SOCIAL CONTEXT AND THE EVOLUTION OF DELAYED REPRODUCTION IN BIRDS

Liam U. Taylor[1*] and Richard O. Prum[1]

[1]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA

[*]Corresponding author: liam.taylor@yale.edu

ABSTRACT

Classic life history theory makes generalized predictions about phenotypic correlations across large clades. Modern comparative tests of these correlations account for the underlying structure of phylogenetic trees. Yet neither life history theory nor phylogenetic comparative methods automatically specify how biological mechanisms generate correlations. This problem is evident in comparative analyses of birds. Birds show a correlation between body size and age at first reproduction, but do not actually grow larger if they delay reproduction. Instead, field studies raise the hypothesis that social contexts—especially cooperative breeding, coloniality, and lekking—generate unique demands for behavioral development, which in turn result in delayed reproduction. Here, we support that hypothesis with a comparative dataset spanning 961 species in 155 avian families. Continuous (Ornstein-Uhlenbeck), discrete (hidden state Markov), and phylogenetic regression models revealed delayed reproduction in colonial birds, a weaker signal in cooperative birds, and the consistent evolution of sexual bimaturism in polygynous, lekking birds. These results show an association between diverse social contexts, sex-specific developmental demands, and life history evolution in birds. Considering this diversity, we discuss how even statistically powerful phylogenetic correlations—whether focused on mass, lifespan, or broad social categories—can ultimately fail to model the history of life history evolution.

KEYWORDS

colony, lek, deferred breeding, recruitment, phylogenetic natural history, sexual bimaturism

Running title: *Evolution of avian delayed reproduction*

Main text word count: 4,472

INTRODUCTION

One aim of life history theory is to explain diversity in core phenotypic traits (e.g., size, survival rate, and fecundity) in terms of predictable, law-like patterns that span large groups of organisms. Famous examples include the *r*-*K* selection spectrum (Pianka 1970) and invariant scaling rules (Charnov 1993). Phylogenetic comparative methods have been developed to remove the confounding effects of phylogenetic history when analyzing these patterns (e.g., phylogenetic generalized least squares, PGLS; Grafen 1989). Where classic life history theory tested trait correlations across vast assemblages of plants, fish, mammals, and birds (e.g., Western and Ssemakula 1982, Stearns 1983, Loveless and Hamrick 1984, Roff 1984, Harvey and Clutton-Brock 1985, Molau 1993), contemporary life history theory pursues the same goal while "accounting for phylogeny" (e.g., Møller 2006, Tökölyi et al. 2014, Friedman 2020). Yet comparative methods do not automatically identify the causal dynamics underlying phenotypic correlations, especially when causal dynamics themselves evolve across the tree of life (Uyeda et al. 2018, Kozłowski et al. 2020).

Consider the classic correlation between size and age at first reproduction. All else being equal, natural selection favors organisms that reproduce as quickly as possible (Williams 1966). But if an organism has an opportunity for development—for example, by growing rather than reproducing, leading to increased future fecundity due to a larger body size—then selection can favor the evolution of delayed reproduction (Williams 1966, Bell 1980, Roff 1984, Stearns 1992). Phylogenetic and non-phylogenetic analyses clearly support a correlation between size and age at first reproduction across mammals and birds (e.g., Western and Ssemakula 1982, Harvey and Clutton-Brock 1985, de Magalhães et al. 2007).

Now, consider the biology of birds. Almost all lineages of birds grow to adult size within their first year of life, many within their first few weeks (Bennett and Owens 2002). But many bird species delay reproduction for several years (Lack 1968). Because few birds actually grow while they delay reproduction, the correlation between size and age at first reproduction cannot represent a direct causal relationship between the two traits (Charnov 2000).

Instead, field studies show that some birds delay reproduction because they undergo unique processes of behavioral development across diverse breeding systems and social contexts. For example, the cooperative-breeding White-winged Chough (~350g, Corcoracidae: *Corcorax melanorhamphos*), starts breeding around four years old, only after establishing a breeding group to assist with incubation and provisioning young (Rowley 1978, Heinsohn and Cockburn 1997). The colonial Wandering Albatross (~7 kg, Diomedeidae: *Diomedea exulans*) starts breeding around 11 years old, only after establishing the central-place foraging skills, nest site, and pair-bonds required for two parents to raise young at pelagic breeding colonies (Hector et al. 1986, Weimerskirch and Jouventin 1987, Pickering 1989, Riotte-Lambert and Weimerskirch 2013). Meanwhile, female Long-tailed Manakins (~20g, Pipridae: *Chiroxiphia linearis*) begin breeding in their first or second year, whereas the lekking males spend a decade navigating the social hierarchies of the lek and developing the content of coordinated, multi-male sexual displays before they start to breed (McDonald 1993, Trainer et al. 2002). Individuals in these species delay reproduction because reproduction requires social development, which extends beyond somatic growth.

Inspired by this natural history, researchers have long suggested that avian life histories are structured by territorial social contexts such as cooperative breeding, coloniality, and lekking (Lack 1968, Orians 1969, Wiley 1974, Gould 1977, Bradley and Wooller 1990, Møller 2006, Hatchwell 2009). More recently, Ancona et al. (2020) found that polygynous lekking birds—which have a sexual asymmetry in social behavior at the lek—have a corresponding sexual asymmetry in age at first reproduction. Here, we ask the broader question of whether delayed reproduction has evolved to a greater extent across multiple, complex social contexts when compared to species that do not live in those social contexts. We analyze the relationship between social context and age at first reproduction across the avian phylogeny using continuous Ornstein-Uhlenbeck models (Butler and King 2004), a new application of discrete hidden Markov models that incorporates underlying evolutionary heterogeneity (Boyko and Beaulieu 2021), and phylogenetic regressions (Grafen 1989, Garland Jr et al. 1993). We conclude that simple life history correlations (e.g., mass *vs.* age at first reproduction) obscure the important role of social context in avian

evolution, while our own, more complex models (social context *vs.* age at first reproduction) obscure an even richer diversity in the developmental processes that influence life histories.

METHODS

Data and trees

We coded female and male age first reproduction for birds as a central, discretized, and annual integer. For example, species that first breed in their second summer after hatch (~23-25 months old) were assigned a value of two. Our core sources were encyclopedias, including all full-length articles in Cornell's Birds of the World (Billerman et al. 2022), The Birds of the Western Palearctic (Cramp et al. 1977), Handbook of Australian, New Zealand, and Antarctic Birds (Marchant and Higgins 1990), and The Birds of Africa (Fry et al. 1982), supplemented with literature on target families or species. See Appendix I for detailed information about character coding, with references and full source quotations in the main data file. Every analysis was conducted on separate female and male datasets.

