

# Michener's group-size paradox in cooperatively breeding birds

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## Abstract

According to Michener's paradox, most altruistic groups in nature should be small and large groups should not exist. This is because per capita productivity is thought to decrease as groups get larger, meaning that the share of indirect fitness available to each group member declines, which favours dispersal. The empirical evidence for a decrease in per capita productivity is contradictory, however, and limited to the social Hymenoptera. I report that per capita reproductive success decreased with increasing group size across 26 cooperatively breeding bird species. Small groups comprising two or three individuals were the most common (79% of 16,101 groups), and these had the highest per capita reproductive success. This close fit between per capita reproductive success and the distribution of group sizes in nature suggests that it may indeed be difficult for large groups to evolve through indirect fitness benefits alone.

**Keywords:** comparative analysis, inclusive fitness, kin selection, diminishing returns, helping behaviour, phylogenetic methods

## Introduction

Thanks to the work of WD Hamilton and others, we have a good understanding of how altruistic groups evolve, both theoretically and empirically (Bourke, 2011, 2014; Hamilton, 1963; Rubenstein & Abbot, 2017; West et al., 2021). We have a poor understanding, however, of how large these groups should be. In fact, according to the empirical work of CD Michener on the social Hymenoptera (bees, wasps, ants), the existence of large groups might even be paradoxical (Michener, 1964). This is due to the law of diminishing returns: On a per capita basis, productivity is most efficient in small groups, so these should predominate in natural populations. Although first described in the social insects, this lesser-known paradox could be of general importance since altruistic groups occur in many animal clades (e.g., birds, mammals, shrimps, and aphids) and at different levels of biological organization (e.g., multicellular groups) (Bourke, 2011, 2014; Rubenstein & Abbot, 2017).

The problem is, Michener's paradox has only been statistically evaluated across species in the social Hymenoptera, and here the evidence it exists is contradictory (Jeanne et al., 2022). Per capita productivity does not decline in species that raise young in large groups (e.g., *Solenopsis* ants, >10,000 individuals), although it may decline in species that raise young in small groups (e.g., *Halictus* bees, <10 individuals). One interpretation of these results is that the existence of large groups is not paradoxical, since there is no general decrease in per capita productivity with group size across social Hymenopterans. The results seem to paint a more nuanced picture, however. If decreasing per capita productivity is a general feature of the biology of species that raise young in small groups, then we still need to explain how the

small-grouped ancestors of species that now breed in large groups (e.g., Burchill & Moreau, 2016; Chak et al., 2017; Rodriguez-Serrano et al., 2012) resolved the paradox. If decreasing per capita productivity is not a general feature of small-grouped species, then we can consider throwing the paradox out with the proverbial bathwater.

I use a phylogenetic comparative approach to assess the evidence for Michener's paradox in cooperatively breeding birds ( $N_{\text{species}} = 26$ ,  $N_{\text{groups}} = 16,101$ ). In these species, totipotent mature offspring often delay dispersal to help raise younger siblings, as in the social Hymenoptera (Rubenstein & Abbot, 2017). Group sizes are small and vary within species (typically from 2 to 10 individuals), and reproductive success has been measured in these different-sized groups (Koenig, 1981; Koenig & Dickinson, 2016; Stacey & Koenig, 1990). I first examine how per capita reproductive success and total reproductive success vary across group sizes. I then use data on the frequency of different group sizes in natural populations to determine whether groups with the highest per capita reproductive success are the most common. Confirming whether Michener's paradox exists matters. If it exists, then it questions our current understanding of how large groups evolved, since this is unlikely to have been through indirect fitness benefits alone.

