HOW LARGE COOPERATIVE BIRD GROUPS AVOID LOCAL COMPETITION

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TEASER

The more the merrier? Perhaps not when it comes to cooperative groups. The more group members, the fewer resources to go around, which should limit group size. So how do large groups escape this conundrum? Using data from cooperative birds, we show that groups can avoid local competition for resources and increase in size by expanding their territory sizes. A large territory means more resources. And more resources means more and merrier group members.

ABSTRACT

Large cooperative groups are a common sight in nature. Their existence is puzzling, however, because local competition should keep groups relatively small. A simple but untested way large groups can avoid local competition is by increasing their resource base. We conducted a systematic review and phylogenetic meta-analysis to look for evidence of this effect in wild populations of cooperatively breeding birds. Across 634 groups from 29 species, group size and resource availability (territory area) were strongly positively correlated (Pearson's r = 0.52). Furthermore, when a specific group changed size, its territory changed size correspondingly (N = 34 groups). Our results support the prediction that large groups can avoid local competition by increasing their resource base and explain a sizeable fraction of group size variation in nature (R^2 = 0.27).

KEY WORDS

comparative study, aves, helper, alloparent, social evolution

INTRODUCTION

Local competition is a big obstacle for cooperation. At least in theory (Taylor 1992; Wilson et al. 1992; Ferrando 2024). When there is strong local competition for resources, relatives are likely to compete. This will reduce the selective advantage of cooperation because helping one relative may be costly to another. This negative effect of local competition, which is captured by extended versions of Hamilton's rule (West et al. 2002), suggests that cooperative groups should remain relatively small. Large groups are likely to experience intense resource competition, leading to conflicts within the group, reduced fitness, dispersal of group members, and, potentially, group extinction (e.g., Curry 1988; Creel and Creel 2015; Sorato et al. 2016; Nelson-Flower et al. 2018; Riehl and Smart 2022; Downing 2024). Since large cooperative groups exist in nature (Rubenstein and Abbot 2017), they must avoid local competition. The question is, how?

An obvious way groups can avoid local competition is by expanding their resource base as they increase in size. This is known as increasing local carrying capacity in the theoretical literature (Platt and Bever 2009; Van Dyken 2010; Van Dyken and Wade 2012). Surprisingly, this prediction is missing empirical support, which could be due to the difficulty of finding a suitable study system. In nature, we should see a positive relationship between group size and resource availability and, when a given group changes size, its resources should change correspondingly. This means that group size needs to vary and be measurable, the resources available to these groups must also be measurable, and ideally, we would be able to follow specific groups to examine how their resources change when group size changes. A tall order.

Thankfully, cooperatively breeding birds have risen to the occasion. In these birds, adult individuals feed young produced by others. Decades of research on many different species and hundreds of groups has produced the data needed to quantify the relationship between group size and resource availability (Stacey and Koenig 1990; Koenig and Dickinson 2016). Group size is measured as the number of adults in a breeding unit and resource availability can be approximated by examining space use (territory area) during the breeding season. The assumption is that territory area is positively correlated with the resources group members need to feed themselves and their group's young during this period.

Our aim is simple. We look for evidence that group size covaries with territory area in cooperative birds using a systematic literature search and phylogenetic meta-analysis. While it seems a foregone conclusion that it must, confirming this relationship is important as it helps us explain variation in cooperative group size in nature, which is poorly understood.

MATERIALS AND METHODS

Overview

We conducted a systematic literature search and phylogenetic meta-analysis to quantitatively estimate the relationship between group size and territory area in cooperative birds. This involved five main steps: (1) outlining study eligibility criteria, (2) search string construction and validation to find studies meeting these criteria, (3) searching Scopus and Web of Science and screening studies, (4) calculating effect sizes and (5) using a phylogenetic meta-analytic model to estimate the mean effect size and investigating how territory size changes when group size changes. This study is pre-registered with the Open Science Foundation.

Eligibility criteria

To quantify the relationship between group size and territory area, studies with data had to: (1) be in English, French, or Finnish; (2) be peer reviewed research papers, pre-prints, PhD / MSc theses, or monographs / books; (3) be on cooperatively breeding birds, defined as species in which adults feed offspring other than their own; (4) be field studies on wild populations without experimental manipulations, such as supplementary feeding, nest box additions, or removal of group members; (5) provide raw data in tables, figures, supplementary information, or report relevant test statistics and sample sizes, and the data should not have been included in another study; (6) group size must be continuous, rather than binary such as small vs large groups, and should reflect the number of adults in the breeding season; (7) territory area must be continuous, not binary such as large vs small, and should reflect space use during the breeding season. This last criterion matters because space use by cooperative birds can be substantially different between breeding and non-breeding seasons (e.g., Seddon et al. 2003; Radford and du Plessis 2004; Sorato et al. 2016). These criteria were used to construct a title and abstract decision tree and a full text decision tree which were used to screen studies (Figure S1).