Life history evolution is more sensitive to changes at younger ages (Williams 1966, Hamilton 1966, Stearns 1992), meaning shifts in younger values (e.g., breeding year one *vs.* two) may be subject to stronger selection than shifts in older values (e.g., breeding year eight *vs.* nine). We therefore used $\log_2$ age values for continuous analyses of age at first reproduction. See Appendix II for analyses using untransformed values.

We assigned each species in our age at first reproduction dataset to one of four social contexts: cooperative, colonial, lekking, or "other." Cooperative breeding was assigned to birds in which breeding territories include extra-pair individuals or multi-pair groups, encompassing both helpers-at-the-nest (e.g., Superb Fairywren *Malurus cyaneus*; Dunn et al. 1995) and communal breeding (e.g., Mexican Jay *Aphelocoma wollweberi*; Brown 1970). Coloniality was assigned to species in which breeding territories maintain nest sites in close proximity to conspecifics, as opposed to foraging or other environmental resources (Perrins and Birkhead 1983). Lekking was assigned to species in which breeding territories maintain sexual display sites rather than nesting or environmental resources (cf., Bradbury 1981). This

broad definition of lekking includes species with aggregated "arena" display sites (e.g., Greater Sage-Grouse *Centrocercus urophasianus*; Wiley 1973) as well as more solitary display sites (e.g., Satin Bowerbird *Ptilonorhynchus violaceus*; Borgia 1985; Prum 1994). Species that were not cooperative, colonial, or lekking were assigned "other."

We made minor updates to the Cockburn (2006) parental care dataset for cooperative breeders, reassigning some species based on our more recent life history sources and including communal breeders as cooperative. We consulted our life history sources, Rolland et al. (1998), and Bradbury (1981) for statements about coloniality and lekking. In cases of hierarchically-structured social groups of cooperative breeders (e.g., Bell Miner *Manorina melanophrys*; Smith and Robertson 1978), we assigned species under the more proximate context of cooperative. For comparing social and mass-based models, we used mass data ($\log_{10}$, not distinguished by sex) from the AVONET dataset (Tobias et al. 2022).

We drew a distribution of 1,000 phylogenetic trees for our final dataset from BirdTree (Fig. 1; Jetz et al. 2012). Data and phylogenies were wrangled, pruned, and visualized with the ape, ggtree, and tidyverse packages in R v4.3.1 (Paradis et al. 2004, Yu et al. 2017, Wickham et al. 2019, R Core Team 2023).

Continuous model comparisons

We first modeled the relationship between social context and avian life history evolution in a continuous framework, using Ornstein-Uhlenbeck (OU) model comparisons (Butler and King 2004, Beaulieu et al. 2012). If cooperative breeding, coloniality, or lekking influences the evolution of delayed reproduction, then we predict that more complicated models—those differentiating age at first reproduction regimes based on social context—will be preferable to simpler models that ignore social context.

We compared seven continuous models for age at first reproduction ($\log_2$) evolution (Table 1): Brownian motion (BM); single regime OU (OU1); cooperative in one regime *vs.* everything else in a second regime (OU2-Cooperative); colonial in one regime *vs.* everything else in a second regime (OU2-

Colonial); lekking in one regime *vs.* everything else in a second regime (OU2-Lekking); cooperative or colonial or lekking in one regime *vs.* everything else in a second regime (OU2-Social); and cooperative *vs.* colonial *vs.* lekking *vs.* other in four separate regimes (OU4-Social). OU regimes differed only by mean (θ) parameters and were assigned based on ancestral state estimates of social context (R package ape, four-state discrete model, symmetrical rates). We fitted continuous models with the three-point algorithm in R package OUwie (Ho and Ané 2014, Beaulieu and O'Meara 2022) and compared BIC scores for each of 1,000 trees.

Discrete model comparisons

Because our trait of interest is discretized—first in terms of annual integer values and further via log transformation—continuous models may offer poor descriptions of our data. We thus supplemented our OU model comparisons with discrete model comparisons. As with our continuous comparisons, we predict that more complicated models linking social context to transitions in delayed reproduction will be preferable to simpler models in which the two traits evolve independently.

Species were binned into three age at first breeding states (1 *vs.* 2 *vs.* 3+ yr, untransformed ages) and two social states (cooperative, colonial, or lekking *vs.* other). We then compared four discrete models: age and social transition rates are independent of one another (H1-Independent); age transition rates depend on social state (H1-Dependent); age and social transition rates are independent, but an unobserved hidden character allows for shifts in age transition rates (H2-Independent); and age transition rates are dependent on both social state and an unobserved hidden character (H2-Dependent).

The H1 models offer a standard comparison of uncorrelated *vs.* unidirectional, dependent character evolution (Pagel 1994). Importantly, the H2 models allow for underlying transition rate variation in our trait of interest (age at first reproduction) extending beyond our favorite covariate ("social" or "other"). This feature makes the H2-Independent model a better null comparison than the H1-Independent model (Maddison and FitzJohn 2015, Uyeda et al. 2018, Boyko and Beaulieu 2021). See

Appendix III for model details. We fitted discrete models with R package corHMM (1 random restarts per run; Beaulieu et al. 2022) and compared AICc scores for each of 1,000 trees.

Regression analyses

We directly compared age at first reproduction ($\log_2$) across social contexts using phylogenetic-corrected ANOVA from R package phytools (Brownian correlation structure; Garland Jr et al. 1993, Revell 2012) with post hoc pairwise t-tests. *P*-values were simulated from 1,000 iterations for each of 1,000 trees. We predicted that cooperative, colonial, and lekking species would have older ages at first reproduction when compared to species outside of those social contexts ("other"). To interpret other modeling results, we also tested whether the sexual difference in age at first reproduction (male – female, untransformed values, overlapping dataset only) was elevated in different social contexts. Given three overlapping comparisons per variable (cooperative *vs.* other, colonial *vs.* other, lekking *vs.* other), the Bonferonni-corrected *P*-value threshold for pairwise t-tests was $\alpha = 0.05/3 = 0.016$,

Lastly, we used PGLS regressions (Grafen 1989) to investigate how strong, purely correlative models (mass *vs.* age at first reproduction) compare to weaker, potentially causal models (social context *vs.* age at first reproduction). We conducted four PGLS regressions with the following formulas: (1) age ~ social_context; (2) age ~ mass; (3) age ~ social_context + mass; and (4) age ~ social_context + mass + social_context * mass. All models used $\log_2$ age values and Martin's correlation structures from R package ape, with fixed α parameters from our OU1 model estimates (see *Methods: continuous model comparisons*). See Appendix II for analyses using Brownian motion correlation structures. We fitted PGLS models in R package nlme (Pinheiro and Bates 2000) and compared using BIC scores for each of 1,000 trees.