## Methods

### Data collection

Studies reporting data on reproductive success (annual number of fledglings) in different-sized groups were identified by screening an existing database of 879 studies on 182 species of cooperatively breeding birds (Supplementary Material). This

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database comprises all known studies (published research, MSc and PhD theses, monographs, and edited volumes) with data on the breeding biology and fitness parameters of cooperative birds and is periodically updated. In addition, I contacted individual researchers to request data. Only studies that reported reproductive success in three or more group sizes were included. Nesting attempts that failed are included in reproductive success estimates. As Michener's paradox concerns the indirect fitness component of Hamilton's rule (per capita reproductive success measures the potential kin-selected benefits helpers stand to gain), only species that raise young in family groups were included. In non-family groups, indirect fitness is not applicable ( $r = 0$ ), and the evolution of cooperation is driven by direct fitness payoffs only. Per capita reproductive success tends to increase with group size in non-family groups, but maximum group sizes are significantly smaller than they are in family groups (Chak et al., 2017; Downing et al., 2020; Hartley & Davies, 1994; Lukas & Clutton-Brock, 2012).

I obtained data on reproductive success across different-sized groups for 26 species (Table 1, Supplementary Table S1). For three of these species (red-cockaded woodpeckers, white-browed sparrow weavers, Tibetan ground tits), data from multiple study populations were available, and these were pooled by taking weighted averages. For superb fairy-wrens and Florida scrub jays, which each have multiple studies reporting overlapping data sets, I extracted data from the study with the largest sample size. For red-winged fairywrens and sociable weavers, which each have studies from the same population but from different study dates and report non-overlapping data sets, the data were pooled by taking weighted averages. Full details of the figures, tables, text fragments from which data were obtained, and the calculations used to pool data are provided in Supplementary Material.

For each of the 26 species for which reproductive success estimates were available, I searched the database for data on the frequency of different-sized groups in natural populations. Group sizes are those from the breeding season, when helping at the nest takes place. Data on the frequency of different-sized groups were available for 23/26 species (Supplementary Table S2). For each species, group size frequencies came from the same study populations as the reproductive success data, except for the white-winged cough. This species was, therefore, excluded from the analyses examining reproductive success in relation to group size frequencies, but it was included in the descriptive statistics of the distribution of different group sizes. For the three species for which the reproductive success estimates from different populations were pooled, the frequency data were also pooled.

### Standardized total reproductive success and per capita reproductive success

To allow comparisons between species, I standardized reproductive success across group sizes (mean = 0 and SD = 1). This was done for each species separately. Per capita reproductive success was calculated by dividing total reproductive success by group size and was then standardized (mean = 0 and SD = 1). Again, this was done for each species separately.

### Model construction

#### Part A: per capita and total reproductive success across group sizes

To determine how per capita reproductive success and total reproductive success vary across group sizes, I constructed

two random slope models using the *MCMCglmm* R package (Hadfield, 2010; R Core Team, 2022). In the first model, per capita reproductive success (standardized, Gaussian) was the response variable, and group size (log transformed) was the fixed effect. I specified a random effect structure that allowed each species to have its own intercept and slope to account for non-independence between data points resulting from multiple observations per species (Schielzeth & Forstmeier, 2009). I also included a random term for phylogeny to account for non-independence between species due to shared evolutionary history (R code model: *rs\_pc\_rs\_modA*). I updated the phylogeny used to estimate phylogenetic variance every 1,000 iterations of the Markov chain. In total, I used 1,300 phylogenies (from Jetz et al., 2012) each iterated 1,000 times and saved the last iteration from each phylogeny. I discarded the first 300 iterations as a burn-in period, giving a posterior distribution of 1,000 iterations (each from a different phylogeny). The second model had the same structure as the first, but with total reproductive success (standardized, Gaussian) as the response variable (R code model: *rs\_t\_rs\_modA*).