Search string development and validation

As we required data on group size and territory area from cooperatively breeding birds, we built three substrings targeting each of these components. For each substring, we identified possible synonyms using a word cloud of the titles and abstracts of 15 benchmark papers (Table S1) which we wanted the search to return. The search string was optimised to return between 1000 and 3000 studies, which is a feasible screening target (Foo et al. 2021). The substrings were then combined in the following way

> (bird* AND (cooperat* OR co-operat* OR help* OR alloparent*)) AND ((territor* OR habitat* OR homerange* OR home-range*) AND (size* OR qualit* OR resource* OR tree*)) AND (group* OR "group size*" OR "number of individuals")

Based on a preliminary search in Web of Science, the miss rate was 33 % (5/15 benchmark papers were missing) and the hit rate was 21 % (the number of studies out of 100 chosen at random that passed to full text screening using our title and abstract decision tree). Although the miss rate was a little high, ideally none of our benchmark papers would have been missing, the hit rate was excellent and modifying the search string to improve the miss rate resulted in an extremely high number of studies being returned (>10 000).

Searches and screening

The search was conducted on 18.3.2024 from the University of Oulu using Scopus (topic search, default settings) and Web of Science (topic search, databases covered: Core Collection, Current Contents Connect, SciELO, Data Citation Index, Grants Index, Korean Journal Database, medline, Policy Citation Index, Preprint Citation Index, ProQuest, Research Commons, Derwent Innovations Index). We used the full range of dates covered by each platform.

The Scopus search returned 370 studies and the Web of Science search returned 1080 studies (Figure S2). After removing 316 duplicates (in Rayyan), the titles and abstracts of 1134 studies were screened. Of these, 956 studies were excluded based on our decision tree. We screened the full text of the remaining 178 studies using our decision tree and included 26 studies. We identified 19 additional relevant studies during full text screening of which four were included. The 1990 and 2016 cooperative breeding books (Stacey and Koenig 1990; Koenig and Dickinson 2016) were also screened, but chapters with relevant data had already been identified in our main search.

Our final sample size was 30 studies. These studies represent 29 different species. The numbers are not identical because two studies reported data for more than one species (Gaston 1976; Chan and Augusteyn 2003) and three species (superb fairywren, green woodhoopoe, laughing kookaburra) were the focus of multiple studies (Table 1).

Effect sizes and within-group changes

We used *Zr* as an effect size. In our case, this is simply the correlation between group size and territory area (ha), normalised using Fisher's z-transformation: 0.5 * ln(1+r / 1-r). The sampling variance of this effect size is 1/(N-3) where N is the number of unique groups studied (Koricheva et al. 2013). The order of preference for our effect size calculations was: (1) Spearman's *r*, Pearson's *r*, or R^2 reported in the results, (2) raw data extracted from tables (main or supplementary), (3) raw data extracted from figures or written in the text.

In summary, 10 studies reported Spearman's *r*, six reported Pearson's *r*, two reported R^2, three reported raw data in Tables, six reported raw data in Figures (three scatterplots, three maps), two reported data in the text, and one study reported raw data in the supplementary information (Table S2). Full details on how each effect size was calculated are provided in the supplementary data extraction file. Territory area was measured in various ways in these studies including polygons estimated statistically and those drawn by hand. As the territory areas of all groups within a study were estimated using the same method, any resulting bias will be within- rather than between-study, and should not affect the strength of each correlation.

We chose to analyse the data at the species level which meant pooling effect sizes for the three species that were the focus of multiple studies: two studies on the superb fairywren, two on the green woodhoopoe, and three on the laughing kookaburra. These were pooled by taking a weighted mean effect size, based on the number of groups studied, and using the combined number of groups studied to calculate the sampling variance (supplementary data extraction file).

Twelve of the thirty studies reported how territory size was adjusted following changes in group size for specific groups. Seven of these studies made qualitative statements. Five studies on four species provided quantitative data: jungle babbler, green woodhoopoe (two studies), grey-crowned babbler, and laughing kookaburra (Table S3). This data took the form of the change in group size between breeding seasons and its corresponding change in territory area (supplementary data extraction file).

Statistical analyses

Publication bias and heterogeneity

There was no a priori expectation that non-significant results would remain unpublished (Nakagawa et al. 2022). The studies in our sample were typically observational, reporting natural history. Consistently, of the 21 studies that tested the relationship between group size and territory area, six found no relationship, 14 found a significant positive relationship and one found a significant negative relationship. However, a trim and fill analysis, which identifies and imputes the number of missing studies needed to create a symmetric funnel plot, estimated that nine studies were missing from our sample. This would change our mean effect size from 0.57 (see results) to 0.43. The fail-safe number ranged from 29 to 1598 depending on the estimation method. This is the number of unpublished non-significant studies needed to make our mean effect size non-significant. Finally, we used Egger's regression accounting for phylogeny to estimate the mean effect size when sampling variance is zero (i.e. the intercept = 0.49, standard error = 0.13, $p < 0.001$). Based on a random effects meta-analytic model that did not include phylogeny, the between-study variance (Tau^2) was 0.09, giving an I^2 value of 63% ($Q = 78.7$, $p < 0.001$).

