Evolution of social organization: phylogenetic analyses of ecology and sexual selection in weavers

Running title: Evolution of social organization

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 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, UK

[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

* Correspondence: Liu Yang, email: liuy353@mail.sysu.edu.cn

ORCID:

Zitan Song: 0000-0001-9739-0233

András Liker: 0000-0001-8545-4869

Yang Liu: 0000-0003-4580-5518

Tamás Székely: 0000-0003-2093-0056

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, both during the non-breeding season (flocking vs solitary foraging) and 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 dataset of 107 weaver species. We showed that both diet and habitat type are associated with spatial distribution and the latter predicts mating system, consistent with Crook's propositions. The best supported phylogenetic path model (PPA) also supported Crook's arguments and uncovered a direct relationship between non-breeding 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 non-breeding 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 last 50 years, these studies have mainly progressed in evolutionary biology and organismal biology (Davies et al. 2012; Rubenstein and Alcock 2019; Wilson 1975). 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 on 9th October 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, 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 non-breeding and breeding seasons. Second, he laid the foundation for comparative analyses by proposing non-independent 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 based on 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 last two decades (Davies et al. 2012; Freckleton et al. 2002; Nunn 2011), 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 non-breeding season (i.e., flocking behavior), (ii) does the non-breeding 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 priori-defined path models to the data.

Material and methods

Data collection

We used primary research papers, 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; Dunning Jr 2007; Frith 2004), and published papers (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 Table S1 and Table S2, and uploaded in Dryad Digital Repository (see Data accessibility).

We used habitat type and diet type to represent nesting site and food resources, respectively, following Crook's definitions (Table S1 and Table 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 and open habitat). Diet type was classified as insectivorous, omnivorous, or granivorous.

We used three variables to represent social organization: (1) breeding distribution, (2) non-breeding 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 non-breeding distribution, solitary refers to foraging solitary, 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 classified 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 non-breeding distribution (R = 0.991).

Statistical analyses

To control for phylogenetic uncertainty, we ran each analysis using 200 phylogenetic trees extracted from 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, non-breeding distribution and mating system as functions of resource distribution and additional covariates using Phylogenetic Generalized Least Squares (PGLS, Freckleton et al. 2002; Martins and Hansen 1997). We first tested the effects of resource distribution on non-breeding distribution by fitting PGLS models (n = 98). We then fitted PGLS models with resource distribution and non-breeding 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 they represent discretized versions of actual (biologically) continuous variables (Symonds and Blomberg 2014; Graber 2013). PGLS are widely used in phylogenetic studies of discrete ordinal variables (Adams et al. 2019; Iglesias-Carrasco et al. 2019; Lifjeld et al. 2019; Liker et al. 2013; Remeš et al. 2015).

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; and 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 GLS 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, non-breeding 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 pre-specified that resource distributions affected breeding distribution, mating system, and/or non-breeding distribution (Fig. S1, also see Emlen and Oring 1977; Jarman 1974). Second, using the best-supported model from the first set, i.e., the models with the lowest 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 non-significant 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 indices: 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 fit indices were obtained using the "*lavaan*" package (Rosseel 2012). All statistical analyses were performed with R 3.6.0 (R Development Core Team; http://cran.r- project.org/).

Results

Resource distribution and social organization

Flocking during the non-breeding 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 non-breeding distribution (Table 1): 78.13% of the 32 species that live in open habitats (Fig. 3a) and 92.31% of the 26 species that have a granivorous diet (Fig. 3b) live in flocks, whereas only 15.63% of the 32 species from closed habitats and 11.43% of the 35 species with insectivorous diet live in flocks (Fig. 3a & b). Furthermore, non-breeding 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 (Fig. 2b, Fig. 4a). We found consistent, albeit non-significant, 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 non-breeding 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 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 also suggests that non-breeding distribution and diet have direct link to mating system, and habitat also directly are related to breeding distribution (Fig. 5b, Table S3, and Table 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 non-breeding season, and non-breeding 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 non-breeding 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 non-breeding 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 Jr 1988), and avoiding food patches that have already been depleted by other members of the group (Beauchamp 2005; Cody 1971). Research has revealed that group foraging in birds and fishes is explained, in part, by increased foraging efficiency (Mariette and Griffith 2013; Pitcher et al. 1982; Rubolini et al. 2015; Ward and Zahavi 1973).

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, 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 non-breeding 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 (Carrascal and Alonso 2006; Walther and Gosler 2001). 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, diluting predation threats, and group defense or enhanced vigilance (Elgar 1989; Siegfried and Underhill 1975). Consistently, species living in open habitat were more likely to live in groups and form large flocks (Rangeley and Kramer 1998; San Jose et al. 1997).

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 non-colonial weavers. Breeding in colonies may facilitate courtship and copulation through reproductive synchrony (Ims 1990), and increase the intensity of sexual selection through pre- and post-copulatory 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).

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).

The first set of PPAs investigated the main associations between resource distribution and social organization, and the possible pathways between non-breeding and breeding social organizations (Fig. 5a, Table 4, Fig. S1). Consistent with Crook (1964), we found that non-breeding season distribution correlated with breeding season distribution and mating system, and both diet and habitat (resource distributions) were associated with non-breeding 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 that a major pathway not envisaged by Crook (1964) which is a direct association between non-breeding distribution and mating system (Table S3, Fig. S2). By including this path, the model had a better fit to the data (Table S3, Fig. S2 and Fig. 5b).

The best-supported path model (Table S3, Fig. 5b, and Fig. S2) indicated that mating system was influenced by both non-breeding and breeding distributions. It is difficult to tease apart tightly evolved traits such as breeding and non-breeding distributions, although one possible reason for the significant influence of non-breeding distribution on mating system is social environment. Components of social system, such as breeding and non-breeding distributions and mating system, could co-evolve (Kappeler, 2019). Species that have flocks in the non-breeding 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 extra-pair 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 (Eberhart-Phillips et al. 2018; Liker et al. 2013; Székely et al. 2014). 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' non-breeding 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 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 (over 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 re-mating (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 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 (Schacht et al. 2017; Székely et al. 2000; Székely et al. 2014). However, teasing apart the complex effects of ecology, life history, and demography on breeding system evolution (and vice versa, see Liker et al. 2013; Safari and Goymann 2021; Székely 2019) remains a challenging task for behavioral ecologists.

Conclusions

Our study using modern phylogenetic comparative approaches confirm a fundamental premise in behavioral ecology and sociobiology by showing that ecology and aggregations are associated with mating system and sexual size dimorphism. Phylogenetic path analyses 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.

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Statement of Authorship

TS, YL, and ZS conceived the study, conducted the analyses, and wrote the manuscript; AL contributed to data analyses and manuscript writing, and reviewed drafts of the paper. All authors reviewed the manuscript and gave final approval for publication.

Data accessibility

Datasets of weaver ecology and social organizations that we analyzed in this study are available at Dryad Digital Repository https://doi.org/10.5061/dryad.7wm37pvq4 and code for analysis available at Zenodo: https://doi.org/10.5281/zenodo.5785586

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Table 1 Non-breeding distribution is predicted by habitat and diet in weavers (n = 98 species).

