

Group formation and the evolutionary pathway to complex sociality in birds

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Other Supplementary Information for this manuscript include the following:

External Supplementary Data Tables S1 to S5 and S9 to S10 (*DowningetalData.xlsx*)

Supplementary Data 1 (R code, *DowningetalRCode.R*)

Supplementary Data 2 (Effect size calculations, *effectSizes.txt*)

Sensitivity Analyses

2.1 Breeding system classification

To explore the effect of classifying cooperative species as breeding either family or non-family group on our results, we estimated the evolutionary transitions between Riehl's four categories of avian cooperative breeding systems using stochastic character mapping in the *phytools* R package. We added category *v*) as non-cooperative breeders ($N_{species} = 4558$) and simulated character histories across the same 1000 phylogenies used to estimate ancestral breeding systems in our BPMMs (i.e. those not discarded as a burn-in), running 10 simulations per tree. We used an equal-rates Q matrix and empirical Bayes estimation. We found that that 27/27 transitions to Riehl's category *iii*) (our non-family groups) were from non-cooperative ancestors (category *v*) while there have been repeated transitions between Riehl's categories *i*), *ii*) and *iv*) (our family groups) – see Supplementary Table 6.

Furthermore, there were no differences between Riehl's categories *i*), *ii*) and *iv*) (our family groups) in terms of division of reproduction (for both females and males), group size (mean and maximum) and reproductive specialization (*Zr fecundity*) while these all differed from

Riehl's category *iii*) (our non-family groups) – see Supplementary Table 7 and the Supplementary Data 1.

Supplementary Table 6. The number of transitions between Riehl's categories estimated using stochastic character mapping. Categories *i*), *ii*) and *iv*) correspond to our family groups, category *iii*) to our non-family groups and category *v*) are non-cooperative species. Transitions are from X to Y.

		Riehl Category (X)				
		<i>i</i>)	<i>ii</i>)	<i>iii</i>)	<i>iv</i>)	<i>v</i>)
Riehl Category (Y)	<i>i</i>)	-	3	0	2	77
	<i>ii</i>)	6	-	0	0	26
	<i>iii</i>)	0	0	-	0	27
	<i>iv</i>)	4	0	1	-	
	<i>v</i>)	5	1	0	1	-

Supplementary Table 7. Differences between cooperative species in division of reproduction (DoR), group size and specialization using Riehl's categories – *i*), *ii*) and *iv*) correspond to our family groups and *iii*) to our non-family groups. The 95% CI is shown in brackets.

	Trait	Reproductive DoR		Group Size		Specialization
	Riehl Cat.	females %	males %	mean	maximum	<i>Zr fecundity</i>
Family groups	<i>i)</i>	0 (0 - 0.4)	3 (0.6 - 19)	2.8 (1.9 - 4.3)	5.6 (4 - 10)	0.22 (-0.12 - 0.46)
	<i>ii)</i>	0.5 (0 - 60)	2 (0.2 - 28)	3.5 (2.1 - 4.8)	6.2 (4.2 - 10.8)	0.27 (-0.02 - 0.71)
	<i>iv)</i>	14 (0 - 84)	12 (2 - 49)	3.7 (2.3 - 5.5)	7.5 (5.4 - 13.9)	0.26 (-0.51 - 0.04)
Non-family groups	<i>iii)</i>	99 (0.6 - 100)	86 (0.5 - 98)	2.6 (1.8 - 4)	4.2 (2.7 - 7)	-0.21 (-0.14 - 0.57)

2.2 Different measures of fecundity and maternal care

(a) Fecundity measures

To explore the effect of group formation on reproductive specialization we examined the relationship between group size and fecundity. We collected data on fecundity which included three different measures: clutch size, number of clutches and egg volume. If relatedness is required for specialization to evolve, then only family groups should be specialized. Our three measures of specialization are likely to be correlated, with the highest productivity being achieved when breeding females can lay larger clutches with smaller eggs more often, as seen

in the ants and higher termites which live in highly related family groups^{63,64}. We only had sufficient data to explore whether the relationship between clutch size and group size was correlated with the relationship between the number of clutches and group size across eight family group cooperative breeders. We found these to be correlated (Spearman's $\rho = 0.60$).