#### Part B: per capita and total reproductive success and the frequency of group sizes

To determine whether groups with the highest per capita reproductive success or those with the highest total reproductive success are the most common in natural populations, I again constructed two random slope models. In the first model, per capita reproductive success (standardized, Gaussian) was the response variable and the percentage of groups (log transformed) was the fixed effect (R code model: *rs\_pc\_rs\_modB*). In the second model, total reproductive success (standardized, Gaussian) was the response variable and the percentage of groups (log transformed) was the fixed effect (R code model: *rs\_t\_rs\_modB*). In both models, I specified a random effect structure, which allowed each species to have its own intercept and slope, and I included a random term for phylogeny, and phylogenetic uncertainty was accounted for by updating the phylogeny used in parameter estimation as described above. Parameter estimates from these models are reported as the posterior modes ( $\beta$ ) and 95% credible intervals (CI) of posterior distributions. Significance is determined by whether the 95% CI includes zero. See Supplementary Methods for details on priors, model convergence, quadratic effects, and study effort.

### Results

Per capita reproductive success decreased significantly with increasing group size across species (random slopes  $\beta = -0.65$ , 95% CI =  $-1.01$  to  $-0.13$ ;  $N_{\text{species}} = 26$ ; Figure 1A). Within species, the relationship was negative in 17/26 cases, and there was no clear relationship in two cases, and it was positive in seven cases (Supplementary Figure S1). In contrast, total reproductive success increased significantly with group size across species (random slopes  $\beta = 1.10$ , 95% CI =  $0.80$  to  $1.53$ ;  $N_{\text{species}} = 26$ ; Figure 1A). The relationship was positive in 24/26 species (Supplementary Figure S2).

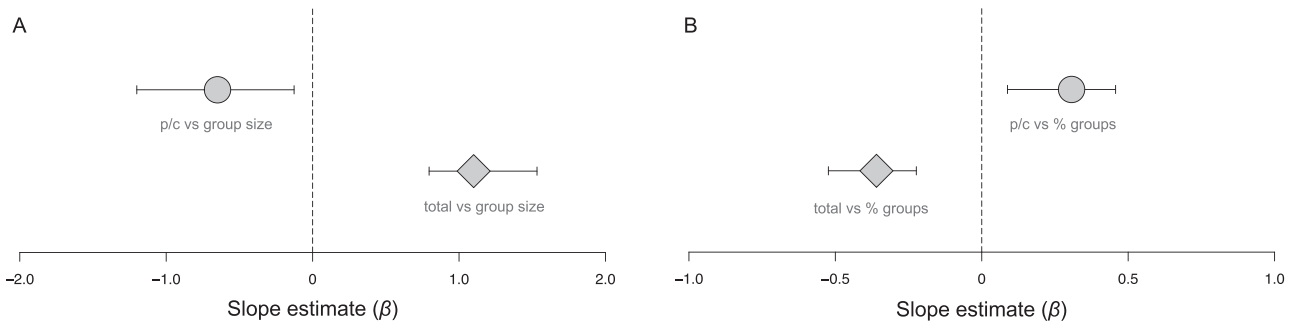
The distribution of group sizes was strongly right skewed, with most groups being small (Figure 2). Of 16,101 groups sampled from 23 species, 79% comprised two or three individuals, 18% comprised four individuals, and 3% comprised five or more individuals. This right-skewed pattern was mirrored within most species (Supplementary Figure S3).