	Estimate (95% CI)	Standard error (95% CI)	t (95% CI)	p (95% CI)
Intercept	1.723 (1.723, 1.723)	0.113 (0.111, 0.114)	15.351 (15.264, 15.437)	0.000 (0.000, 0.000)
Habitat	0.203 (0.203, 0.203)	0.094 (0.094, 0.094)	2.169 (2.166, 2.172)	**0.033 (0.032, 0.033)**
Diet	0.460 (0.459, 0.461)	0.098 (0.098, 0.098)	4.700 (4.691, 4.709)	**0.000 (0.000, 0.000)**

Non-breeding distribution was scored as solitary to flocking, habitat was scored as open to close, and diet was scored as insectivorous to granivorous. Phylogenetically corrected least-squares analyses (PGLS) using 200 iterations. Estimate, SE, and t value of probability of PGLS are shown. λ, mean (95% CI) = 0.002 (0.000, 0.005). R^2, mean (95% CI) = 0.341 (0.340, 0.342). Significant p values are in bold.

Table 2 Spatial distribution during breeding and non-breeding season in weavers (n = 93 species).

	Estimate (95% CI)	Standard error (95% CI)	t (95% CI)	p (95% CI)
Intercept	-0.419 (-0.432, -0.407)	0.342 (0.334, 0.350)	-1.227 (-1.249, -1.205)	0.229 (0.220, 0.237)
Non-breeding distribution	0.426 (0.423, 0.430)	0.126 (0.125, 0.126)	3.390 (3.354, 3.426)	**0.001 (0.001, 0.002)**
Habitat	0.267 (0.262, 0.272)	0.132 (0.132, 0.133)	2.022 (1.981, 2.063)	0.056 (0.050, 0.061)
Diet	0.075 (0.068, 0.081)	0.136 (0.135, 0.136)	0.552 (0.506, 0.599)	0.601 (0.570, 0.633)

Breeding distribution was scored as solitary to colonial, non-breeding distribution was scored as solitary to flocking, and habitat was scored as open to closed. Phylogenetically corrected least-squares analyses (PGLS) using 200 iterations. Estimate, SE, and t value of probability of PGLS are shown. λ, mean (95% CI) = 0.242 (0.218, 0.266). R^2, mean (95% CI) = 0.291 (0.289, 0.292). Significant p values are in bold.

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

	Estimate (95% CI)	Standard error (95% CI)	Z or F (95% CI)	p (95% CI)
Mating system[a] (n = 83 species)				
Intercept	-0.153 (-0.223, -0.084)	0.853 (0.842, 0.865)	-0.232 (-0.323, -0.142)	0.682 (0.645, 0.719)
Breeding distribution	0.897 (0.885, 0.910)	0.282 (0.278, 0.285)	3.218 (3.150, 3.286)	**0.003 (0.003, 0.004)**
Breeding plumage[a] (n = 105 species)				
Intercept	0.021 (-0.068, 0.110)	0.672 (0.653, 0.691)	-0.120 (-0.255, 0.014)	0.499 (0.457, 0.540)
Breeding distribution	0.513 (0.501, 0.524)	0.217 (0.213, 0.222)	2.378 (2.325, 2.430)	**0.026 (0.022, 0.029)**
SSD in wing length[b] (n = 93 species)				
Breeding distribution (BD)			8.387 (8.272, 8.503)	0.001 (0.001, 0.001)
BD (solitary)	0.036 (0.035, 0.037)	0.027 (0.027, 0.027)		
BD (mixed)	0.100 (0.099, 0.101)	0.031 (0.030, 0.031)		
BD (colony)	0.063 (0.062, 0.064)	0.027 (0.027, 0.028)		
SSD in tarsus length[b] (n = 88 species)				
Breeding distribution (BD)			3.054 (2.988, 3.120)	0.058 (0.054, 0.062)
BD (solitary)	0.032 (0.032, 0.033)	0.014 (0.014, 0.014)		
BD (mixed)	0.047 (0.047, 0.048)	0.017 (0.017, 0.018)		
BD (colony)	0.052 (0.052, 0.053)	0.014 (0.014, 0.014)		
SSD in body mass[b] (n = 68 species)				
Breeding distribution (BD)			2.026 (1.887, 2.166)	0.186 (0.173, 0.199)
BD (solitary)	0.079 (0.076, 0.081)	0.034 (0.032, 0.036)		
BD (mixed)	0.105 (0.101, 0.109)	0.043 (0.041, 0.045)		
BD (colony)	0.134 (0.132, 0.135)	0.033 (0.030, 0.035)		

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[a]: The model was fitted using the package "*phyloglm*" and 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.

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[b]: The model was fitted using the package “*caper*” with Pagel’s λ maximum likelihood branch length transformation and 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.

α, mean (95% CI): mating system, 0.039 (0.037, 0.041); breeding plumage, 0.087 (0.081, 0.092). λ, mean (95% CI): SSD in wing, 0.687 (0.679, 0.694); SSD in tarsus, 0.367 (0.357, 0.376); SSD in mass, 0.211 (0.173, 0.250). R^2, mean (95% CI): mating system, 0.498 (0.492, 0.504); breeding plumage, 0.302 (0.292, 0.311); SSD in wing, 0.157 (0.155, 0.159); SSD in tarsus, 0.067 (0.066, 0.068); SSD in mass, 0.058 (0.054, 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). Phylogenetically corrected least-squares analyses (PGLS) using 200 iterations. Estimate, SE, z, and F value of probability of PGLS are shown. Significant p values are in bold.

Table 4 Results of candidate model selection for the first set of phylogenetic path analyses on social organization in weavers (mean ± SE). See Material and methods for details.

Path model	Fisher's C	df	Pc	AICc	CFI	TLI	RMSEA	SRMR
Crook's H	**29.052 ± 0.310**	**10**	**0.003 ± 0.000**	**57.617 ± 0.364**	**0.857 ± 0.002**	**0.742 ± 0.004**	**0.173 ± 0.002**	**0.131 ± 0.001**
AH 1	44.535 ± 0.387	12	0.000 ± 0.000	72.306 ± 0.448	0.586 ± 0.002	0.408 ± 0.003	0.28 ± 0.001	0.218 ± 0.001
AH 2	39.185 ± 0.361	12	0.000 ± 0.000	66.120 ± 0.418	0.623 ± 0.002	0.462 ± 0.003	0.267 ± 0.001	0.216 ± 0.001
AH 3	57.144 ± 0.481	10	0.000 ± 0.000	90.613 ± 0.565	0.775 ± 0.002	0.493 ± 0.005	0.243 ± 0.001	0.142 ± 0.001
AH 4	46.642 ± 0.286	10	0.000 ± 0.000	78.278 ± 0.336	0.702 ± 0.002	0.463 ± 0.004	0.251 ± 0.001	0.172 ± 0.001
AH 5	46.805 ± 0.483	10	0.000 ± 0.000	78.47 ± 0.568	0.809 ± 0.003	0.569 ± 0.006	0.223 ± 0.002	0.124 ± 0.001
AH 6	29.854 ± 0.251	10	0.002 ± 0.000	58.559 ± 0.295	0.964 ± 0.001	0.918 ± 0.003	0.094 ± 0.002	0.074 ± 0.001

Model codes correspond to diagrams presented in Fig. S1. For each model, we report the AICc value, CFI, TLI, RMSEA, and SRMR. For p-values of Fishers' *C* statistic, 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 highlighted in bold.

Figure captions

Figure. 1 Social organization in relation to diet and habitat in weavers based on Crook (1964).

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) Non-breeding distribution, habitat, and diet (n = 98 species). Non-breeding distributions were scored as: (1) solitary foraging, (2) family parties or small mixed species foraging flocks, or (3) large foraging groups in non-breeding 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 photos: Handbook of the Birds of the World (del Hoyo et al. 2018).

