicts breeding distribution and mating system (fig. 5A). The best-supported model has a poor fit to the data (see "Material and Methods").

Adding further connections to the aforementioned best model improved its fit to the data (see "Material and Methods"; table S3; fig. S2). In the second set of path models, three models passed Fisher's C statistics (i.e., showed acceptable model fit). Of these, the best-fit model (with the lowest AICc value) supports the main components of Crook's hypothesis (fig. S2). In addition to the associations suggested by Crook, the latter model suggests
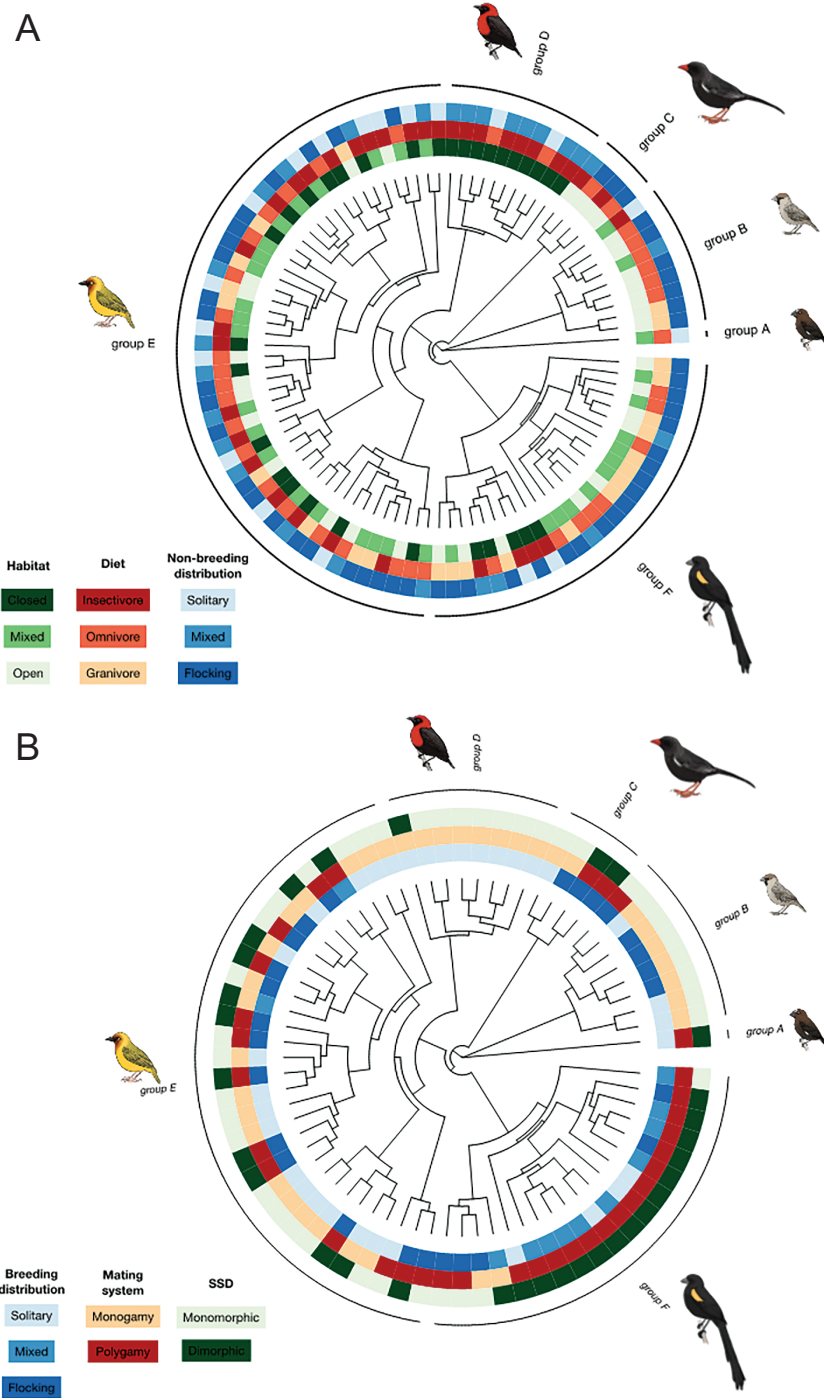
Figure 2: Phylogenetic distribution of diet, habitat type, distribution, and social behavior in weavers. Groups A–F represent different genera of the family Ploceidae. *A*, Nonbreeding distribution, habitat, and diet ($n = 98$ species). Nonbreeding distributions were scored as (1) solitary foraging, (2) family parties or small mixed-species foraging flocks, or (3) large foraging groups in nonbreeding season. Breeding distributions were scored as (1) solitary nesting, (2) small colony formation, or (3) colonial formation (for details, see table S1). *B*, Breeding distribution, mating system, and sexual size dimorphism (SSD) relative to breeding distribution in weavers ($n = 71$ species). Breeding distributions were scored as (1) solitary nesting, (2) small colony formation, or (3) colonial formation. Mating system was scored as (0) monogamy or (1) polygamy. SSD was quantified as $\log_{10}$(male wing length) $-$ $\log_{10}$(female wing length) and split into "monomorphic" when SSD was less than 0.07 (the median SSD) and "dimorphic" when SSD was greater than 0.07. Credit for bird pictures: Kelai Lee.

Table 1: Nonbreeding distribution is predicted by habitat and diet in weavers ($n = 98$ species)

	Estimate (95% CI)	SE (95% CI)	t (95% CI)	P (95% CI)
Intercept	1.723 (1.723–1.723)	.113 (.111–.114)	15.351 (15.264–15.437)	.000 (.000–.000)
Habitat	.203 (.203–.203)	.094 (.094–.094)	2.169 (2.166–2.172)	**.033 (.032–.033)**
Diet	.460 (.459–.461)	.098 (.098–.098)	4.700 (4.691–4.709)	**.000 (.000–.000)**

Note: Nonbreeding distribution was scored as solitary to flocking, habitat was scored as open to closed, and diet was scored as insectivorous to granivorous. Phylogenetic generalized least squares (PGLS) analyses using 200 iterations. Estimate, SE, and t value of probability of PGLS are shown. λ, mean (95% confidence interval [CI]) = 0.002 (0.000–0.005). R^2, mean (95% CI) = 0.341 (0.340–0.342). Significant P values are in bold.

that nonbreeding distribution and diet have direct links to mating system and that habitat is also directly related to breeding distribution (fig. 5*B*; tables S3, S4).