RESULTS

Data and trees

We compiled age at first reproduction values for 961 species (941 female values, 947 male values) across 36/41 orders and 155/249 families in the Clements v2022 taxonomy (Clements et al. 2022). Of the 94 families with no available data, 68 were in order Passeriformes. The female dataset included 126 cooperative, 198 colonial, and 27 lekking species (Fig. S1). The male dataset included 126 cooperative, 199 colonial, and 30 lekking species (Fig. 1).

Age at first reproduction values ranged from <1 yr (coded as 1 yr, see Appendix I) to >10 yr. Species with the highest estimated ages at first reproduction included colonial tubenoses such as *Thalassarche chrysostoma* (Procellariiformes: Diomedeidae, 13 yr female and male), the cooperative old-world vulture *Gypaetus barbatus* (Accipitriformes: Accipitridae, 10 yr female and male), the lekking manakin *Chiroxiphia linearis* (Passeriformes: Pipridae, 2 yr female, 11 yr male), and the lekking parrot *Strigops habroptila* (Psittaciformes: Strigopidae, 10 yr female and male).

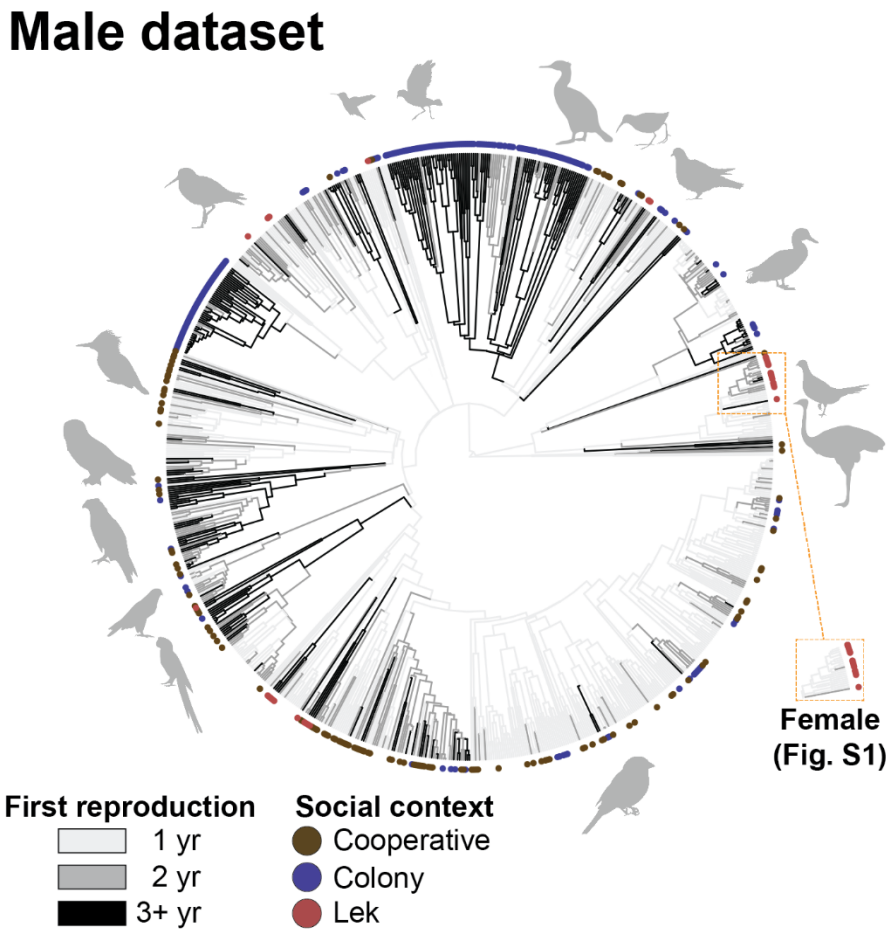

Figure 1. Avian phylogeny showing male age at first reproduction. Tips colored by social context. Binned ancestral ages estimated using corHMM (H1-Independent model). Orange box highlights differences between male and female ages in lekking pheasants and grouse (Galliformes: Phasianidae). Example phylogeny from 1,000 trees used for analysis. Silhouettes from phylopic.org.

Continuous model comparisons

All OU models greatly outperformed the simplest BM model in both female and male datasets for avian age at first reproduction evolution (Table 1). For the female dataset, the best model from our set included a separate OU regime for colonial taxa only (OU2-Colony), followed closely by models that allowed a separate regime spanning all cooperative, colonial, or lekking taxa (OU2-Social), or distinct regimes for each social context (OU4-Social, Table 1). Distinguishing cooperative-breeding taxa alone (OU2-Cooperative) was no better than a simple OU1 model for both female and male data. Distinguishing lekking taxa (OU2-Lek) was preferred to the OU1 model for males but not females. The best of our

continuous models for the male dataset distinguished separate regimes for each of our social contexts (OU4-Social, Table 1). Whenever estimated separately, central (θ) OU parameters for age at first reproduction were elevated in cooperative, colonial, and/or lekking regimes (Table S1).

Table 1. Continuous model comparisons for the evolution of delayed reproduction in birds. Multi-regime Ornstein-Uhlenbeck models (OU2, OU4) divide lineages based on social context, allowing different central (θ) parameters for age at first reproduction. ΔBIC scores (median with rounded 5th, 95th percentiles) were calculated separately given the minimum BIC score in each of 1,000 trees.

Model	Regimes	ΔBIC, female		ΔBIC, male	
BM	1	222.7	(169, 404)	213.1	(171, 317)
OU1	1	44.4	(35, 79)	69.5	(61, 87)
OU2-Cooperative	2	50.2	(40, 86)	75.8	(67, 94)
OU2-Colony	2	**0**	**(0, 4)**	38.7	(34, 43)
OU2-Lek	2	47.8	(37, 84)	44.6	(35, 65)
OU2-Social	2	2.8	(0, 21)	18.2	(13, 25)
OU4-Social	4	2.1	(0, 5)	**0**	**(0, 0)**

Discrete model comparisons

Across female and male datasets, a dependent model (H1-Dependent) in which age at first reproduction transition parameters depend on simplified social context (i.e., cooperative, colonial, or lekking *vs.* other) was preferred to an independent model (H1-Independent) in which transitions were unrelated (Table 2). Importantly, the simple social-dependence model (H1-Dependent) was worse than a model in which age transitions depend on a hidden character state unrelated to our social context classification (H2-Independent, Table 2). The best discrete model for both females and males combined these patterns of variation, making age transitions dependent on both our social character states and additional hidden states (H2-Dependent, Table 2). In H1- and H2-Dependent models, almost all median upward age transition rates were elevated in "social" lineages, whereas downward transitions were elevated in "other" lineages (Appendix III). The exceptions were age 1-2 and 2-1 transition rates in hidden state 2 of the H2-Dependent model, which was estimated with wide uncertainty across trees (Appendix III).