To ensure that our finding that females in family and non-family groups differ in reproductive specialization was not due to differences in available fecundity measures, we compared family and non-family groups only using data on clutch size and group size ($Zr\ clutch$) and recovered the same result: breeding females in family groups increased their investment in fecundity as groups became larger ($Zr\ clutch = 0.21$, CI = 0.05 to 0.36, $N_{species} = 22$) while fecundity decreased with group size in non-family groups ($Zr\ clutch = -0.20$ CI = -0.40 to -0.06; $N_{species} = 12$; $P_{family\ vs.\ non-family} < 0.001$). It was not possible to compare family and non-family groups in terms of number of clutches and egg volume due to limited data for non-family groups (1 observation for egg size and 2 observations for re-nesting).

(b) Measures of maternal care

Investment in maternal care was measured either as provisioning, brooding or incubation effort. In ants and higher termites where division of labour is at its most extreme, queens invest little in any of these behaviours^{63,64}, suggesting that reductions in all three behaviours should be correlated. We explored the correlation between the relationship between brooding effort and group size and the relationship between provisioning effort and group size across five species (all family group cooperative breeders). As predicted, we found them to be highly correlated (Spearman's $\rho = 0.80$). Data are currently too limited to explore the correlations between other measures of maternal care – typically only one measure is recorded per species.

Limited data for non-family groups for the correlation between brooding and group size (1 species) and the correlation between incubation and group size (4 observations) meant that it was not possible to compare family and non-family groups for these measures of $Zr\ care$. However, we compared the correlation between provisioning effort and group size ($Zr\ provisioning$) between family and non-family groups and confirmed our finding: breeding females in both family and non-family groups reduce their investment in care with increasing group size (family: $Zr\ provisioning = -0.32$, CI = -0.53 to -0.15; non-family: $Zr\ provisioning = -0.10$ CI = -0.51 to 0.04; $N_{species} = 44$; $P_{family\ vs.\ non-family} = 0.82$).

2.3 Uncertainty in ancestral state estimation and different polyandry measures

In section 1.1a, we used a multinomial BPMM to estimate the posterior probability that each node on each phylogeny was in one of three states: family group cooperative breeder, non-family group cooperative breeder or non-cooperative. If the posterior probability for one of these states was greater than 0.67 we assigned the node to that state. We explored the sensitivity of our results to this cut-off by relaxing and restricting this value (see the Supplementary Data 1). We relaxed the cut-off by assigning each node the state with the highest posterior probability (any value > 0.33) and we restricted this cut-off by only assigning nodes to a given state if one state had a posterior probability > 0.9 (any nodes that did not meet this cut-off were assigned as unknown). The > 0.33 assignments had the effect of increasing the number of transitions from non-cooperative ancestors to family and non-family group cooperative breeding systems (195 family group origins and 33 non-family group origins averaged across 1000 trees) while the 0.9 assignments decreased the number of transitions (60 family group origins and 7 non-family group origins averaged across 1000 trees). The change in the number of assignments results from differences the number of nodes classified as unknown.

We then explored how these different levels of uncertainty in our ancestral state estimations of breeding systems influenced our estimates of ancestral polyandry. Our measure of polyandry was the percentage of broods that contained one or more chicks sired by multiple males inside or outside the group, commonly referred to as the percentage of extra-pair paternity per brood ($\% EPP\ br.$). For transitions to family group cooperative breeders from non-cooperative ancestors and for species that remained non-cooperative, we found similar values of ancestral $\% EPP\ br.$ across the different cut-off values (Supplementary Table 8). For transitions to non-family cooperative breeders from non-cooperative ancestors ancestral $\% EPP\ br.$ for the 0.90 cut-off was estimated to be twice as high as those for the >0.33 and 0.67 cut-offs. This is likely to result from the loss of statistical power in the number of non-family origins ($N_{origins} = 7$) and does not alter our conclusion that non-family groups were founded by females with higher rates of ancestral polyandry compared with family groups ($P_{family\ vs.\ non-family} = 0.08$).