**Table 1.** The species included in this study and their group size ranges in the wild.

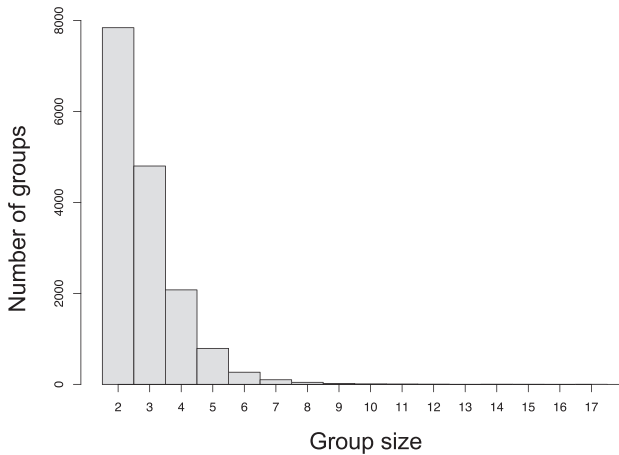
Species	Group size range	Study location	Sources
Seychelles warbler ( <i>Acrocephalus sechellensis</i> )	2–6	Cousin Island, Seychelles	Brouwer et al. (2006); Borger et al. (2023)
Rufous vanga ( <i>Schetba rufa</i> )	2–5	Ampijoroa Forest Station, Madagascar	Asai et al. (2001); Eguchi (personal communication) (2023)
Pied kingfisher ( <i>Ceryle rudis</i> )	2–5	Winam Gulf, Lake Victoria, Kenya	Reyer (1980)
White-fronted bee-eater ( <i>Merops bullockoides</i> )	2–7	Lake Nakuru National Park, Kenya	Emlen (1990); Emlen and Wrege (1991)
Green woodhoopoe ( <i>Phoeniculus purpureus</i> )	2–17	Lake Naivasha, Kenya	Ligon and Ligon (1978)
Placid greenbul ( <i>Phyllastrephus placidus</i> )	2–7	Taita Hills, Kenya	Van de Loock (2019); Cousseau (personal communication) (2023)
Karoo scrub-robin ( <i>Erythropterygia coryphaeus</i> )	2–5	Koebeg Nature Reserve, South Africa	Lloyd et al. (2009); Lloyd (personal communication) (2023)
Sociable weaver ( <i>Philetairus socius</i> )	2–8	Benfontein Game Farm, South Africa	Covas et al. (2008); D'Amelio et al. (2022)
White-browed sparrow weaver ( <i>Plocepasser mahali</i> )	2–9	Tswalu Kalahari Reserve, South Africa and Luangwa Valley, Zambia	Capilla-Lasheras et al. (2021); Lewis (1981)
Brown treecreeper ( <i>Climacteris picumnus</i> )	2–7	Warraderry State Forest, Australia	Doerr and Doerr (2006, 2007)
White-winged chough ( <i>Corcorax melanorhamphos</i> )	2–14	Mt. Ainslie and Black Mountain, Australia	Boland et al. (1997); Rowley (1978)
Superb fairy-wren ( <i>Malurus cyaneus</i> )	2–6	Australian National Botanic Gardens, Australia	Brouwer et al. (2020)
Laughing kookaburra ( <i>Dacelo novaeguineae</i> )	2–8	near Canberra, Australia	Legge (2000); Legge and Cockburn (2000)
Red-winged fairy-wren ( <i>Malurus elegans</i> )	2–9	Smith's Brook Reserve, Australia	Russell and Rowley (2000)
White-breasted Robin ( <i>Eopsaltria georgiana</i> )	2–6	Smith's Brook Reserve, Australia	Russell et al. (2004)
Chestnut-crowned babbler ( <i>Pomatostomus ruficeps</i> )	2–15	Fowlers Gap, Australia	Browning et al. (2012)
Grey-crowned babbler ( <i>Pomatostomus temporalis</i> )	2–9	Coomalie Farm, Australia	Eguchi et al. (2007); Eguchi (personal communication) (2023)
Apostlebird ( <i>Struthidea cinerea</i> )	3–17	Central Southern New South Wales, Australia	Woxvold (2004)
Carrion crow ( <i>Corvus corone</i> )	2–9	Northern Spain	Baglione et al. (2002); Canestrari et al. (2008)
Azure-winged magpie ( <i>Cyanopica cyanus</i> )	2–11	Near Badajoz, Spain	Valencia et al. (2003)
Red-cockaded woodpecker ( <i>Picoides borealis</i> )	2–7	Sandhills and Marine Corps Base Camp Lejeune, USA	Walters and Garcia (2016)
Pygmy nuthatch ( <i>Sitta pygmaea</i> )	2–5	Near Flagstaff, AZ, USA	Sydeman et al. (1988)
Florida scrub jay ( <i>Aphelocoma coerulescens</i> )	2–8	Archbold Biological Station, USA	Fitzpatrick and Bowman (2016); Woolfenden and Fitzpatrick (1990)
Toucan barbet ( <i>Semornis ramphastinus</i> )	2–4	Reserva Natural La Planada, Colombia	Restrepo and Mondragón (1998)
Hoatzin ( <i>Opisthocomus hoazin</i> )	2–7	Fundo Pecuario Masaguara, Venezuela	Strahl (1988); Strahl and Schmitz (1990)
Tibetan ground tit ( <i>Pseudopodoces humilis</i> )	2–5	Damxung County and Tianjun County, China	Zhao et al. (2019)