Table 2. Discrete model comparisons for the evolution of delayed reproduction in birds. Dependent models allow age at first reproduction transition rate parameters to vary with respect to social state, while more complicated models (H2) allow those parameters to vary with respect to a hidden character state. ΔAICc scores (median with rounded 5th, 95th percentiles in parentheses) were calculated separately given the minimum AICc score in each of 1,000 trees.

Model	Transition dependency	ΔAICc, female		ΔAICc, male	
H1-Independent	None	74.8	(54, 96)	74.2	(59, 93)
H1-Dependent	Age|Social	33.1	(13, 53)	31.3	(16, 49)
H2-Independent	Age|Hidden	21.5	(0, 45)	29.2	(13, 48)
H2-Dependent	Age|Social,Hidden	**0**	**(0, 5)**	**0**	**(0, 0)**

Regression analyses

Phylogenetic ANOVAs for age at first reproduction across social contexts were significant for female, male, and difference datasets (median $P < 0.01$). Post hoc pairwise t-tests showed that colonial birds had significantly higher ages at first reproduction when compared to "other" taxa (i.e., neither cooperative, nor colonial, nor lekking) across both females and males (Table 3). Age at first reproduction was not significantly different between cooperative and "other" species.

Only the male dataset showed significantly higher ages at first reproduction for lekking taxa (Table 3). This sexual disparity was supported directly by tests of the difference between male and female ages. Unlike cooperative or colonial birds, lekking birds showed elevated age at first reproduction in males relative to female (Table 3).

Table 3. Post hoc pairwise comparisons following significant phylogenetic ANOVAs of avian age at first reproduction (female or male, $\log_2$,) or difference in age at first reproduction (male - female, untransformed) across social contexts. Post hoc pairwise *T* values compare species in each social context with species coded as "other" (e.g., cooperative *vs.* other). Uncorrected pairwise *P*-values (median with 5th, 95th percentiles; median $P < 0.016$ in bold) were simulated for each of 1,000 trees.

	Female			Male			Difference, male - female		
Social context	***T***	***P***		***T***	***P***		***T***	***P***	
Cooperative	-3.5	0.16	(0.13, 0.18)	-3.9	0.11	(0.09, 0.13)	-0.72	0.78	(0.76, 0.81)
Colony	**-18.3**	**<0.01**	**(<0.01, <0.01)**	**-18.5**	**<0.01**	**(<0.01, <0.01)**	0.59	0.92	(0.91, 0.94)
Lek	-0.7	0.81	(0.79, 0.83)	**-7.6**	**<0.01**	**(<0.01, 0.01)**	**-18.3**	**<0.01**	**(<0.01, <0.01)**

Simple PGLS models using only mass data were substantially better at fitting age at first reproduction values than models using social context alone for both male and female datasets (Tables 4, S5). Cooperative breeding, coloniality, and lekking were associated with significantly higher ages at first reproduction in the female and male Social models and the male Social+Mass model (Tables 4, S5). For social contexts in the Social*Mass model, only colony breeding was significant for females and only lekking was significant for males. The marginally significant effect of lekking in the female Social model (median "lek" effect in female Social model = 0.4, $P = 0.046$) disappeared in the female Social+Mass and Social*Mass models, whereas lekking remained significant with larger effect across male models (median "lek" effect in male Social model = 1.1, $P < 0.01$; Tables 4, S5). Whereas the significance and effect of social context terms on age at first reproduction varied across trees and models, mass was a significant term across the entire range of trees, models, correlations structures, and alternate age values (Table S5).

The only significant interaction in the Social*Mass PGLS model was Colony*Mass in females (Tables 4, S5; median interaction term = -0.2; $P = 0.04$). However, intercepts and mass coefficients varied whenever separate Mass models were fit to taxa in different social contexts (Table S6). Notably, there was a significant correlation between mass and age at first reproduction for females across 27 lekking species, but no significant correlation for males across 30 lekking species (Fig. S2).

Table 4. Phylogenetic generalized least squares (PGLS) models for age at first reproduction. ΔBIC scores (median with rounded 5th, 95th percentiles in parentheses) were calculated separately given the minimum BIC score in each of 1,000 trees. Significant terms had median $P < 0.05$ across 1,000 trees.

	Female			**Male**		
Model	**ΔBIC**		**Significant terms**	**ΔBIC**		**Significant terms**
Social	115.4	(67, 169)	cooperative, colony, lek	100.1	(51, 138)	cooperative, colony, lek
Mass	**0**	**(0, 88)**	mass	2.5	(0, 13)	mass
Social+Mass	7.1	(0, 23)	mass, cooperative, colony	**0**	**(0, 6)**	mass, cooperative, colony, lek
Social*Mass	27.1	(0, 45)	mass, colony, colony*mass	26.1	(11, 30)	mass, lek

DISCUSSION

Our comparative analyses are consistent with the hypothesis that complex social contexts—coloniality, lekking, and, in one analysis, cooperative breeding—are associated with the evolution of delayed reproduction in birds. Both continuous (OU) and discrete (hidden Markov models) model comparisons showed that models incorporating social context offer better descriptions of age at first reproduction evolution than models ignoring social context (Tables 1-2). Continuous model parameters (Table S1) and discrete model transition rates (Appendix III) revealed that delayed reproduction was elevated in lineages that live in these complex social contexts. Phylogenetic ANOVAs further clarified these results, showing an elevated age at first reproduction in both females and males of colony-nesting species (Table 3). Lekking, however, was more strongly associated with delayed reproduction in males relative to females across species (Tables 1, 4) and associated with longer delays in males relative to females within species (Table 3). When mass and social context was included in PGLS models, they showed significantly delayed reproduction for females and males in colonial species, males in lekking species, and an additional signal of delayed reproduction in cooperative birds across sexes (Table 4).