Finally, we explored the effect of excluding chicks sired by multiple males inside the social group on our estimates of ancestral polyandry by only considering broods with chicks sired by males outside the group as being polyandrous (extra-group paternity per brood: % *EGP br.*). Again, we did this across the different cut-off values in our certainty of ancestral breeding systems. For species that remained non-cooperative, measures of ancestral % *EGP br.* and % *EPP br.* were consistent across the different cut-off values (Table S8). For transitions to family group cooperative breeders from non-cooperative ancestors, polyandry rates were slightly lower when estimated using % *EGP br.* across all cut-off values (13%, 6% and 8% lower for the 0.33, 0.67 and 0.90 cut-offs respectively). This makes sense given that family groups sometimes have multiple male breeders (see Fig. 3b in the main text), which occurs due to female-breeder turnover within the group providing opportunities for fathers and sons to mate with the same female³⁷. For transitions to non-family group cooperative breeders from non-cooperative ancestors, however, polyandry rates were much lower when estimated using % *EGP br.* across all cut-off values (33%, 28% and 84% lower for the 0.33, 0.67 and 0.90 cut-offs respectively). One interpretation of these results is that in non-cooperative species extra-pair partners are recruited as group members during transitions to non-family cooperative breeding systems, resulting in reduced estimates of polyandry when % *EGP br.* is used versus % *EPP br.*

Supplementary Table 8. Uncertainty in ancestral state estimation and different polyandry measures. Polyandry for cooperative breeders was estimated either as the % of broods that contained chicks sired by multiple males (% *EPP br.*) or as the % of broods that contained chicks sired by males outside the group only (% *EGP br.*). The 95% CI is shown in brackets.

Node Cut-off	0.33		0.67		0.90	
	% <i>EPP br.</i>	% <i>EGP br.</i>	% <i>EPP br.</i>	% <i>EGP br.</i>	% <i>EPP br.</i>	% <i>EGP br.</i>
nonCoop to nonCoop	18 (7 - 55)	16 (4 - 54)	20 (7 - 50)	19 (6 - 56)	17 (6 - 52)	16 (6 - 56)
nonCoop to Family	20 (5 - 55)	7 (1 - 36)	17 (4 - 50)	11 (1 - 36)	12 (4 - 60)	4 (0 - 37)
nonCoop to nonFam	49 (13 - 87)	16 (4 - 68)	41 (14 - 93)	13 (1 - 73)	99 (11 - 100)	15 (0 - 87)

Causality of Helper Effects

Positive correlations between the fecundity and survival of breeding females in relation to increasing group size may be a by-product of parental or territory quality, rather than a

consequence of being helped⁴. Specifically, experienced breeders on high quality territories may have higher fecundity, reduced workloads, and survive for longer and consequently have larger groups through the recruitment of philopatric offspring as helpers. However, a range of experimental evidence suggests a causal role for helpers (Supplementary Table 9): helper removal experiments have demonstrated breeding females adjust their fecundity and care in response to group size; food supplement experiments have demonstrated that breeders adjust their investment in care in response to foraging costs; clutch manipulation experiments have demonstrated that breeders adjust their investment in care in response to group size; and cross fostering experiments have demonstrated that breeding females adjust their fecundity in response to group size.

Supplementary References:

63. Wilson, E. O. *The Insect Societies* (Belknap Press, Cambridge, MA, 1971).
64. Bignell, D. E., Roisin, Y. & Lo, N. Eds. *Biology of Termites: a Modern Synthesis* (Springer, London, 2010).