Figure. 3 Non-breeding distribution of weavers relative to (a) habitat, (b) diet, and (c) breeding distribution (Table S1). The number of species is shown.

Figure. 4 Breeding distribution in weavers relative to (a) mating system, (b) breeding plumage, and (c) sexual size dimorphism. Mean ± stand error and number of species are shown, and dots indicate outliers. The number of species is shown.

Figure. 5 Phylogenetic path models of social organization in weavers (n = 75). (a) The best-supported model from the first set (Table 4 and Figure S1) and (b) the best-supported model from the second set (Table S3 and Figure S2). 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, significant; grey, non-significant; model AH2.5 in Table S3).

Figure 1

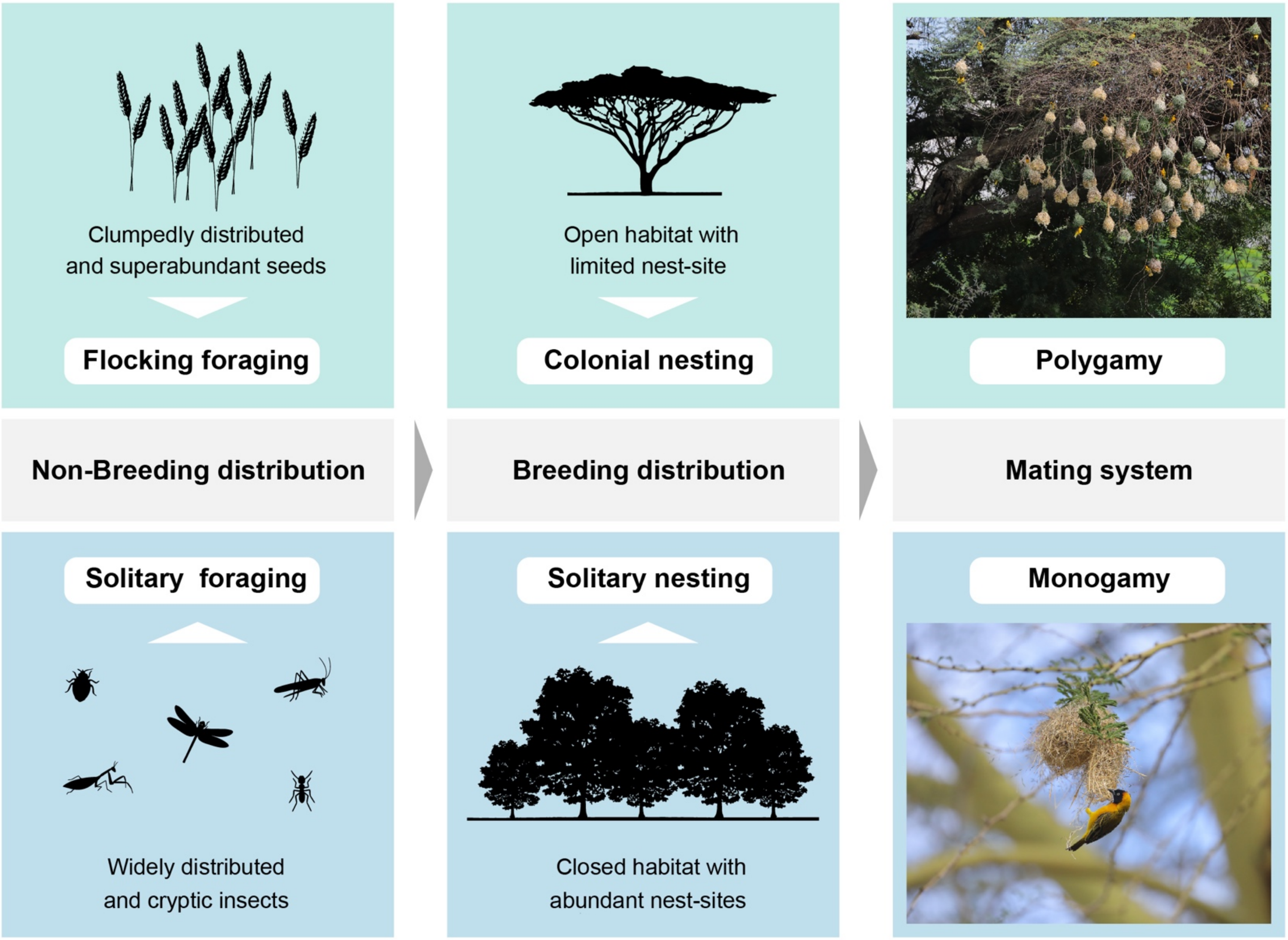

Clumpedly distributed
and superabundant seeds
Flocking foraging
Open habitat with
limited nest-site
Colonial nesting
Polygamy
Non-Breeding distribution
Breeding distribution
Mating system
Solitary foraging
Solitary nesting
Monogamy
Widely distributed
and cryptic insects
Closed habitat with
abundant nest-sites