Discussion

Our work produced two main results. First, our phylogenetic comparative analyses support the main component of Crook's proposition: both diet and habitat predict social organization in the nonbreeding season, and nonbreeding distribution predicts coloniality and, ultimately, mating system and sexual dimorphism in weavers. Second, using confirmatory PPAs, we reveal novel relationships suggesting a direct link between spatial distribution during the nonbreeding season and mating system.

Resource Distribution and Social Organization

Crook (1964) proposed two key hypotheses to explain why some weavers live in flocks during the nonbreeding season: (1) improved feeding efficiency and (2) reduced predation risk. Improved feeding efficiency can occur when groups are more efficient at finding food patches (Krebs 1974), copying foraging locations (Krebs 1973; Waite and Grubb 1988), and avoiding food patches that have already been depleted by other members of the group (Cody 1971; Beauchamp 2005). Research has revealed that group foraging in birds and fishes is explained, in part, by increased foraging efficiency (Ward and Zahavi 1973; Pitcher et al. 1982; Mariette and Griffith 2013; Rubolini et al. 2015).

Our results show that increasing composition of seeds in the diet is associated with more flocking, presumably to exploit temporarily available food patches. Seeds often have clumped distribution (Guo et al. 1998), and consistently, a high proportion of granivorous birds in open habitats have been observed to form flocks (Zarco and Cueto 2017), and group size tends to increase with seed density (Grzybowski 1983). Additionally, accessing locally abundant resources results in less conflict (Shen et al. 2014); therefore, granivorous weavers could form large flocks. Furthermore, insectivorous birds might not benefit as much as granivorous birds from being gregarious because their food is more evenly spaced (Ulyshen 2011; Zarco and Cueto 2017).

Reduced predation may contribute to (or drive) aggregations during the nonbreeding season. Consistent with Crook's suggestion, we found that weavers in open savanna were more likely to forage in flocks than forest-dwelling weavers. Birds normally prefer to feed near cover to escape predators (Walther and Gosler 2001; Carrascal and Alonso 2006). In open habitats, because of less vegetation cover, animals are more vulnerable to predators (Caro et al. 2004), and vigilance in savanna habitat increases with distance from the forest edge (Campos et al. 2009). There are additional benefits to flocking: reduced predation threats through predator confusion, diluted predation threats, and group defense or enhanced vigilance (Siegfried and Underhill 1975; Elgar 1989). Consistently, species living in open habitat were more likely to live in groups and form large flocks (San Jose et al. 1997; Rangeley and Kramer 1998).

Coloniality occurs in approximately 13% of all birds, and various hypotheses have been put forward to explain it (Bennett and Owens 2002). Our findings of stronger association between coloniality and flocking than between coloniality, habitat, or diet (table 2; fig. 5) suggest that sociality itself may be a selective factor promoting coloniality. In other words, if a species spends most of its time socializing outside the breeding season, the social interactions between population members can create a selection to seek closeness and tight interactions during breeding. This intriguing result then suggests that coloniality may evolve—at least in certain species—as a general tendency to seek close interactions and perhaps physical contacts with other members of the population (see below).