These results provide quantitative support for the claim that social contexts influence life history evolution in birds (Gould 1977 p. 345:347, Bradley and Wooller 1990, Møller 2006). Field studies show how different behavioral processes within each social context can give rise to delayed breeding. For example, young seabirds of all sexes must first gain experience with colony nesting territories (Ainley et al. 1983) and establish a pair-bond (Pickering 1989) to begin breeding among conspecifics in dense island colonies. Meanwhile, male—but not female—reproduction in lekking species requires developing display sites and displays (e.g., McDonald 1989, Collis and Borgia 1993). Consistent with this developmental asymmetry in behavioral demands and previous comparative studies of polygynous birds (Wiley 1974, Ancona et al. 2020), our results for lekking lineages showed delays in male—relative to female—reproduction. Research in fish, mammals, and birds has long tied sex-related demands in social development to the evolution of sex-related life histories (e.g., blackbirds: Selander 1965, grouse, as recapitulated in Fig. 1: Wiley 1974, ungulates: Gould 1977, Spotted Hyenas: Holekamp and Strauss 2020,

309 Orangutans: Kralick et al. 2023, guppies: Rodd et al. 1997, wrasses: Robertson 1972, Lowe et al. 2021).
310 The multiple origins of lekking in birds allows for broader, comparative analyses of such socially-
311 mediated life history evolution (Fig. 1; Ancona et al. 2020)

312 On the one hand, we support a general association between social context and delayed
313 reproduction. On the other hand, our results teach us that these even these claims are not sufficiently
314 specific. Some of our continuous and discrete models lump cooperation, colonies, and leks into a simple
315 "social" category (Tables 1-2). Yet colony-breeding is neither homologous nor analogous to lekking in
316 birds, and these social contexts had different consequences for female and male life histories. Meanwhile,
317 our simple "other" category included diverse social dynamics (e.g., social networks in parrots; Penndorf
318 et al. 2023) that did not feature as characters in our analyses.

319 Furthermore, our analyses of cooperative species may have been hindered by our use of a single
320 category for both communal breeders and helpers-at-the-nest. Obligate communal breeders require extra-
321 pair assistance to provision and protect young (e.g., Rowley 1978, Heinsohn and Cockburn 1997). The
322 need to establish a cooperative breeding group may thus cause delayed reproduction. Alternatively,
323 functional helpers-at-the-nest often assist conspecifics only after failing to disperse to their own territories
324 (e.g., Pruett-Jones and Lewis 1990, Dunn et al. 1995, Margraf and Cockburn 2013). In such cases,
325 cooperation can be part consequence, rather than cause, of delayed reproduction. We also represented age
326 at first reproduction as a static value within species. Reproductive patterns within cooperative species,
327 such as the decision to help or disperse, often fluctuate widely with environmental factors such as rainfall
328 (Koenig et al. 1992, Rubenstein 2011, Welklin et al. 2023). Our simple trait categorizations thus neglect
329 factors known to affect life histories in birds.

330 In fact, we know that our simplified social character states explained only a portion of
331 evolutionary patterns in avian delayed reproduction. The best discrete evolutionary models allowed for
332 hidden state variation, independent from the classes of social variation we recognized (Table 2). One
333 critical feature left out of our models is foraging development, which tunes a parent's ability to
334 simultaneously provision young and stay alive (Ashmole 1963, Wunderle 1991, Becker et al. 2008).

Foraging development is further imbricated with social context. For example, scavenging opportunities in raptors can be regulated by dominance hierarchies (Dwyer and Cockwell 2011); pelagic seabirds must develop central-place foraging skills to breed at their island colonies (Coulson 2002, Collet et al. 2020); and some species learn how to forage directly from others (Slagsvold and Wiebe 2011). Snow (1971) argued that frugivory contributes to the evolution of polygynous leks by making it easier for a single parent to forage for dependent offspring. For lekking birds, then, it may be the ease of foraging—rather than the high demand for foraging development—that ultimately contributes to sex-related delayed reproduction.

No details of this underlying ecological and evolutionary diversity are represented, informed, predicted, or explained by our most powerful PGLS model: the significant regression between mass and age at first reproduction in birds (Table 4). We know the model is merely correlative rather than causal, because most birds do not grow any larger while they delay reproduction across years (Lack 1968, Bennett and Owens 2002). Phylogenetic correction has nothing to do with it; a correlation neither guarantees nor replaces a basic, biological fact about organismal diversity (cf., Uyeda et al. 2018).

One ad hoc response is to appeal to lifespan, arguing that low mortality rates can independently explain the separate evolution of delayed reproduction and large body size (Pianka 1970, with opposite logic in Møller 2006), thus generating an equally universal scaling law (Charnov 1993, 2000). But lifespan cannot independently explain the evolution of delayed reproduction; an organism of any given lifespan should still evolve to reproduce as quickly as possible (Williams 1966, Lehtonen 2016; with specific exceptions in declining populations and variable environments, Caswell 1982, Tuljapurkar 1990). What underpins the evolution of delayed reproduction is not simply variation in lifespan, but rather variation in "some more important development" (Williams 1966 p. 87:88) before an organism starts breeding (Wittenberger 1979, Bell 1980). Although expected lifespan can tune the reproductive costs and benefits of development (Stearns and Koella 1986), it neither predicts nor explains the form of that development. Configured and refigured by behavior, society, and sex at colonies, leks, and elsewhere, the form of development is precisely what varies among lineages of birds. General rules about evolution will

never help us if we already know that individual lineages have evolved different rules, and evolve according to those different rules. It is clear we have much more to learn about life histories than anything a universal regression—phylogenetic or otherwise—purports to teach.

ETHICS

This work did not require ethical approval from a human subject or animal welfare committee.

DATA ACCESSIBILITY

All data and analysis code are available from: https://github.com/ltaylor2/Avian_Delayed_Reproduction

AUTHORS' CONTRIBUTIONS

L.U.T.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing - original draft; R.O.P: investigation, resources, supervision, writing - review & editing.

CONFLICT OF INTEREST DECLARATION

We declare we have no competing interests.

FUNDING

This work was supported by NSF GRFP grant no. #DGE1752134 for L.U.T. and the W.R. Coe fund from Yale University.

ACKNOWLEDGEMENTS

We are grateful to the Yale Center for Research Computing for guidance and the use of research computing infrastructure (McCleary HPC). Josef Uyeda provided valuable feedback on some of our analyses. We thank Stephen Stearns, Martha Muñoz, and the summer fellows at the Bowdoin Scientific Station on Kent Island for helpful comments on the manuscript.

382 **LITERATURE CITED**

383 Ainley, D. G., R. E. LeResche, and W. J. Sladen. 1983. Breeding Biology of the Adélie Penguin.
384 University of California Press, Berkeley.

385 Ancona, S., A. Liker, M. C. Carmona-Isunza, and T. Székely. 2020. Sex differences in age-to-maturation
386 relate to sexual selection and adult sex ratios in birds. Evolution Letters 4:44–53.

387 Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b:458–473.

388 Beaulieu, J. M., D.-C. Jhwueng, C. Boettiger, and B. C. O'Meara. 2012. Modeling Stabilizing Selection:
389 Expanding the Ornstein–Uhlenbeck Model of Adaptive Evolution. Evolution 66:2369–2383.

390 Beaulieu, J. M., and B. O'Meara. 2022. OUwie: Analysis of evolutionary rates in an OU framework. R.

391 Beaulieu, J., B. O'Meara, J. Oliver, and J. Boyko. 2022. corHMM: Hidden Markov Models of Character
392 Evolution. R package. v2.8.