Figure 2a

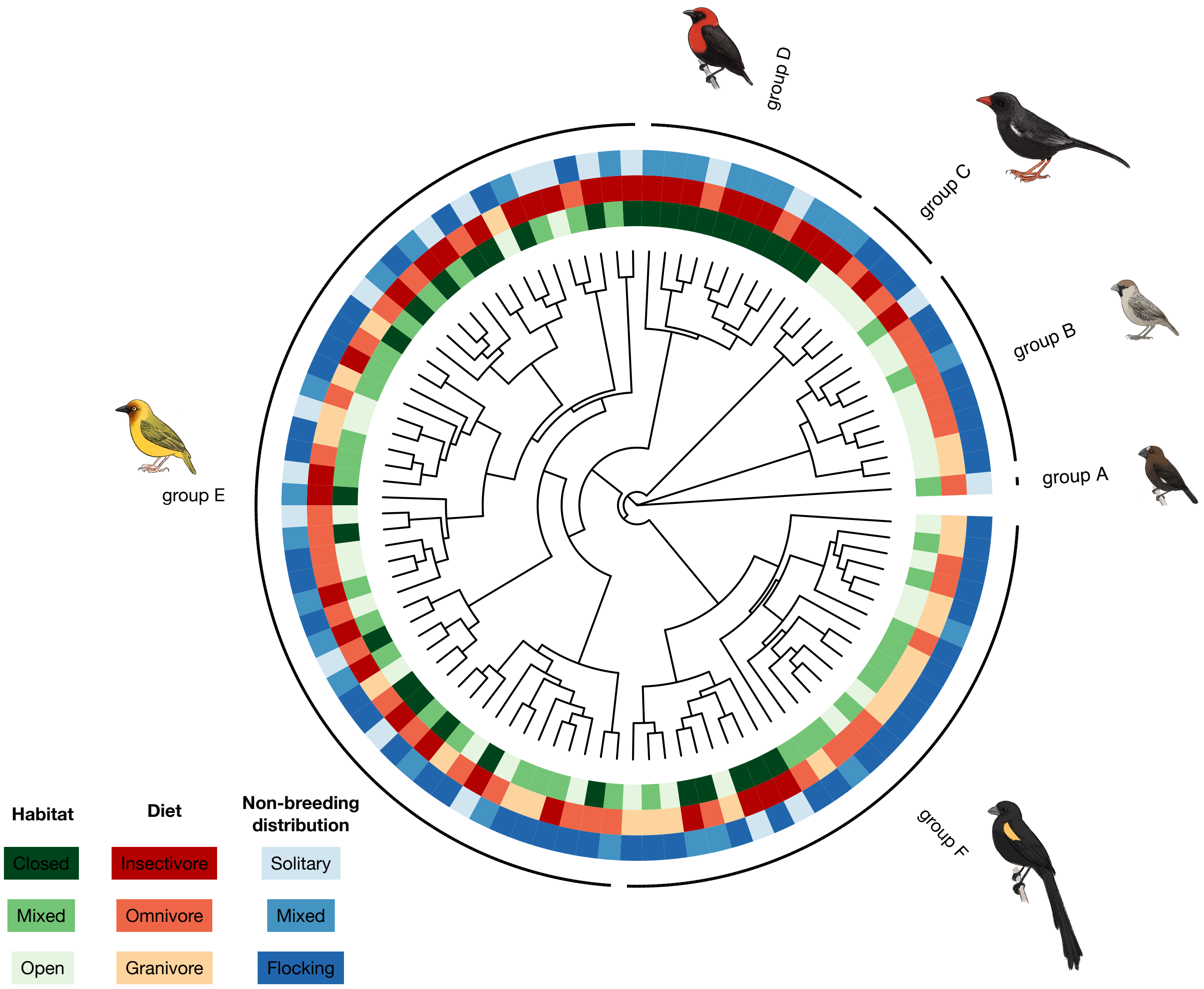

group D
group C
group B
group A
group E
group F
Habitat
Closed
Mixed
Open
Diet
Insectivore
Omnivore
Granivore
Non-breeding distribution
Solitary
Mixed
Flocking

Figure 2b

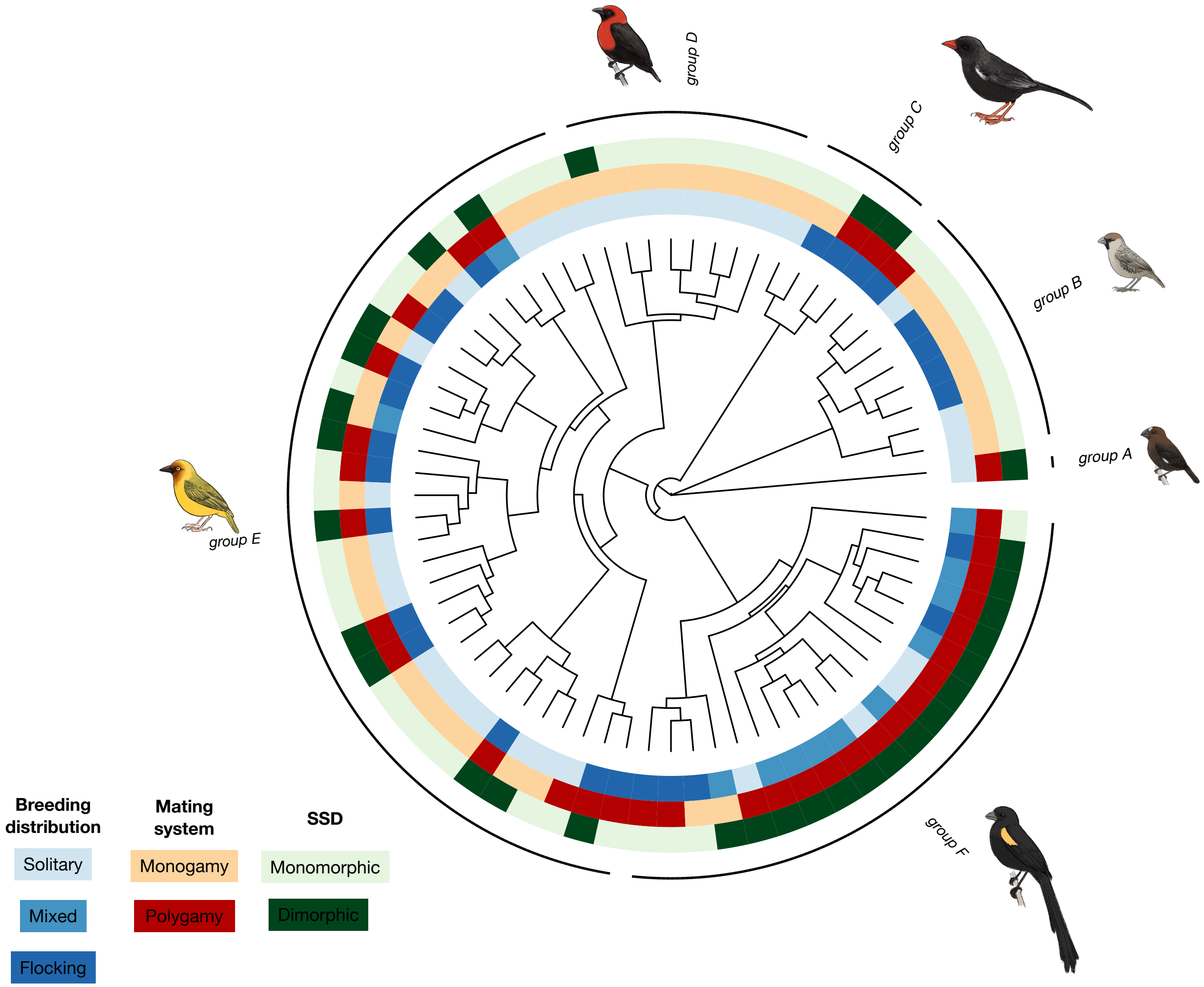

group D
group C
group B
group A
group E
group F
Breeding distribution
Solitary
Mixed
Flocking
Mating system
Monogamy
Polygamy
SSD
Monomorphic
Dimorphic