Our results showed that colony-breeding weavers had higher degrees of sexual dimorphism and more distinct breeding plumage than noncolonial weavers. Breeding in colonies may facilitate courtship and copulation through reproductive synchrony (Ims 1990) and increase the intensity of sexual selection through pre- and postcopulatory sexual competition (Hoi and Hoi-Leitner 1997; Waas et al. 2000). Interestingly, we found that weavers that breed in medium-sized colonies exhibit the largest extent of sexual dimorphism and breeding plumage change, which indicates that high levels of coloniality may constrain sexual selection; this is consistent with the findings of previous studies on seed bugs and fungus beetles (Conner 1989; McLain 1992).
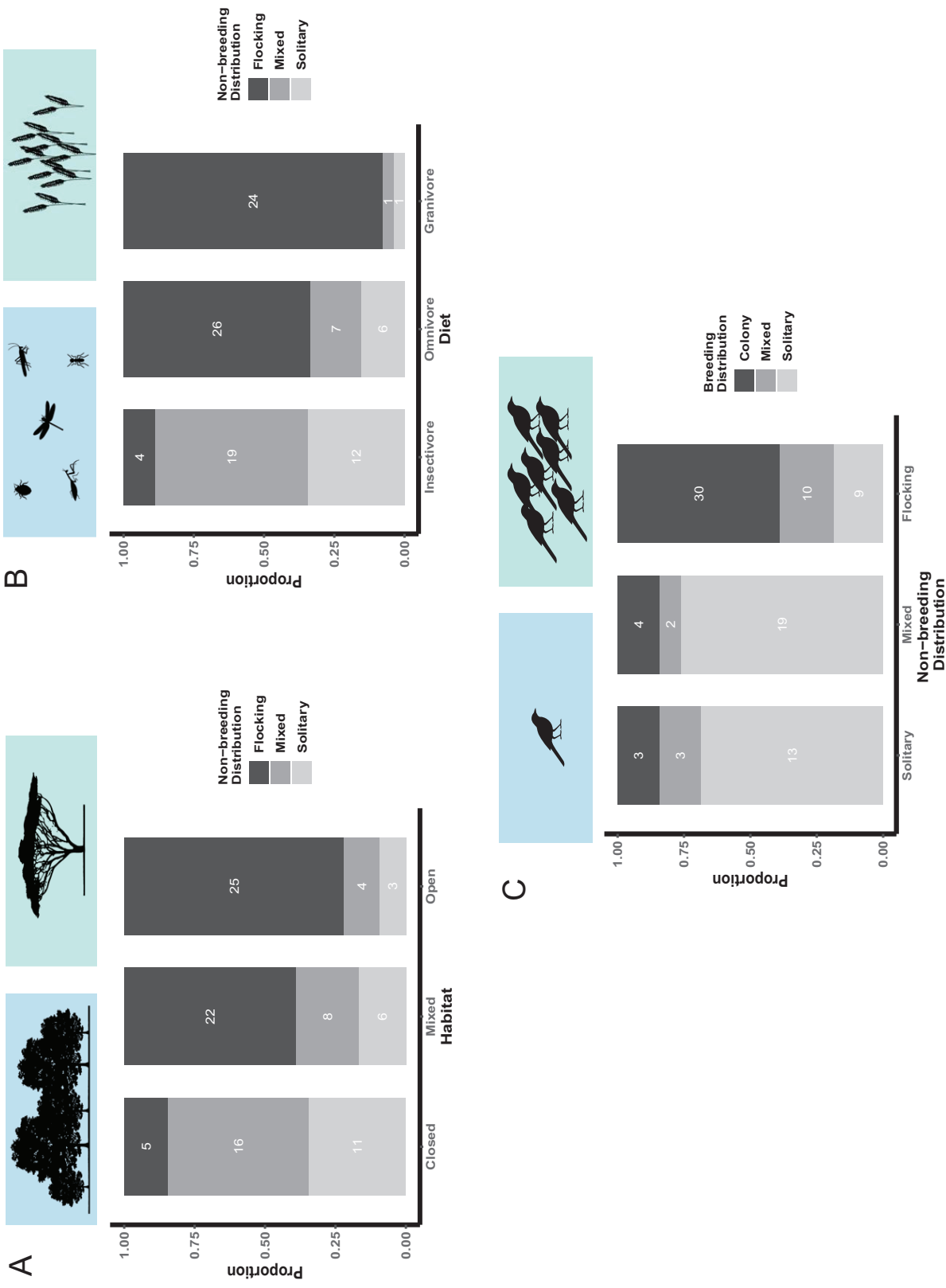
Figure 3: Nonbreeding distribution of weavers relative to habitat (*A*), diet (*B*), and breeding distribution (*C*; table S1). The number of species is shown.

Table 2: Spatial distribution during breeding and nonbreeding seasons in weavers (*n* = 93 species)

	Estimate (95% CI)	SE (95% CI)	*t* (95% CI)	*P* (95% CI)
Intercept	−.419 (−.432 to −.407)	.342 (.334 to .350)	−1.227 (−1.249 to −1.205)	.229 (.220 to .237)
Nonbreeding distribution	.426 (.423 to .430)	.126 (.125 to .126)	3.390 (3.354 to 3.426)	**.001 (.001 to .002)**
Habitat	.267 (.262 to .272)	.132 (.132 to .133)	2.022 (1.981 to 2.063)	.056 (.050 to .061)
Diet	.075 (.068 to .081)	.136 (.135 to .136)	.552 (.506 to .599)	.601 (.570 to .633)

Note: Breeding distribution was scored as solitary to colonial, nonbreeding distribution was scored as solitary to flocking, and habitat was scored as open to closed. Phylogenetic generalized least squares (PGLS) analyses using 200 iterations. Estimate, SE, and *t* value of probability of PGLS are shown. λ, mean (95% confidence interval [CI]) = 0.242 (0.218 to 0.266). R^2, mean (95% CI) = 0.291 (0.289 to 0.292). Significant *P* values are in bold.

Exploring Causal Relationships Using PPAs

Crook (1964) formulated his hypotheses based on the influence of several aspects of ecology on social organization. Without proper statistical analysis, however, it is difficult to disentangle a multivariate hypothesis that assumes causal and covariant effects among a set of variables. In standard path analyses, direct effects could be interpreted as indicators of possible direct causal relationships between variables in a model (Grace 2006).

Table 3: Relationship between breeding distribution (BD) and sexual size dimorphism (SSD) in weavers

	Estimate (95% CI)	SE (95% CI)	*Z* or *F* (95% CI)	*P* (95% CI)
Mating system (*n* = 83 species):[a]				
Intercept	−.153 (−.223 to −.084)	.853 (.842 to .865)	−.232 (−.323 to −.142)	.682 (.645 to .719)
BD	.897 (.885 to .910)	.282 (.278 to .285)	3.218 (3.150 to 3.286)	**.003 (.003 to .004)**
Breeding plumage (*n* = 105 species):[a]				
Intercept	.021 (−.068 to .110)	.672 (.653 to .691)	−.120 (−.255 to .014)	.499 (.457 to .540)
BD	.513 (.501 to .524)	.217 (.213 to .222)	2.378 (2.325 to 2.430)	**.026 (.022 to .029)**
SSD in wing length (*n* = 93 species):[b]				
BD	...	...	8.387 (8.272 to 8.503)	.001 (.001 to .001)
BD (solitary)	.036 (.035 to .037)	.027 (.027 to .027)	...	...
BD (mixed)	.100 (.099 to .101)	.031 (.030 to .031)	...	...
BD (colony)	.063 (.062 to .064)	.027 (.027 to .028)	...	...
SSD in tarsus length (*n* = 88 species):[b]				
BD	...	...	3.054 (2.988 to 3.120)	.058 (.054 to .062)
BD (solitary)	.032 (.032 to .033)	.014 (.014 to .014)	...	...
BD (mixed)	.047 (.047 to .048)	.017 (.017 to .018)	...	...
BD (colony)	.052 (.052 to .053)	.014 (.014 to .014)	...	...
SSD in body mass (*n* = 68 species):[b]				
BD	...	...	2.026 (1.887 to 2.166)	.186 (.173 to .199)
BD (solitary)	.079 (.076 to .081)	.034 (.032 to .036)	...	...
BD (mixed)	.105 (.101 to .109)	.043 (.041 to .045)	...	...
BD (colony)	.134 (.132 to .135)	.033 (.030 to .035)	...	...