393 Becker, P. H., T. Dittmann, J.-D. Ludwigs, B. Limmer, S. C. Ludwig, C. Bauch, A. Braasch, and H.
394 Wendeln. 2008. Timing of initial arrival at the breeding site predicts age at first reproduction in a
395 long-lived migratory bird. Proceedings of the National Academy of Sciences 105:12349–12352.

396 Bell, G. 1980. The Costs of Reproduction and Their Consequences. The American Naturalist 116:45–76.

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

399 Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg. 2022. Birds of the World.
400 Cornell Lab of Ornithology, Ithaca.

401 Borgia, G. 1985. Bower quality, number of decorations and mating success of male satin bowerbirds
402 (*Ptilonorhynchus violaceus*): an experimental analysis. Animal Behaviour 33:266–271.

403 Boyko, J. D., and J. M. Beaulieu. 2021. Generalized hidden Markov models for phylogenetic comparative
404 datasets. Methods in Ecology and Evolution 12:468–478.

405 Bradbury, J. W. 1981. The Evolution of Leks. Pages 138–169 *in* R. D. Alexander and D. W. Tinkle,
406 editors. Natural Selection and Social Behavior. Chiron Press, New York.

407 Bradley, J. S., and R. D. Wooller. 1990. Philopatry and Age of First-breeding in Long-lived Birds. Pages
408 1657–1665 Acta XX Congressus Internationalis Ornithologici. Christchurch, New Zealand.

409 Brown, J. L. 1970. Cooperative breeding and altruistic behaviour in the mexican jay, *Aphelocoma*
410 *ultramarina*. Animal Behaviour 18:366–378.

411 Butler, M. A., and A. A. King. 2004. Phylogenetic comparative analysis: a modeling approach for
412 adaptive evolution. The American Naturalist 164:683–695.

413 Caswell, H. 1982. Life History Theory and the Equilibrium Status of Populations. The American
414 Naturalist 120:317–339.

415 Charnov, E. L. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology.
416 Oxford University Press, New York.

417 Charnov, E. L. 2000. Evolution of life-history variation among species of altricial birds. Evolutionary
418 Ecology Research 2:375–383.

419 Clements, J. F., T. S. Schulenberg, M. J. Iliff, T. A. Fredericks, J. A. Gerbracht, D. Lepage, S. M.
420 Billerman, B. L. Sullivan, and C. L. Wood. 2022. The eBird/Clements checklist of Birds of the
421 World.

422 Cockburn, A. 2006. Prevalence of different modes of parental care in birds. Proceedings of the Royal
423 Society B: Biological Sciences 273:1375–1383.

424 Collet, J., A. Prudor, A. Corbeau, L. Mendez, and H. Weimerskirch. 2020. First explorations: ontogeny of
425 central place foraging directions in two tropical seabirds. Behavioral Ecology 31:815–825.

426 Collis, K., and G. Borgia. 1993. The Costs of Male Display and Delayed Plumage Maturation in the Satin
427 Bowerbird (*Ptilonorhynchus violaceus*). Ethology 94:59–71.

428 Coulson, J. C. 2002. Colonial breeding in seabirds. Pages 100–127 *in* E. A. Schreiber and J. Burger,
429 editors. Biology of marine birds. CRC Press, Boca Raton.

430 Cramp, S., D. Brooks, and C. Perrins. 1977. Handbook of the Birds of Europe, the Middle East, and
431 North Africa: The Birds of the Western Palearctic. Oxford University Press, Oxford.

432 Dunn, P. O., A. Cockburn, and R. A. Mulder. 1995. Fairy-wren helpers often care for young to which
433 they are unrelated. Proceedings of the Royal Society of London. Series B: Biological Sciences
434 259:339–343.

435 Dwyer, J. F., and S. G. Cockwell. 2011. Social Hierarchy of Scavenging Raptors on the Falkland Islands,
436 Malvinas. Journal of Raptor Research 45:229–235.

437 Friedman, J. 2020. The Evolution of Annual and Perennial Plant Life Histories: Ecological Correlates and
438 Genetic Mechanisms. Annual Review of Ecology, Evolution, and Systematics 51:461–481.

439 Fry, C. H., E. K. Urban, S. Keith, R. Safford, and F. Hawkins. 1982. The Birds of Africa. Academic
440 Press, Cambridge.

441 Garland Jr, T., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance
442 by computer simulation. Systematic biology 42:265–292.

443 Gould, S. J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, Mass.

444 Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of
445 London. B, Biological Sciences 326:119–157.

446 Hamilton, W. D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology
447 12:12–45.

448 Harvey, P. H., and T. H. Clutton-Brock. 1985. Life history variation in primates. Evolution 39:559–581.

449 Hatchwell, B. J. 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history.
450 Philosophical Transactions of the Royal Society B: Biological Sciences 364:3217–3227.

451 Hector, J. A. L., J. P. Croxall, and B. K. Follett. 1986. Reproductive endocrinology of the wandering
452 albatross *Diomedea exulans* in relation to biennial breeding and deferred sexual maturity. Ibis
453 128:9–22.

454 Heinsohn, R., and A. Cockburn. 1997. Helping is costly to young birds in cooperatively breeding white-
455 winged choughs. Proceedings of the Royal Society of London. Series B: Biological Sciences
456 256:293–298.

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

459 Holekamp, K. E., and E. D. Strauss. 2020. Reproduction Within a Hierarchical Society from a Female's
460 Perspective. Integrative and Comparative Biology 60:753–764.

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

463 Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The Evolution of
464 Delayed Dispersal in Cooperative Breeders. The Quarterly Review of Biology 67:111–150.

465 Kozłowski, J., M. Konarzewski, and M. Czarnoleski. 2020. Coevolution of body size and metabolic rate
466 in vertebrates: a life-history perspective. Biological Reviews 95:1393–1417.

467 Kralick, A. E., C. A. O'Connell, M. L. Bastian, M. K. Hoke, B. S. Zemel, T. G. Schurr, and M. W.
468 Tocheri. 2023. Beyond Dimorphism: Body Size Variation among Adult Orangutans is not
469 Dichotomous by Sex. Integrative and Comparative Biology:icad015.

470 Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

471 Lehtonen, J. 2016. The Lambert W function in ecological and evolutionary models. Methods in Ecology
472 and Evolution 7:1110–1118.

473 Loveless, M. D., and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant
474 populations. Annual review of ecology and systematics 15:65–95.

475 Lowe, J. R., G. R. Russ, A. A. Bucol, R. A. Abesamis, and J. H. Choat. 2021. Geographic variability in
476 the gonadal development and sexual ontogeny of *Hemigymnus*, *Cheilinus* and *Oxycheilinus*
477 wrasses among Indo-Pacific coral reefs. Journal of Fish Biology 99:1348–1363.