Figure 3a

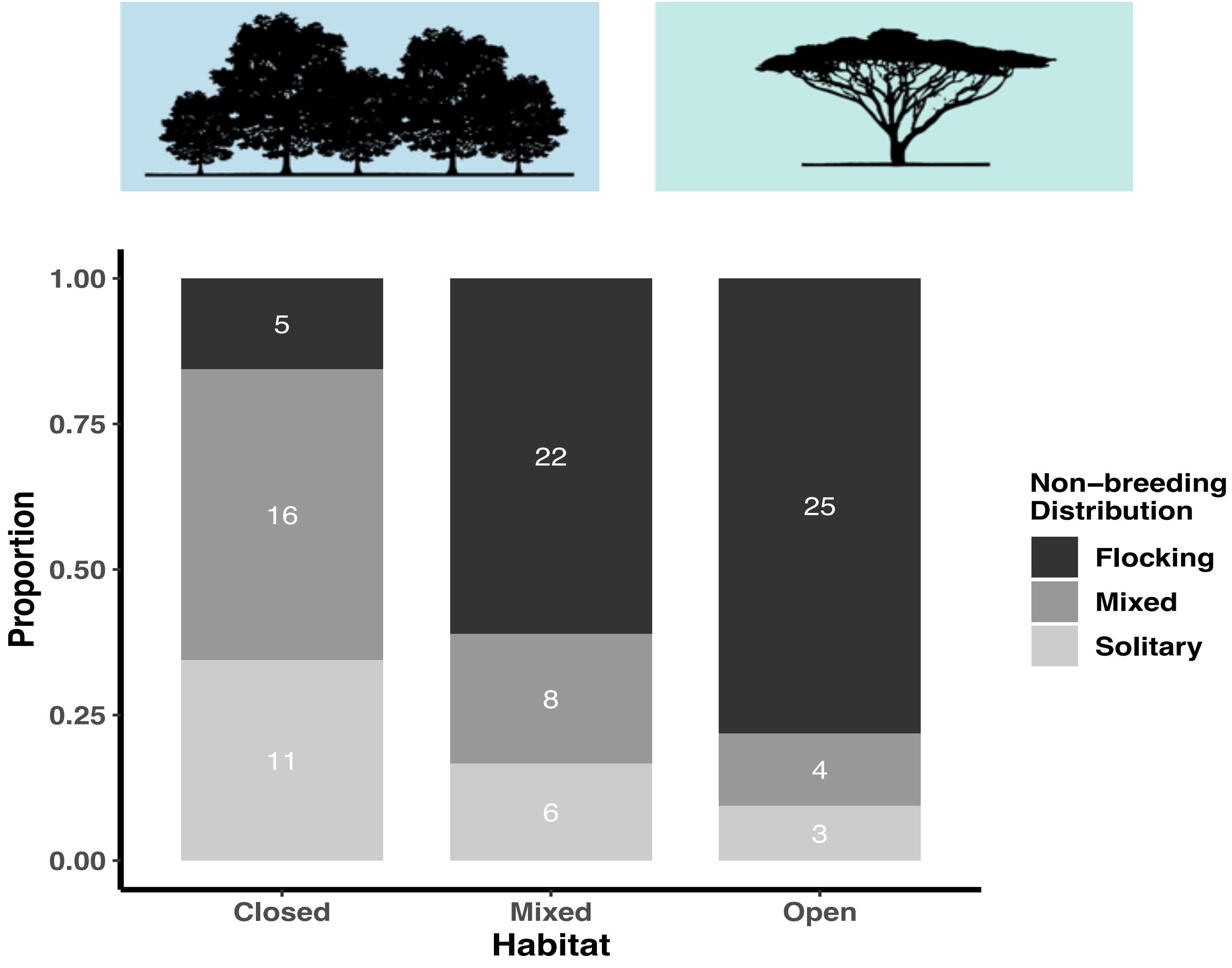
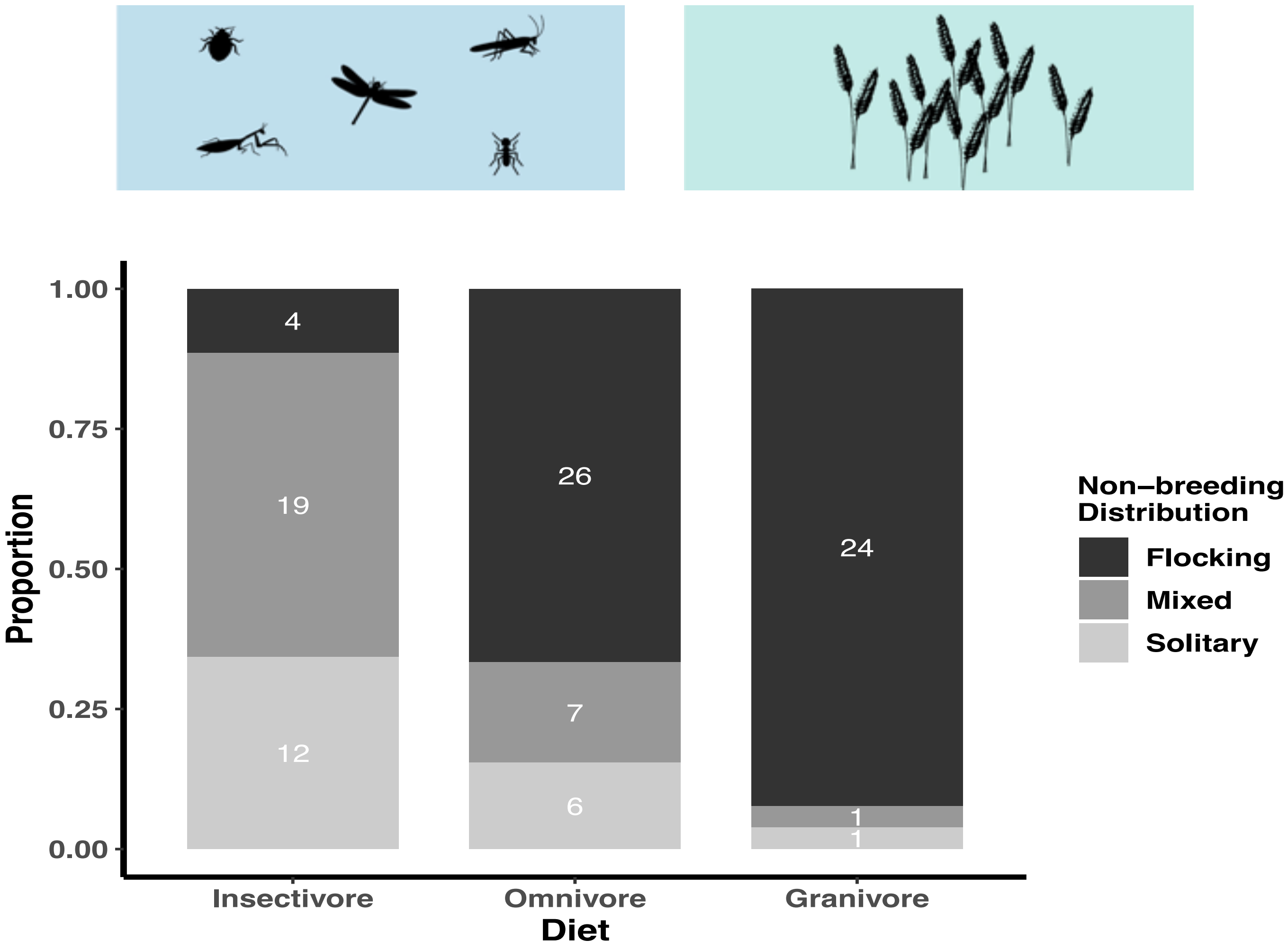
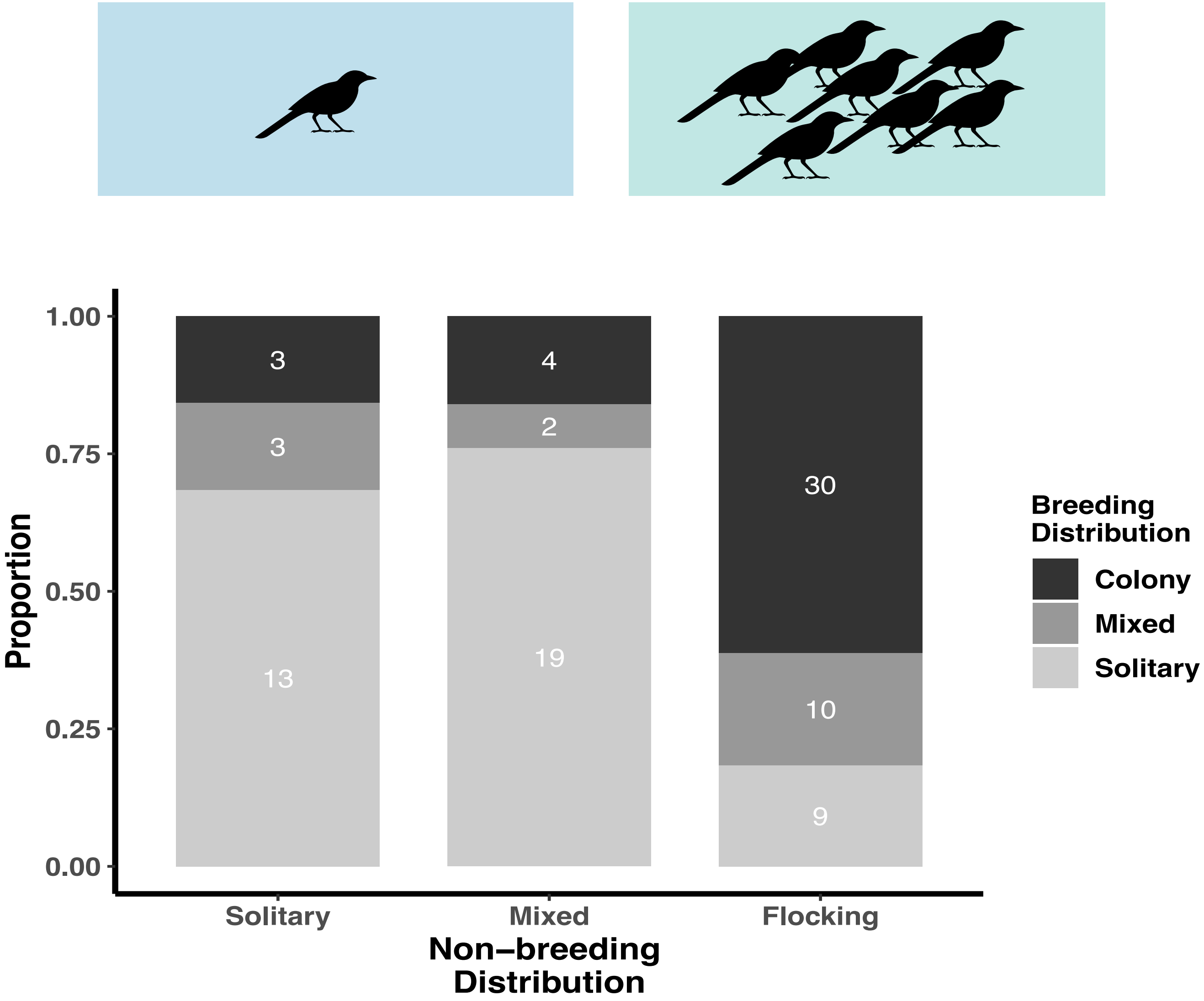