Note: α, mean (95% confidence interval [CI]): mating system = 0.039 (0.037 to 0.041); breeding plumage = 0.087 (0.081 to 0.092). λ, mean (95% CI): SSD in wing = 0.687 (0.679 to 0.694); SSD in tarsus = 0.367 (0.357 to 0.376); SSD in mass = 0.211 (0.173 to 0.250). R^2, mean (95% CI): mating system = 0.498 (0.492 to 0.504); breeding plumage = 0.302 (0.292 to 0.311); SSD in wing = 0.157 (0.155 to 0.159); SSD in tarsus = 0.067 (0.066 to 0.068); SSD in mass = 0.058 (0.054 to 0.062). Breeding distribution was scored as solitary or colonial, mating system was scored as monogamy or polygamy, and breeding plumage was scored as permanent or changing (table S1). Phylogenetic generalized least squares (PGLS) analyses using 200 iterations. Estimate, SE, *Z* value, and *F* value of probability of PGLS are shown. Significant *P* values are in bold.

[a] Fitted using the package phyloglm. Significance was verified using the *Z* value of the regression coefficient, and the phylogenetic signal for a binary variable was measured by α (Ives and Garland 2014). The higher the α, the lower the phylogenetic signal.

[b] Fitted using the package caper with Pagel's λ maximum likelihood branch-length transformation. Significance was verified using the *F* value of the regression coefficient, and the phylogenetic signal for continuous and ordinal variables was measured by Pagel's λ (Münkemüller et al. 2012). The higher the λ, the higher the phylogenetic signal.
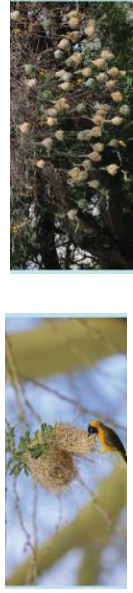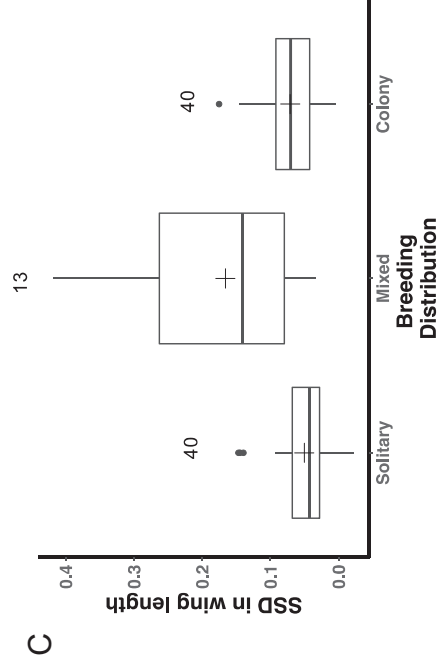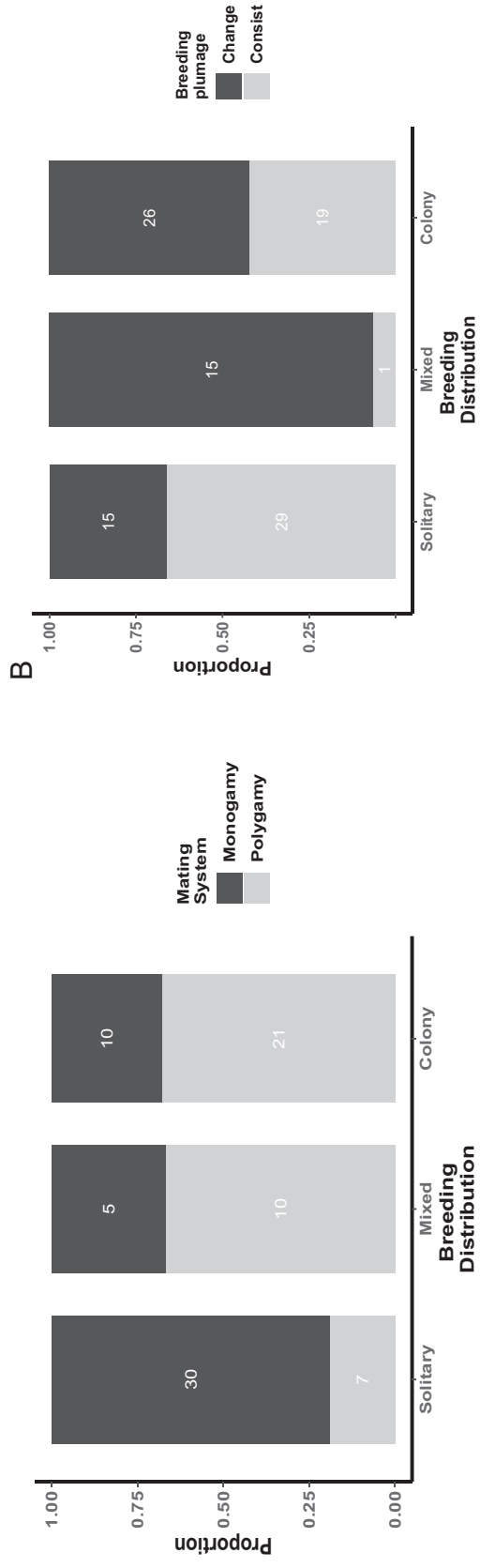
Figure 4: Breeding distribution in weavers relative to mating system (*A*), breeding plumage (*B*), and sexual size dimorphism (*C*). Mean ± SE and number of species are shown, and dots indicate outliers.