The most common group sizes were those with the highest per capita reproductive success (random slopes  $\beta = 0.31$ , 95% CI = 0.09 to 0.46;  $N_{\text{species}} = 22$ ; Figure 1B), while the rarest group sizes had the highest total reproductive success (random slopes  $\beta = -0.36$ , 95% CI =  $-0.52$  to  $-0.22$ ;  $N_{\text{species}} = 22$ ; Figure 1B). This indicates that small groups, which are the most common, have higher per capita reproductive success than

large groups, which are comparatively rare, even though large groups leave behind more descendants. Within species, the relationship between per capita reproductive success and the frequency of different group sizes was positive in 14/22 cases (Supplementary Figure S4), while the relationship between total reproductive success and the frequency of different group sizes was negative in 18/22 cases (Supplementary Figure S5).



**Figure 1.** The slopes ( $\beta$ ) and 95% credible intervals of (A) the relationship between standardized per capita reproductive success (p/c vs. group size) or standardized total reproductive success (total vs. group size) and log group size ( $N_{\text{species}} = 26$ ) and (B) the relationships between standardized per capita reproductive success (p/c vs. % groups) or standardized total reproductive success (total vs. % groups) and the log percentage of different-sized groups ( $N_{\text{species}} = 22$ ).



**Figure 2.** The number of different-sized groups across 23 cooperative bird species ( $N_{\text{groups}} = 16,101$ ).

**Discussion**

Cooperative birds appear to breed in group sizes that maximize their per capita reproductive success. Across 26 species, there was a significant negative relationship between per capita reproductive success and group size (Figure 1A). Small groups of two to three individuals were the most common group sizes in most species, making up 79% of all sampled groups (Figure 2), and these had higher per capita reproductive success than larger groups (Figure 1B). Groups with more than four members were rare, comprising just 3% of all sampled groups, even though these produce more offspring on average than smaller groups. These results suggest that the existence of large groups may indeed be paradoxical, since groups should remain small when considering per capita reproductive success.

While per capita reproductive success decreased with increasing group size on average across species, the relationship was positive in 9/26 species (Supplementary Figure S1). Similarly, per capita reproductive success was highest in the most common group sizes when averaged across species, but in 8/22 species, rarer group sizes had higher per capita reproductive success (Supplementary Figure S4). The species bucking the trend were the same in both cases. One explanation for the opposing patterns seen in these species is that they are the result of sampling bias: Reproductive success has not been measured in the largest group sizes known to occur in these

species, while it has been in the other species (Supplementary Table S2). More data from the rarest group sizes are needed to confirm this. Alternatively, these species may have shared aspects of their ecology, which account for their distinctiveness (Table 1).

From an indirect fitness perspective, it makes sense to disperse from large groups. In family groups, decreasing per capita reproductive success means that the share of indirect fitness benefits available to each helper is reduced as groups get larger, resulting in a smaller  $b$  term (the indirect fitness benefit of staying to help) in Hamilton’s rule (Hamilton, 1963). Consequently, the Hamiltonian condition for staying and helping ( $rb > c$ , where  $r$  = relatedness and  $c$  = the fitness cost of staying to help) is harder to satisfy, and individuals are increasingly likely to disperse and breed independently, although this will depend on the exact value of  $c$ . Thinking of this as an  $N$ -player game, group size will not evolve from  $N$  to  $N + 1$  because the indirect benefits of helping are smaller than the direct gains from dispersing. This implies that kin selection alone is unlikely to drive the evolution of large group sizes.