Main analysis

We estimated the mean effect size using a phylogenetic meta-analytic model in the metafor R package (Viechtbauer 2010; R Core Team 2025). Our *Zr* effect sizes ($N = 29$) were weighted by the inverse of their sampling variances and we included phylogeny (from Claramunt et al. 2025, Figure S3) as a random term to account for non-independence between species. Two species were missing from the phylogeny we used: *Climacteris affinis* and *Cyanocorax formosus*. These were swapped with two species in the same genus that were in the phylogeny: *Climacteris picumnus* and *Cyanocorax cyanomelas*.

To test for within-group changes, we used linear regression with the change in territory area for each group as the response variable and the corresponding change in group size as the predictor. This model treats each group as an independent datapoint even though there are dependencies in the data. However, due to the limited number of studies (N = 5) and the number of groups studied (N = 34), it was not possible to use a random intercepts and slopes model or to estimate the slope for each study separately and then pool these (two-stage analysis). This represents a clear avenue for future research.

Sensitivity analyses

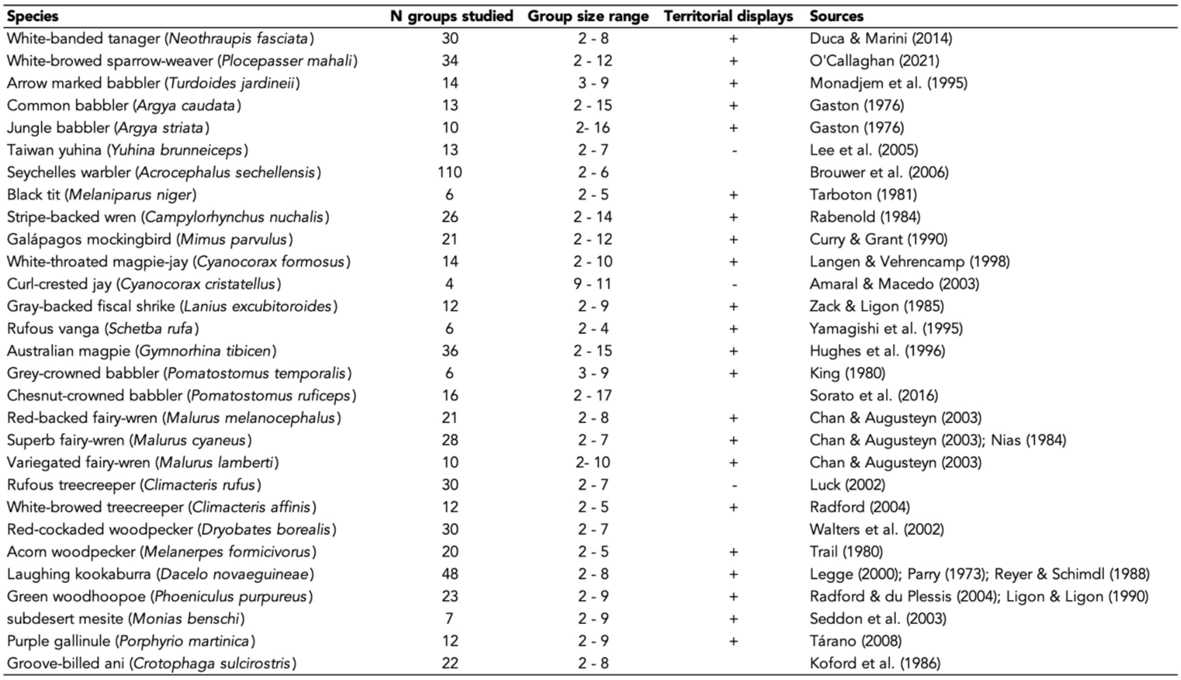
It was unclear whether the group size estimates for four of the species in our sample included juveniles: arrow marked babbler, red-cockaded woodpecker, rufous vanga, and Seychelles warbler. For each, it seemed likely that group size was the number of adults only, however, we re-estimated the mean effect size excluding these four species. Note that our effect size estimate for the Seychelles warbler had the additional issue that it was based on simulated data from reported means and standard errors (supplementary data extraction file).

For our within-group analysis, one study accounted for 65% of the data (22/34 groups). We therefore re-ran our linear regression excluding this study to get an estimate of the relationship between changes in group size and territory size that gives approximately equal weight to each of the other studies (N = 12 groups from four studies).