Table 4: Results of candidate model selection for the first set of phylogenetic path analyses on social organization in weavers (mean ± SE)

Path model	Fisher's C	df	Pc	AICc	CFI	TLI	RMSEA	SRMR
Crook's H	**29.052 ± .310**	**10**	**.003 ± .000**	**57.617 ± .364**	**.857 ± .002**	**.742 ± .004**	**.173 ± .002**	**.131 ± .001**
AH 1	44.535 ± .387	12	.000 ± .000	72.306 ± .448	.586 ± .002	.408 ± .003	.28 ± .001	.218 ± .001
AH 2	39.185 ± .361	12	.000 ± .000	66.120 ± .418	.623 ± .002	.462 ± .003	.267 ± .001	.216 ± .001
AH 3	57.144 ± .481	10	.000 ± .000	90.613 ± .565	.775 ± .002	.493 ± .005	.243 ± .001	.142 ± .001
AH 4	46.642 ± .286	10	.000 ± .000	78.278 ± .336	.702 ± .002	.463 ± .004	.251 ± .001	.172 ± .001
AH 5	46.805 ± .483	10	.000 ± .000	78.47 ± .568	.809 ± .003	.569 ± .006	.223 ± .002	.124 ± .001
AH 6	29.854 ± .251	10	.002 ± .000	58.559 ± .295	.964 ± .001	.918 ± .003	.094 ± .002	.074 ± .001

Note: See "Material and Methods" for details. Model codes correspond to diagrams presented in figure S1. For each model, we report the corrected Akaike information criterion (AICc) value, Bentler's comparative fit index (CFI), Tucker-Lewis index (TLI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR). For P values of Fishers' C statistic (Pc), significance indicates that the model was rejected by the data. Models were based on 75 weaver species. Supported models (with the lowest AICc values that contained all paths) are shown in bold.

The first set of PPAs investigated the main associations between resource distribution and social organization and the possible pathways between nonbreeding and breeding social organizations (figs. 5A, S1; table 4). Consistent with Crook (1964), we found that nonbreeding season distribution correlated with breeding season distribution and mating system, and both diet and habitat (resource distributions) were associated with nonbreeding distribution. However, all models in the first set of PPAs had a poor fit to the data (see "Results"). In the second set of PPAs, we found a major pathway not envisaged by Crook (1964), which is a direct association between nonbreeding distribution and mating system (table S3; fig. S2). By including this path, the model had a better fit to the data (table S3; figs. 5B, S2).

The best-supported path model (table S3; figs. 5B, S2) indicated that mating system was influenced by both nonbreeding and breeding distributions. It is difficult to tease apart tightly evolved traits such as breeding and nonbreeding distributions, although one possible reason for the significant influence of nonbreeding distribution on mating system is social environment. Components of social system, such as breeding and nonbreeding distributions and mating system, could coevolve (Kappeler 2019). Species that have flocks in the nonbreeding season show less territorial behavior and higher mutual tolerance for conspecific individuals, which promotes coloniality (Kappeler 2019). Furthermore, group living may result in reproductive synchrony (Ims 1990; Smith 2004), and reproductive synchrony could further promote extrapair paternity and polygamy (Grunst et al. 2017). Additionally, the availability of potential mate and breeding density could affect the balance between mating effort and parental care, and this could influence mating system evolution (Emlen and Oring 1977; Reynolds 1987; Székely et al. 2000). Furthermore, recent studies found that a population's social environment could influence breeding strategies. For example, mating system variation in plovers and other shorebirds is driven by skewed adult sex ratios (Liker et al. 2013; Székely et al. 2014; Eberhart-Phillips

et al. 2018). Therefore, ecological factors, such as diet and habitat, may act in concert with demographic factors, such as adult sex ratio, to influence mating systems.

Our study used 200 phylogenetic trees to control for phylogenetic uncertainty and Pagel's λ to estimate phylogenetic signal in the models (Molina-Venegas and Rodríguez 2017). The influence of diet and habitat on weavers' nonbreeding distribution showed limited phylogenetic signal (table 1), which indicated that flocking behavior is influenced by ecology rather than phylogenetic constraints. We used scores to quantify ecology and social organization, which is consistent with most comparative analyses in this research field (Liker et al. 2013; Remeš et al. 2015; Vági et al. 2019), although we did not consider trait variation within populations. As more data become available for each weaver population, follow-up studies could use finer-resolution data and consider population-level analyses.

From a broader perspective, our analyses showed both the power and the limitation of intuition-based behavioral ecology. Crook did not use quantitative methods and simply inferred patterns from observing co-occurrence of traits across weavers. Luckily, the ecology and social behavior of weavers were varied, and there were independent transitions in traits across the phylogeny. The size of the clade (more than 100 extant species) and the independent evolutionary changes certainly contributed to the consistency between Crook's intuition and the phylogenetically controlled analyses.