1.00
0.75
0.50
0.25
0.00
Proportion
5
16
11
22
8
6
25
4
3
Closed
Mixed
Open
Habitat
Non−breeding Distribution
Flocking
Mixed
Solitary

Figure 3b



Proportion
1.00
0.75
0.50
0.25
0.00
4
19
12
26
7
6
24
1
1
Insectivore
Omnivore
Granivore
Diet
Non–breeding
Distribution
Flocking
Mixed
Solitary

Figure 3c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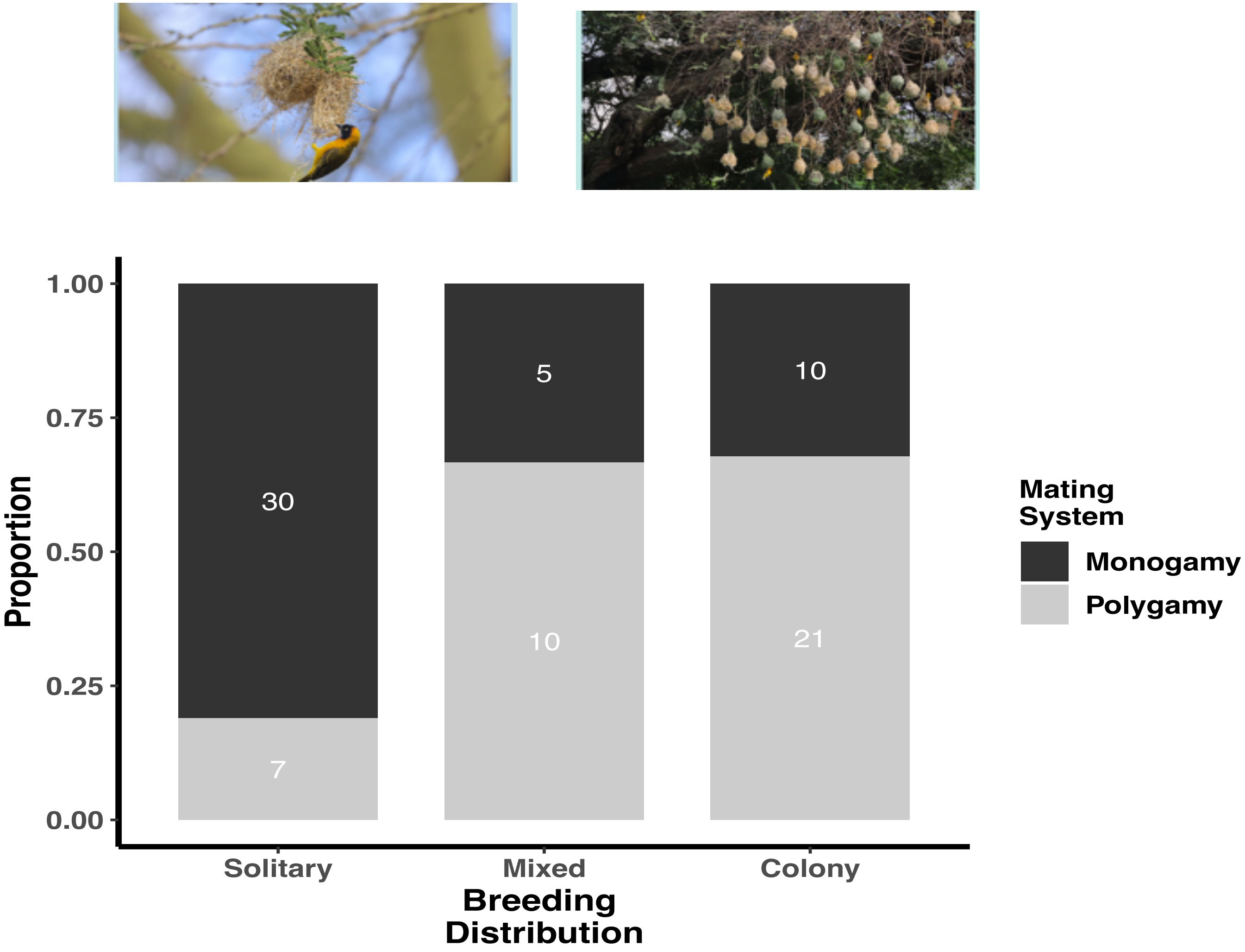
0.75
0.50
0.25
0.00
Proportion
3
3
13
4
2
19
30
10
9
Solitary
Mixed
Flocking
Non−breeding Distribution
Breeding Distribution
Colony
Mixed
Solitary