Although the species included in this study all breed cooperatively in families, within-group relatedness varies from  $<0.2$  in azure-winged magpies (Valencia et al., 2003) to  $>0.4$  in laughing kookaburras (Legge, 2000). This could affect average or maximum group sizes because the indirect fitness component of helping will be lower in some species than others. However, differences in average  $r$  between species should not affect the finding that per capita reproductive success decreases with increasing group size. This is because the value of reproductive success in each group size would be multiplied by a constant value of  $r$ , meaning that the slope of the relationship remains unchanged. This would not be the case if  $r$  changes with group size. We do not know how  $r$  varies with group size in cooperative birds, but it is likely to decrease due to breeder turnover, extra-pair mating, and immigration (Kingma et al., 2021). This would make staying in a large group even less beneficial, from an indirect fitness perspective.

One way to make staying and helping worthwhile is if the direct fitness benefits associated with territory inheritance or improved survival due to reduced predation and lighter workloads compensate for the low indirect fitness of being in a large group (García-Ruiz et al., 2022). These, and other and group augmentation effects, are well documented in the empirical literature, in various animal clades (e.g., Bouwma et al., 2006; Downing et al., 2021;



Kingma et al., 2014; Leadbeater et al., 2011; Smith et al., 2007; Woolfenden & Fitzpatrick, 1978). There is evidence, however, that individuals in large groups are less likely to inherit a breeding position, and there may be increased competition for resources in larger groups, which lowers the survival of group members, negating the direct fitness benefits of group living (Brouwer et al., 2006; Creel & Creel, 2015; Mumme et al., 2015; Shreeves & Field, 2002; Wilson et al., 1992). There are additional parameters influenced by group size that fall less clearly into the direct vs. indirect fitness dichotomy. For example, safe haven effects and the probability of group extinction. Since the many parameters at play may change in non-intuitive directions with increasing group size and depending on ecological conditions (Shen et al., 2017) and on whose perspective is taken (Shen et al., 2023), predicting group size is clearly challenging.

Considering these results in the wider social evolution context, and assuming that declining per capita reproductive success is a general feature of the biology of species that raise young in small groups, how did the small-grouped ancestors of species that now breed in large groups resolve Michener's paradox? One possibility is if totipotency is lost when groups are relatively small. Groups can then get larger because dispersal is never an option for helpers as all fitness is indirect. Per capita productivity would then stop being a currency selection that keeps track of, and other parameters, such as the trade-off between helper size and number, can be adjusted to maximize colony efficiency. Our current understanding of group size evolution is the opposite. Large group size is thought to drive the loss of totipotency among helpers (the size-complexity hypothesis) (Bourke, 2011; Jeon & Choe, 2003; Powers & Lehman, 2017). However, if groups can only get larger through direct and not indirect fitness benefits, this cannot be the case. Of course, birds are totipotent, and their groups are minuscule compared with those of some social insects. We need more theory and data to determine why and to discover which aspects of group size evolution are generalizable across clades and which are not.

## Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

## Data availability

The data underlying this article are available in the article and its online [Supplementary Material](#).

## Author contributions

Philip Downing (Conceptualization [Lead], Data curation [Lead], Formal analysis [Lead], Funding acquisition [Lead], Investigation [Lead], Methodology [Lead], Project administration [Lead], Resources [Lead], Software [Lead], Supervision [Lead], Validation [Lead], Visualization [Lead], Writing—original draft [Lead], Writing—review & editing [Lead])

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## Conflicts of interest

I declare no conflicts of interest.

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