Social Organization beyond Crook's Hypotheses

Weavers that live in open habitat usually breed in colonies and are polygynous, with females usually providing more care than males. Coloniality facilitates male desertion and remating (Danchin and Wagner 1997), which is advantageous for males. Females that breed in open habitat remain in colonial formation regardless of whether they are constrained by
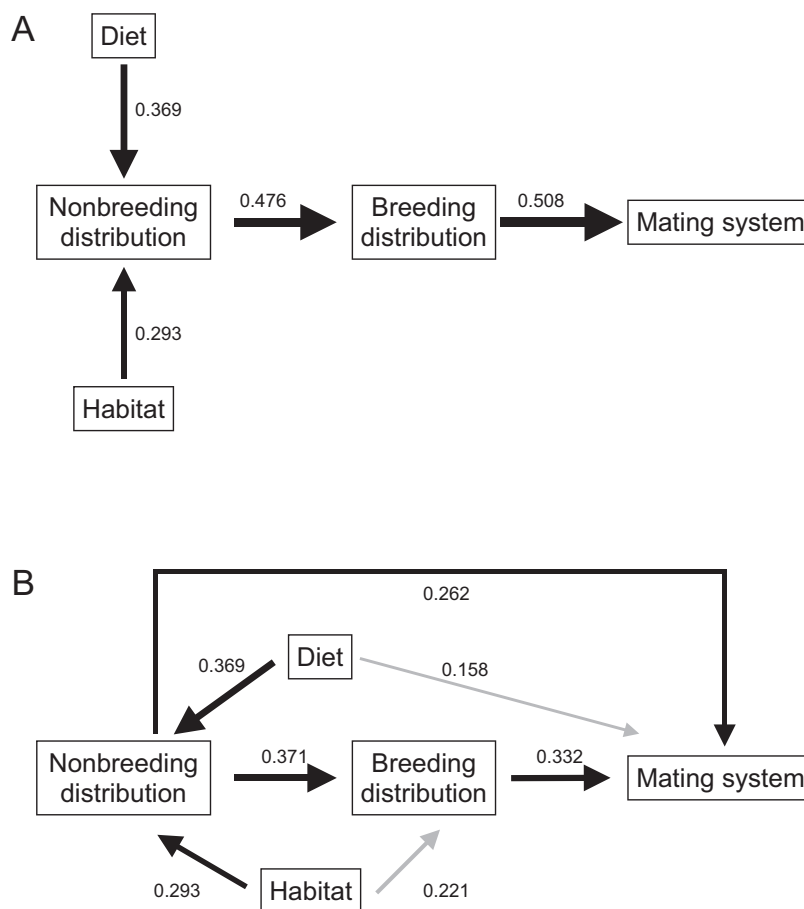
Figure 5: Phylogenetic path models of social organization in weavers ($n = 75$). *A* shows the best-supported model from the first set (table 4; fig. S1), and *B* shows the best-supported model from the second set (). Arrows indicate direct effects; the strength of the effect is indicated by numeric values and line thickness. Arrow color indicates the significance of the effect (black indicates significant, and gray indicates non-significant; model AH2.5 in table S3).

the clumped resource distribution. However, whether the clumped resource distribution constraint forces females to breed in colonies over the antagonistic interests between sexes needs be further investigated.

Crook (1964) suggested that clumped resources are locally superabundant; therefore, a single parent could raise an entire clutch, which promotes polygamy. However, in our study we failed to find a direct relationship between either habitat type or diet with weaver mating system. Indeed, recent studies on mating system evolution emphasized the link between parental care and social monogamy, which indicates that paternal care and monogamy are coadapted (Lukas and Clutton-Brock 2013; Sinervo et al. 2020). Male parental care behaviors can increase female fecundity, which shows that parental conflict may be symmetric between sexes (West and Capellini 2016). In addition, recent studies have suggested the influence of mating opportunities and adult sex ratios on breeding strategies (Székely et al. 2000,

2014; Schacht et al. 2017). However, teasing apart the complex effects of ecology, life history, and demography on breeding system evolution (and vice versa; see Liker et al. 2013; Székely 2019; Safari and Goymann 2021) remains a challenging task for behavioral ecologists.

Conclusions

Our study using modern phylogenetic comparative approaches confirms a fundamental premise in behavioral ecology and sociobiology by showing that ecology and aggregations are associated with mating system and sexual size dimorphism. PPAs confirmed Crook's (1964) conjectures and additionally revealed novel relationships. We suggest three major follow-up studies. First, it will be informative to quantitatively test how resource availability and spatial distribution influence flock size and how colony size influences the costs and benefits of these relationships.

Second, climate change seems to produce extreme changes in natural ecosystems, and it will be informative to determine how climatic variations influence Crook's scenario. Finally, beyond weavers, it will be important to ascertain the generality and validity of Crook's scenario in shaping social organization across a wide range of organisms.

Acknowledgments

Statement of Authorship

T.S., Y.L., and Z.S. conceived the study, conducted the analyses, and wrote the manuscript; A.L. contributed to data analyses and manuscript writing and reviewed drafts of the manuscript. All authors reviewed the manuscript and gave final approval for publication.

Data and Code Availability

Data sets of weaver ecology and social organizations that we analyzed in this study are available at the Dryad Digital Repository (https://doi.org/10.5061/dryad.7wm37pvq4; Song 2022), and code for analysis is available at Zenodo (https://doi.org/10.5281/zenodo.5785586).

Literature Cited

Adams, D. M., C. Nicolay, and G. S. Wilkinson. 2019. Patterns of sexual dimorphism and mating systems. Pages 221–236 *in* T. H. Fleming, L. Davalos, and M. Mello, eds. Phyllostomid bats: a unique mammalian radiation. University of Chicago Press, Chicago.

Beauchamp, G. 2005. Does group foraging promote efficient exploitation of resources? Oikos 111:403–407.

Bennett, P. M., and I. P. F. Owens. 2002. Evolutionary ecology of birds: life histories, mating systems and extinction. Oxford University Press, Oxford.

Bentler, P. M. 1990. Comparative fit indexes in structural models. Psychological Bulletin 107:238–246.

———. 1995. EQS structural equations program manual. Multivariate Software, Los Angeles.

Browne, M. W., and R. Cudeck. 1992. Alternative ways of assessing model fit. Sociological Methods and Research 21:230–258.

Campos, D. P., L. A. Bander, A. Raksi, and D. T. Blumstein. 2009. Perch exposure and predation risk: a comparative study in passerines. Acta Ethologica 12:93–98.

Caro, T., C. Graham, C. Stoner, and J. Vargas. 2004. Adaptive significance of antipredator behaviour in artiodactyls. Animal Behaviour 67:205–228.

Carrascal, L. M., and C. L. Alonso. 2006. Habitat use under latent predation risk: a case study with wintering forest birds. Oikos 112:51–62.

Cody, M. L. 1971. Finch flocks in the Mohave Desert. Theoretical Population Biology 2:142–158.

Conner, J. 1989. Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 43:1378–1386.