Figure 4a


1.00
0.75
0.50
0.25
0.00
Proportion
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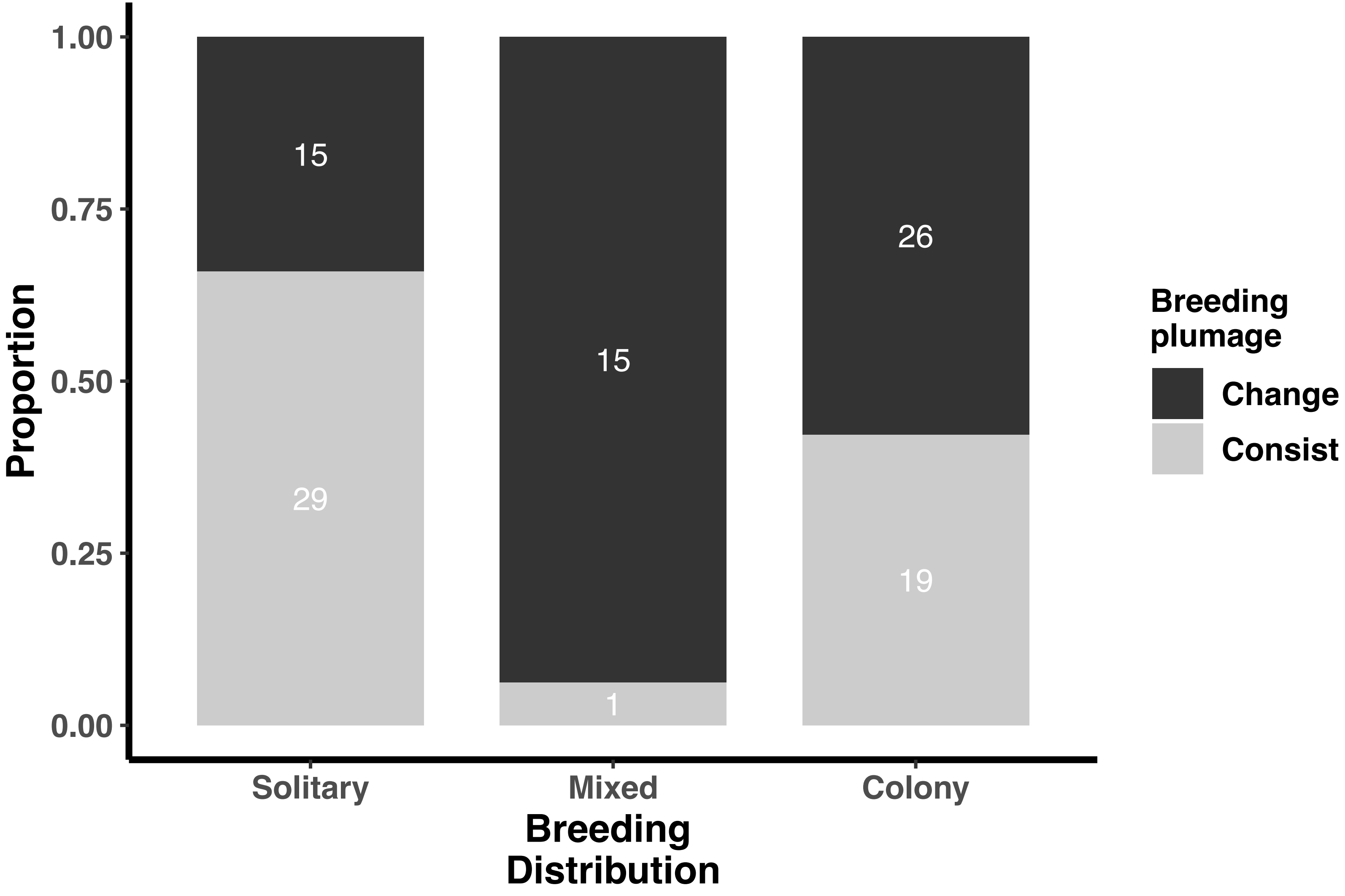
5
10
10
21
Solitary
Mixed
Colony
Breeding Distribution
Mating System
Monogamy
Polygamy

Figure 4b



Proportion
1.00
0.75
0.50
0.25
0.00
15
29
15
1
26
19
Solitary
Mixed
Colony
Breeding Distribution
Breeding plumage
Change
Consist

Figure 4c

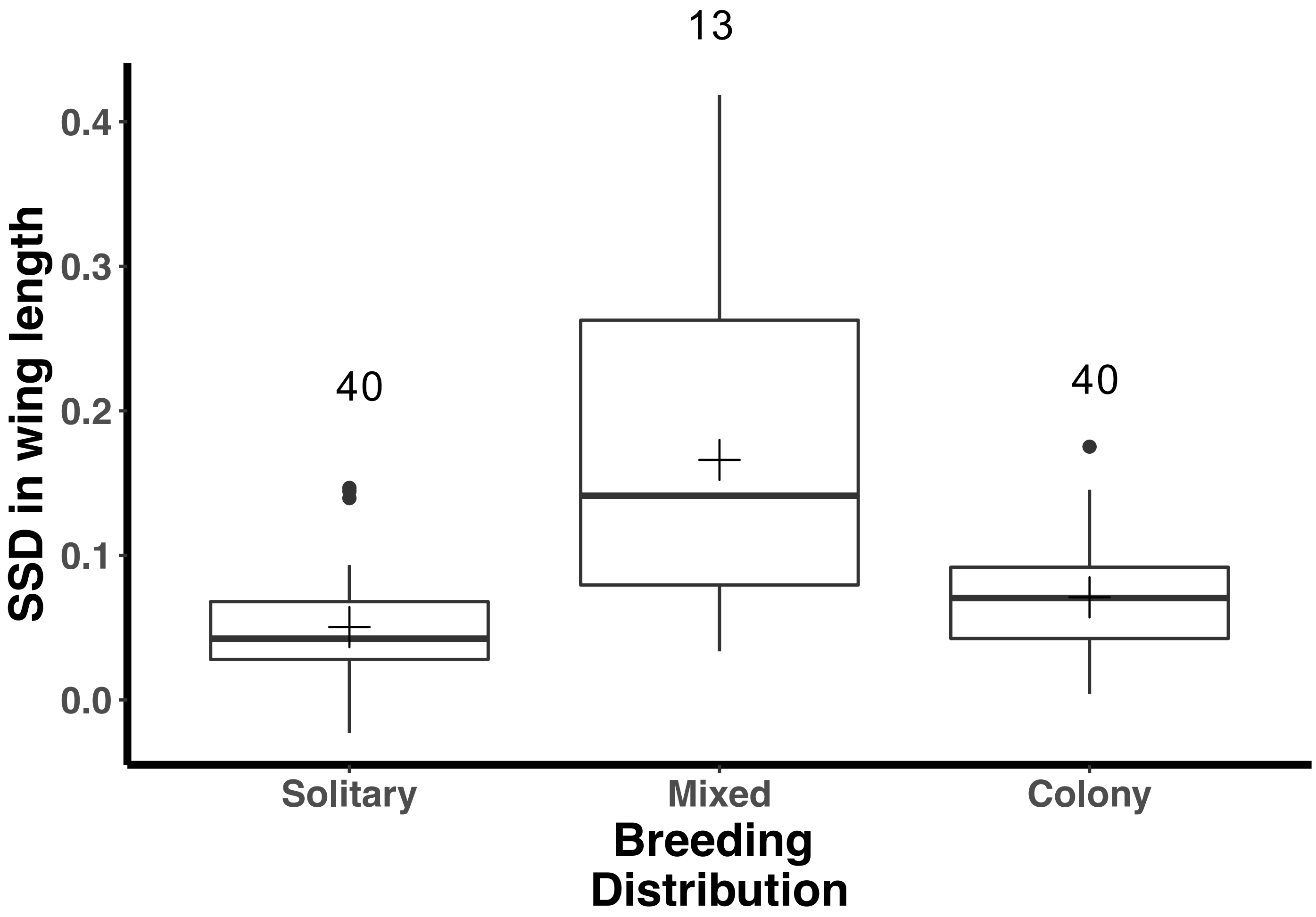

13
40
40
0.4
0.3
0.2
0.1
0.0
SSD in wing length
Solitary
Mixed
Colony
Breeding Distribution