478 Maddison, W. P., and R. G. FitzJohn. 2015. The Unsolved Challenge to Phylogenetic Correlation Tests
479 for Categorical Characters. Systematic Biology 64:127–136.

480 de Magalhães, J. P., J. Costa, and G. M. Church. 2007. An analysis of the relationship between
481 metabolism, developmental schedules, and longevity using phylogenetic independent contrasts.
482 The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences 62:149–160.

483 Marchant, S., and P. J. Higgins. 1990. The Handbook of Australian, New Zealand and Antarctic Birds.
484 Oxford University Press, Melbourne.

Margraf, N., and A. Cockburn. 2013. Helping behaviour and parental care in fairy-wrens (<i>Malurus</i). Emu - Austral Ornithology 113:294–301.

McDonald, D. B. 1989. Cooperation under sexual selection: age-graded changes in a lekking bird. The American Naturalist 134:709–730.

McDonald, D. B. 1993. Demographic consequences of sexual selection in the long-tailed manakin. Behavioral Ecology 4:297–309.

Molau, U. 1993. Relationships between Flowering Phenology and Life History Strategies in Tundra Plants. Arctic and Alpine Research 25:391–402.

Møller, A. P. 2006. Sociality, age at first reproduction and senescence: comparative analyses of birds. Journal of Evolutionary Biology 19:682–689.

Orians, G. H. 1969. On the Evolution of Mating Systems in Birds and Mammals. The American Naturalist 103:589–603.

Pagel, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proceedings of the Royal Society of London. Series B: Biological Sciences 255:37–45.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Penndorf, J., K. M. Ewart, B. C. Klump, J. M. Martin, and L. M. Aplin. 2023. Social network analysis reveals context-dependent kin relationships in wild sulphur-crested cockatoos *Cacatua galerita*. Journal of Animal Ecology 92:171–182.

Perrins, C. M., and T. R. Birkhead. 1983. Social Systems: Territoriality and Coloniality. Pages 7–32 Avian Ecology. Blackie, Glasgow.

Pianka, E. R. 1970. On r- and K-Selection. The American Naturalist 104:592–597.

Pickering, S. P. C. 1989. Attendance patterns and behaviour in relation to experience and pair-bond formation in the Wandering Albatross *Diomedea exulans* at South Georgia. Ibis 131:183–195.

Pinheiro, J. S., and D. M. Bates. 2000. Mixed-Effects Models in S and S-PLUS. Springer-Verlag, New York.

Pruett-Jones, S. G., and M. J. Lewis. 1990. Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. Nature 348:541–542.

Prum, R. O. 1994. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). Evolution 48:1657–1675.

R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in ecology and evolution 3:217–223.

Riotte-Lambert, L., and H. Weimerskirch. 2013. Do naive juvenile seabirds forage differently from adults? Proceedings of the Royal Society B: Biological Sciences 280:20131434.

Robertson, D. R. 1972. Social control of sex reversal in a coral-reef fish. Science 177:1007–1009.

Rodd, F. H., D. N. Reznick, and M. B. Sokolowski. 1997. Phenotypic Plasticity in the Life History Traits of Guppies: Responses to Social Environment. Ecology 78:419–433.

Roff, D. A. 1984. The evolution of life history parameters in teleosts. Canadian Journal of Fisheries and Aquatic Sciences 41:989–1000.

Rolland, C., E. Danchin, and M. de Fraipont. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. The American Naturalist 151:514–529.

Rowley, I. 1978. Communal activities among white-winged choughs *Corcorax melanorhamphus*. Ibis 120:178–197.

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

Selander, R. K. 1965. On Mating Systems and Sexual Selection. The American Naturalist 99:129–141.

Slagsvold, T., and K. L. Wiebe. 2011. Social learning in birds and its role in shaping a foraging niche. Philosophical Transactions of the Royal Society B: Biological Sciences.

Smith, A. J., and B. I. Robertson. 1978. Social Organization of Bell Miners. Emu - Austral Ornithology 78:169–178.

Snow, D. W. 1971. Evolutionary Aspects of Fruit-Eating by Birds. Ibis 113:194–202.

Stearns, S. C. 1983. The Influence of Size and Phylogeny on Patterns of Covariation among Life-History Traits in the Mammals. Oikos 41:173–187.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40:893–913.

Tobias, J. A., C. Sheard, A. L. Pigot, A. J. Devenish, J. Yang, F. Sayol, M. H. Neate-Clegg, N. Alioravainen, T. L. Weeks, and R. A. Barber. 2022. AVONET: morphological, ecological and geographical data for all birds. Ecology Letters 25:581–597.

Tökölyi, J., J. Schmidt, and Z. Barta. 2014. Climate and mammalian life histories. Biological Journal of the Linnean Society 111:719–736.

Trainer, J. M., D. B. McDonald, and W. A. Learn. 2002. The development of coordinated singing in cooperatively displaying long-tailed manakins. Behavioral Ecology 13:65–69.

Tuljapurkar, S. 1990. Delayed reproduction and fitness in variable environments. Proceedings of the National Academy of Sciences 87:1139–1143.

Uyeda, J. C., R. Zenil-Ferguson, and M. W. Pennell. 2018. Rethinking phylogenetic comparative methods. Systematic Biology 67:1091–1109.

Weimerskirch, H., and P. Jouventin. 1987. Population Dynamics of the Wandering Albatross, *Diomedea exulans*, of the Crozet Islands: Causes and Consequences of the Population Decline. Oikos 49:315–322.

Welklin, J. F., S. M. Lantz, S. Khalil, N. M. Moody, J. Karubian, and M. S. Webster. 2023. Photoperiod and rainfall are associated with seasonal shifts in social structure in a songbird. Behavioral Ecology 34:136–149.

Western, D., and J. Ssemakula. 1982. Life history patterns in birds and mammals and their evolutionary interpretation. Oecologia 54:281–290.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, and J. Hester. 2019. Welcome to the Tidyverse. Journal of Open Source Software 4:1686.

Wiley, R. H. 1973. Territoriality and Non-Random Mating in Sage Grouse, *Centrocercus urophasianus*. Animal Behaviour Monographs 6:85–169.

Wiley, R. H. 1974. Evolution of social organization and life-history patterns among grouse. The Quarterly review of biology 49:201–227.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton.

Wittenberger, J. F. 1979. A Model for Delayed Reproduction in Iteroparous Animals. The American Naturalist 114:439–446.

Wunderle, J., Joseph. 1991. Age-specific foraging proficiency in birds. Current Ornithology 8:273–324.

Yu, G., D. K. Smith, H. Zhu, Y. Guan, and T. T.-Y. Lam. 2017. ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. Methods in Ecology and Evolution 8:28–36.