Craig, A. 2010. Family Ploceidae (weavers). Pages 74–197 *in* J. del Hoyo, A. Elliott, and D. A. Christie, eds. Handbook of the birds of the world. Vol. 15. Weavers to new world warblers. Lynx, Barcelona.

Cramp, S., and K. Simmons. 1988. Birds of Europe, the middle east and north Africa. Oxford University Press, Oxford.

Crook, J. H. 1964. The evolution of social organisation and visual communication in the weaver birds (Ploceinae). Behaviour 10:1–178.

Danchin, E., and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology and Evolution 12:342–347.

Darwin, C. 1871. The descent of man and selection in relation to sex. J. Murray, London.

Davies, N. B., J. R. Krebs, and S. A. West. 2012. An introduction to behavioural ecology. 5th ed. Wiley-Blackwell, Hoboken, NJ.

Dunning, J. B., Jr. 2007. CRC handbook of avian body masses. 2nd ed. CRC, Boca Raton, FL.

Eberhart-Phillips, L. J., C. Küpper, M. C. Carmona-Isunza, O. Vincze, S. Zefania, M. Cruz-López, A. Kosztolányi, et al. 2018. Demographic causes of adult sex ratio variation and their consequences for parental cooperation. Nature Communications 9:1651.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biological Reviews 64:13–33.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

Fairbairn, D. J., W. U. Blanckenhorn, and T. Székely. 2007. Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

———. 2004. Inferring phylogenies. Sinauer, Sunderland, MA.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160:712–726.

Frith, C. B. 2004. The birds of Africa. Vol. 7. Academic Press, San Diego.

Futuyma, D., and M. Kirkpatrick. 2017. Evolution. 4th ed. Sinauer, Sunderland, MA.

Gonzalez-Voyer, A., M. González-Suárez, C. Vilà, and E. Revilla. 2016. Larger brain size indirectly increases vulnerability to extinction in mammals. Evolution 70:1364–1375.

Graber, S. 2013. Phylogenetic comparative methods for discrete responses in evolutionary biology. Master's thesis. University of Zurich, Zurich.

Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge.

Grunst, M. L., A. S. Grunst, R. A. Gonser, and E. M. Tuttle. 2017. Breeding synchrony and extrapair paternity in a species with alternative reproductive strategies. Journal of Avian Biology 48:1087–1094.

Grzybowski, J. A. 1983. Sociality of grassland birds during winter. Behavioral Ecology and Sociobiology 13:211–219.

Guo, Q., P. W. Rundel, and D. W. Goodall. 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. Journal of Arid Environments 38:465–478.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Ho, L., and C. Ané. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. Systematic Biology 63:397–408.

Hoi, H., and M. Hoi-Leitner. 1997. An alternative route to coloniality in the bearded tit: females pursue extra-pair fertilizations. Behavioral Ecology 8:113–119.

Hooper, D., J. Coughlan, and M. R. Mullen. 2008. Structural equation modelling: guidelines for determining model fit. Electronic Journal of Business Research Methods 6:53–60.

Iglesias-Carrasco, M., M. D. Jennions, S. Y. Ho, and D. A. Duchêne. 2019. Sexual selection, body mass and molecular evolution interact to predict diversification in birds. Proceedings of the Royal Society B 286:20190172

Ims, R. A. 1990. The ecology and evolution of reproductive synchrony. Trends in Ecology and Evolution 5:135–140.

Ives, A. R., and T. Garland. 2014. Phylogenetic regression for binary dependent variables. Pages 231–261 in L. Z. Garamszegi, ed. Modern phylogenetic comparative methods and their application in evolutionary biology. Springer, Berlin.

Jarman, P. 1974. The social organisation of antelope in relation to their ecology. Behaviour 48:215–267.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Kappeler, P. M. 2019. A framework for studying social complexity. Behavioral Ecology and Sociobiology 73:13.

Krebs, J. R. 1973. Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). Canadian Journal of Zoology 51:1275–1288.

———. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). Behaviour 51:99–134.

Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Lifjeld, J. T., J. Gohli, T. Albrecht, E. Garcia-del-Rey, L. E. Johannessen, O. Kleven, P. Z. Marki, et al. 2019. Evolution of female promiscuity in Passerides songbirds. BMC Evolutionary Biology 19:1–14.

Liker, A., R. P. Freckleton, and T. Székely. 2013. The evolution of sex roles in birds is related to adult sex ratio. Nature Communications 4:1587.

Lukas, D., and T. H. Clutton-Brock. 2013. The evolution of social monogamy in mammals. Science 341:526–530.

Mariette, M. M., and S. C. Griffith. 2013. Does coloniality improve foraging efficiency and nestling provisioning? a field experiment in the wild zebra finch. Ecology 94:325–335.

Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. American Naturalist 149:646–667.

McLain, D. K. 1992. Population density and the intensity of sexual selection on body length in spatially or temporally restricted natural populations of a seed bug. Behavioral Ecology and Sociobiology 30:347–356.

Molina-Venegas, R., and M. Á. Rodríguez. 2017. Revisiting phylogenetic signal: strong or negligible impacts of polytomies and branch length information? BMC Evolutionary Biology 17:53.

Münkemüller, T., S. Lavergne, B. Bzeznik, S. Dray, T. Jombart, K. Schiffers, and W. Thuiller. 2012. How to measure and test phylogenetic signal. Methods in Ecology and Evolution 3:743–756.

Nunn, C. L. 2011. The comparative approach in evolutionary anthropology and biology. University of Chicago Press, Chicago.

Orme, D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. https://cran.r-project.org/web/packages/caper/vignettes/caper.pdf.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877.

Pitcher, T., A. Magurran, and I. Winfield. 1982. Fish in larger shoals find food faster. Behavioral Ecology and Sociobiology 10:149–151.

Rangeley, R. W., and D. L. Kramer. 1998. Density-dependent antipredator tactics and habitat selection in juvenile pollock. Ecology 79:943–952.