Figure 5a

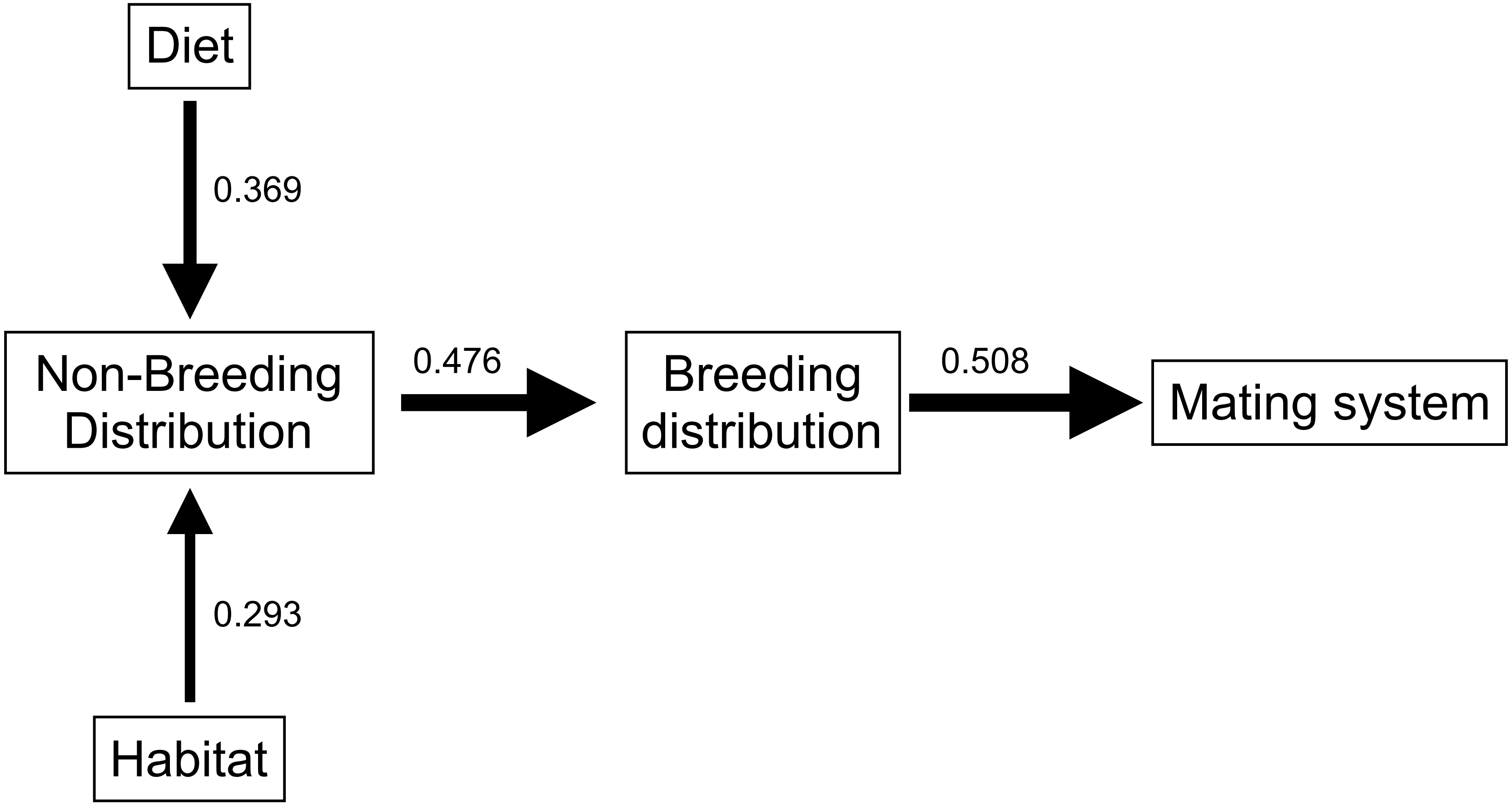
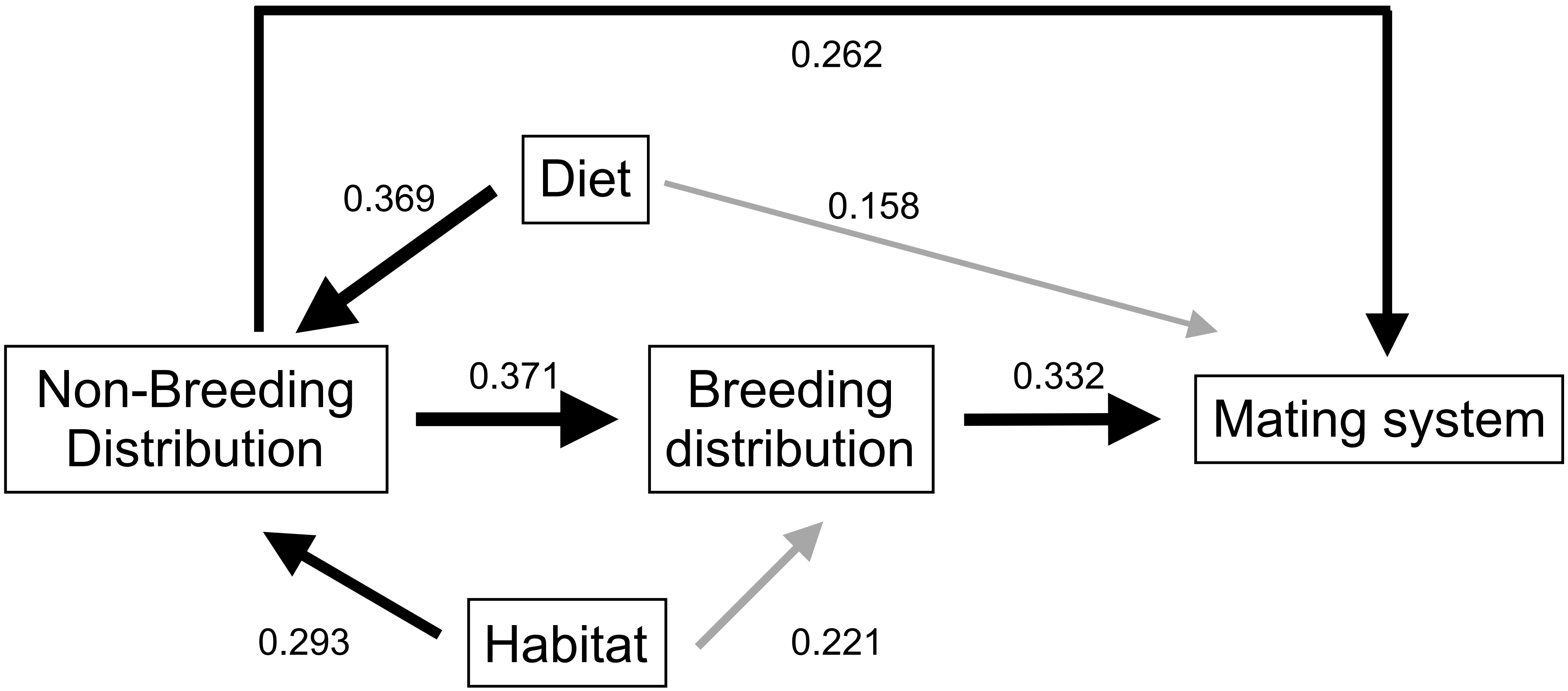

Diet
0.369
Non-Breeding Distribution
0.476
Breeding distribution
0.508
Mating system
0.293
Habitat

Figure 5b


0.262
Diet
0.369
0.158
Non-Breeding Distribution
0.371
Breeding distribution
0.332
Mating system
Habitat
0.293
0.221