DUPLICATE FIGURES AND TABLES

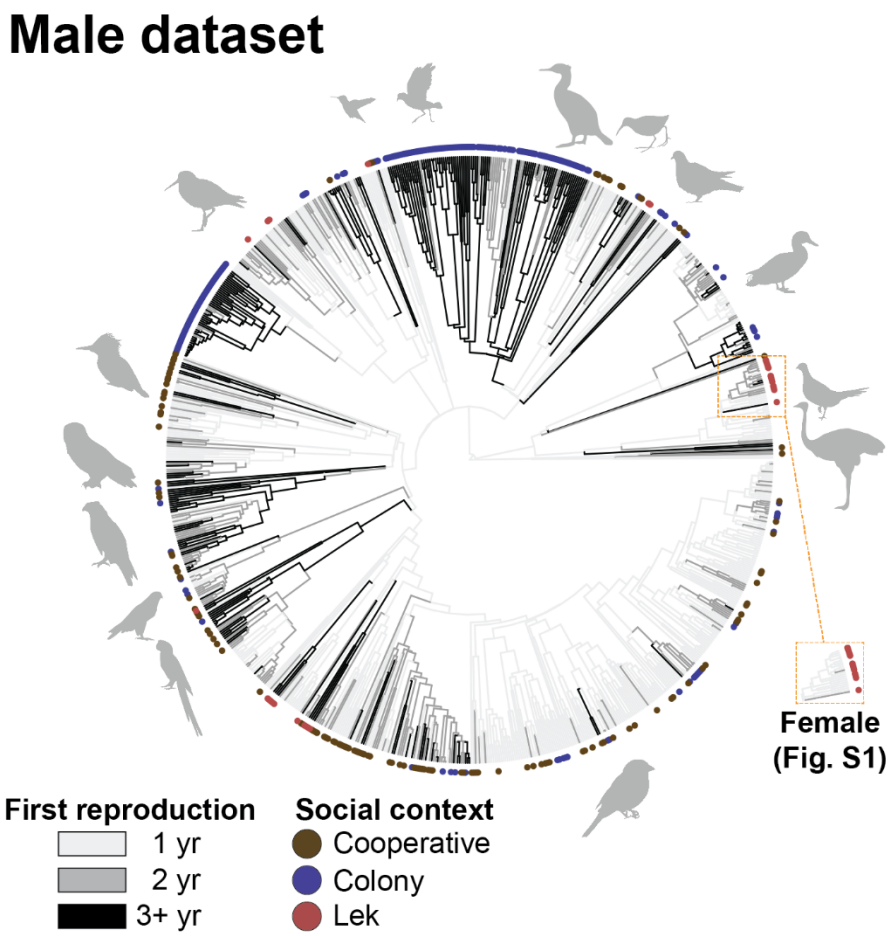

Figure 1. Avian phylogeny showing male age at first reproduction. Tips colored by social context. Binned ancestral ages estimated using corHMM (H1-Independent model). Orange box highlights differences between male and female ages in lekking pheasants and grouse (Galliformes: Phasianidae). Example phylogeny from 1,000 trees used for analysis. Silhouettes from phylopic.org.

Table 1. Continuous model comparisons for the evolution of delayed reproduction in birds. Multi-regime Ornstein-Uhlenbeck models (OU2, OU4) divide lineages based on social context, allowing different central (θ) parameters for age at first reproduction. ΔBIC scores (median with rounded 5th, 95th percentiles) were calculated separately given the minimum BIC score in each of 1,000 trees.

Model	Regimes	ΔBIC, female		ΔBIC, male	
BM	1	222.7	(169, 404)	213.1	(171, 317)
OU1	1	44.4	(35, 79)	69.5	(61, 87)
OU2-Cooperative	2	50.2	(40, 86)	75.8	(67, 94)
OU2-Colony	2	**0**	**(0, 4)**	38.7	(34, 43)
OU2-Lek	2	47.8	(37, 84)	44.6	(35, 65)
OU2-Social	2	2.8	(0, 21)	18.2	(13, 25)
OU4-Social	4	2.1	(0, 5)	**0**	**(0, 0)**

Table 2. Discrete model comparisons for the evolution of delayed reproduction in birds. Dependent models allow age at first reproduction transition rate parameters to vary with respect to social state, while more complicated models (H2) allow those parameters to vary with respect to a hidden character state. ΔAICc scores (median with rounded 5th, 95th percentiles in parentheses) were calculated separately given the minimum AICc score in each of 1,000 trees.

Model	Transition dependency	ΔAICc, female		ΔAICc, male	
H1-Independent	None	74.8	(54, 96)	74.2	(59, 93)
H1-Dependent	Age|Social	33.1	(13, 53)	31.3	(16, 49)
H2-Independent	Age|Hidden	21.5	(0, 45)	29.2	(13, 48)
H2-Dependent	Age|Social,Hidden	**0**	**(0, 5)**	**0**	**(0, 0)**

Table 3. Post hoc pairwise comparisons following significant phylogenetic ANOVAs of avian age at first reproduction (female or male, $\log_2$,) or difference in age at first reproduction (male - female, untransformed) across social contexts. Post hoc pairwise *T* values compare species in each social context with species coded as "other" (e.g., cooperative *vs.* other). Uncorrected pairwise *P*-values (median with 5th, 95th percentiles; median $P < 0.016$ in bold) were simulated for each of 1,000 trees.

	Female			**Male**			**Difference, male - female**		
Social context	***T***	***P***		***T***	***P***		***T***	***P***	
Cooperative	-3.5	0.16	(0.13, 0.18)	-3.9	0.11	(0.09, 0.13)	-0.72	0.78	(0.76, 0.81)
Colony	**-18.3**	**<0.01**	**(<0.01, <0.01)**	**-18.5**	**<0.01**	**(<0.01, <0.01)**	0.59	0.92	(0.91, 0.94)
Lek	-0.7	0.81	(0.79, 0.83)	**-7.6**	**<0.01**	**(<0.01, 0.01)**	**-18.3**	**<0.01**	**(<0.01, <0.01)**

Table 4. Phylogenetic generalized least squares (PGLS) models for age at first reproduction. ΔBIC scores (median with rounded 5th, 95th percentiles in parentheses) were calculated separately given the minimum BIC score in each of 1,000 trees. Significant terms had median $P < 0.05$ across 1,000 trees.

	Female			**Male**		
Model	**ΔBIC**		**Significant terms**	**ΔBIC**		**Significant terms**
Social	115.4	(67, 169)	cooperative, colony, lek	100.1	(51, 138)	cooperative, colony, lek
Mass	**0**	**(0, 88)**	mass	2.5	(0, 13)	mass
Social+Mass	7.1	(0, 23)	mass, cooperative, colony	**0**	**(0, 6)**	mass, cooperative, colony, lek
Social*Mass	27.1	(0, 45)	mass, colony, colony*mass	26.1	(11, 30)	mass, lek