Remeš, V., R. P. Freckleton, J. Tökölyi, A. Liker, and T. Székely. 2015. The evolution of parental cooperation in birds. Proceedings of the National Academy of Sciences of the USA 112:13603–13608.

Reynolds, J. D. 1987. Mating system and nesting biology of the red-necked Phalarope *Phalaropus lobatus*: what constrains polyandry? Ibis 129:225–242.

Rosseel, Y. 2012. lavaan: an R package for structural equation modeling. Journal of Statistical Software 48:1–36.

Rubenstein, D. R., and J. Alcock. 2019. Animal Behavior. Sinauer, Sunderland, MA.

Rubolini, D., I. Maggini, R. Ambrosini, S. Imperio, V. H. Paiva, G. Gaibani, N. Saino et al. 2015. The effect of moonlight on Scopoli's shearwater *Calonectris diomedea* colony attendance patterns and nocturnal foraging: a test of the foraging efficiency hypothesis. Ethology 121:284–299.

Safari, I., and W. Goymann. 2021. The evolution of reversed sex roles and classical polyandry: insights from coucals and other animals. Ethology 127:1–13.

San Jose, C., S. Lovari, and N. Ferrari. 1997. Grouping in roe deer: an effect of habitat openness or cover distribution? Acta Theriologica 42:235–239.

Santos, J. C. 2012. Fast molecular evolution associated with high active metabolic rates in poison frogs. Molecular Biology and Evolution 29:2001–2018.

Santos, J. C., and D. C. Cannatella. 2011. Phenotypic integration emerges from aposematism and scale in poison frogs. Proceedings of the National Academy of Sciences of the USA 108:6175–6180.

Schacht, R., K. L. Kramer, T. Székely, and P. M. Kappeler. 2017. Adult sex ratios and reproductive strategies: a critical re-examination of sex differences in human and animal societies. Philosophical Transactions of the Royal Society B 372:1729.

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

Shipley, B. 2013. The AIC model selection method applied to path analytic models compared using ad-separation test. Ecology 94:560–564.

Siegfried, W. R., and L. Underhill. 1975. Flocking as an anti-predator strategy in doves. Animal Behaviour 23:504–508.

Sinervo, B., A. S. Chaine, and D. B. Miles. 2020. Social games and genic selection drive mammalian mating system evolution and speciation. American Naturalist 195:247–274.

Smith, H. G. 2004. Selection for synchronous breeding in the European starling. Oikos 105:301–311.

Song, Z. 2022. Data from: Evolution of social organization: phylogenetic analyses of ecology and sexual selection in weavers. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.7wm37pvq4.

Stoffel, M. A., S. Nakagawa, and H. Schielzeth. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution 8:1639–1644.

Symonds, M. R., and S. P. Blomberg. 2014. A primer on phylogenetic generalised least squares. Pages 105–130 *in* L. Z. Garamszegi, ed. Modern phylogenetic comparative methods and their application in evolutionary biology. Springer, Berlin.

Székely, T. 2019. Why study plovers? the significance of non-model organisms in avian ecology, behaviour and evolution. Journal of Ornithology 160:923–933.

Székely, T., A. J. Moore, and J. Komdeur. 2010. Social behaviour: genes, ecology and evolution. Cambridge University Press, Cambridge.

Székely, T., J. N. Webb, and I. C. Cuthill. 2000. Mating patterns, sexual selection and parental care: an integrative approach. Pages 194–223 *in* M. Apollonio, M. Festa-Bianchet, and D. Mainardi, eds. Vertebrate mating systems. World Science, London.

Székely, T., F. J. Weissing, and J. Komdeur. 2014. Adult sex ratio variation: implications for breeding system evolution. Journal of Evolutionary Biology 27:1500–1512.

Tucker, L. R., and C. Lewis. 1973. A reliability coefficient for maximum likelihood factor analysis. Psychometrika 38:1–10.

Ulyshen, M. D. 2011. Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. Forest Ecology and Management 261:1479–1489.

Vági, B., Z. Végvári, A. Liker, R. P. Freckleton, and T. Székely. 2019. Parental care and the evolution of terrestriality in frogs. Proceedings of the Royal Society B 286:20182737.

von Hardenberg, A., and A. Gonzalez-Voyer. 2013. Disentangling evolutionary cause-effect relationships with phylogenetic confirmatory path analysis. Evolution 67:378–387.

Waas, J. R., M. Caulfield, P. W. Colgan, and P. T. Boag. 2000. Colony sound facilitates sexual and agonistic activities in royal penguins. Animal Behaviour 60:77–84.

Waite, T. A., and T. C. Grubb Jr. 1988. Copying of foraging locations in mixed-species flocks of temperate-deciduous woodland birds: an experimental study. Condor 90:132–140.

Walther, B., and A. Gosler. 2001. The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: *Parus*). Oecologia 129:312–320.

Ward, P., and A. Zahavi. 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. Ibis 115:517–534.

West, H. E., and I. Capellini. 2016. Male care and life history traits in mammals. Nature Communications 7:1–10.

West, S. G., A. B. Taylor, and W. Wu. 2012. Model fit and model selection in structural equation modeling. Pages 209–231 *in* R. H. Hoyle, ed. Handbook of structural equation modeling. Guilford, New York.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Harvard University Press, Cambridge, MA.

Zarco, A., and V. R. Cueto. 2017. Winter flock structure in the central monte desert, Argentina. Ardea 105:89–97.

Associate Editor: J. Albert C. Uy
Editor: Erol Akçay

"In the breeding season all weavers establish territories and the factors responsible for their dispersion are probably related to those determining the off-season dispersion of the species." A conclusion drawn by British behavioral ecologist John Hurrel Crook (1930–2011) in his landmark study on the social organization of weavers (or weaverbirds, family Ploceidae). Village weaver (*Ploceus cucullatus*), a typical colonial breeder commonly found at sub-Saharan Africa. (Photographed by Chao Zhao.)