RESULTS

In total, 634 different cooperative bird groups were studied in the 29 species in our sample (Table 1). The number of groups studied per species ranged from four to 110. The Seychelles warbler was the most intensively studied species, with more than twice as many groups sampled as the next best studied species (the laughing kookaburra). The curl-crested jay was the least intensively studied species. In 27 species, the correlation between group size and territory area was positive and in 17 of these it was significant (Figure 1). In two species, the superb fairy wren and the acorn woodpecker, there was a non-significant negative correlation between group size and territory area.

Table 1. The 29 cooperative bird species included in this study with sources and details on the number of groups studied, the range of observed group sizes during the breeding season, and the presence / absence (+ / -) of territorial displays.



Species	N groups studied	Group size range	Territorial displays	Sources
White-banded tanager (*Neothraupis fasciata*)	30	2 - 8	+	Duca & Marini (2014)
White-browed sparrow-weaver (*Plocepasser mahali*)	34	2 - 12	+	O'Callaghan (2021)
Arrow marked babbler (*Turdoides jardineii*)	14	3 - 9	+	Monadjem et al. (1995)
Common babbler (*Argya caudata*)	13	2 - 15	+	Gaston (1976)
Jungle babbler (*Argya striata*)	10	2- 16	+	Gaston (1976)
Taiwan yuhina (*Yuhina brunneiceps*)	13	2 - 7	-	Lee et al. (2005)
Seychelles warbler (*Acrocephalus sechellensis*)	110	2 - 6		Brouwer et al. (2006)
Black tit (*Melaniparus niger*)	6	2 - 5	+	Tarboton (1981)
Stripe-backed wren (*Campylorhynchus nuchalis*)	26	2 - 14	+	Rabenold (1984)
Galápagos mockingbird (*Mimus parvulus*)	21	2 - 12	+	Curry & Grant (1990)
White-throated magpie-jay (*Cyanocorax formosus*)	14	2 - 10	+	Langen & Vehrencamp (1998)
Curl-crested jay (*Cyanocorax cristatellus*)	4	9 - 11	-	Amaral & Macedo (2003)
Gray-backed fiscal shrike (*Lanius excubitoroides*)	12	2 - 9	+	Zack & Ligon (1985)
Rufous vanga (*Schetba rufa*)	6	2 - 4	+	Yamagishi et al. (1995)
Australian magpie (*Gymnorhina tibicen*)	36	2 - 15	+	Hughes et al. (1996)
Grey-crowned babbler (*Pomatostomus temporalis*)	6	3 - 9	+	King (1980)
Chesnut-crowned babbler (*Pomatostomus ruficeps*)	16	2 - 17		Sorato et al. (2016)
Red-backed fairy-wren (*Malurus melanocephalus*)	21	2 - 8	+	Chan & Augusteyn (2003)
Superb fairy-wren (*Malurus cyaneus*)	28	2 - 7	+	Chan & Augusteyn (2003); Nias (1984)
Variegated fairy-wren (*Malurus lamberti*)	10	2- 10	+	Chan & Augusteyn (2003)
Rufous treecreeper (*Climacteris rufus*)	30	2 - 7	-	Luck (2002)
White-browed treecreeper (*Climacteris affinis*)	12	2 - 5	+	Radford (2004)
Red-cockaded woodpecker (*Dryobates borealis*)	30	2 - 7		Walters et al. (2002)
Acorn woodpecker (*Melanerpes formicivorus*)	20	2 - 5	+	Trail (1980)
Laughing kookaburra (*Dacelo novaeguineae*)	48	2 - 8	+	Legge (2000); Parry (1973); Reyer & Schimdl (1988)
Green woodhoopoe (*Phoeniculus purpureus*)	23	2 - 9	+	Radford & du Plessis (2004); Ligon & Ligon (1990)
subdesert mesite (*Monias benschi*)	7	2 - 9	+	Seddon et al. (2003)
Purple gallinule (*Porphyrio martinica*)	12	2 - 9	+	Tárano (2008)
Groove-billed ani (*Crotophaga sulcirostris*)	22	2 - 8		Koford et al. (1986)

Across species and accounting for phylogeny, the mean correlation between group size and territory area was significantly positive (*Zr* = 0.57, 95% CI = 0.39 to 0.76; Figure 1). This corresponds to a Pearson's correlation of 0.52, which is considered to reflect a strong relationship (<0.5 is medium and <0.1 is small). The R^2 value based on this correlation coefficient is 0.27. The mean effect size after excluding four species whose group size measures might have included juveniles (arrow marked babbler, red-cockaded woodpecker, rufous vanga, and Seychelles warbler) was slightly higher than our mean estimate including them (*Zr* = 0.61, 95% CI = 0.44 to 0.77).

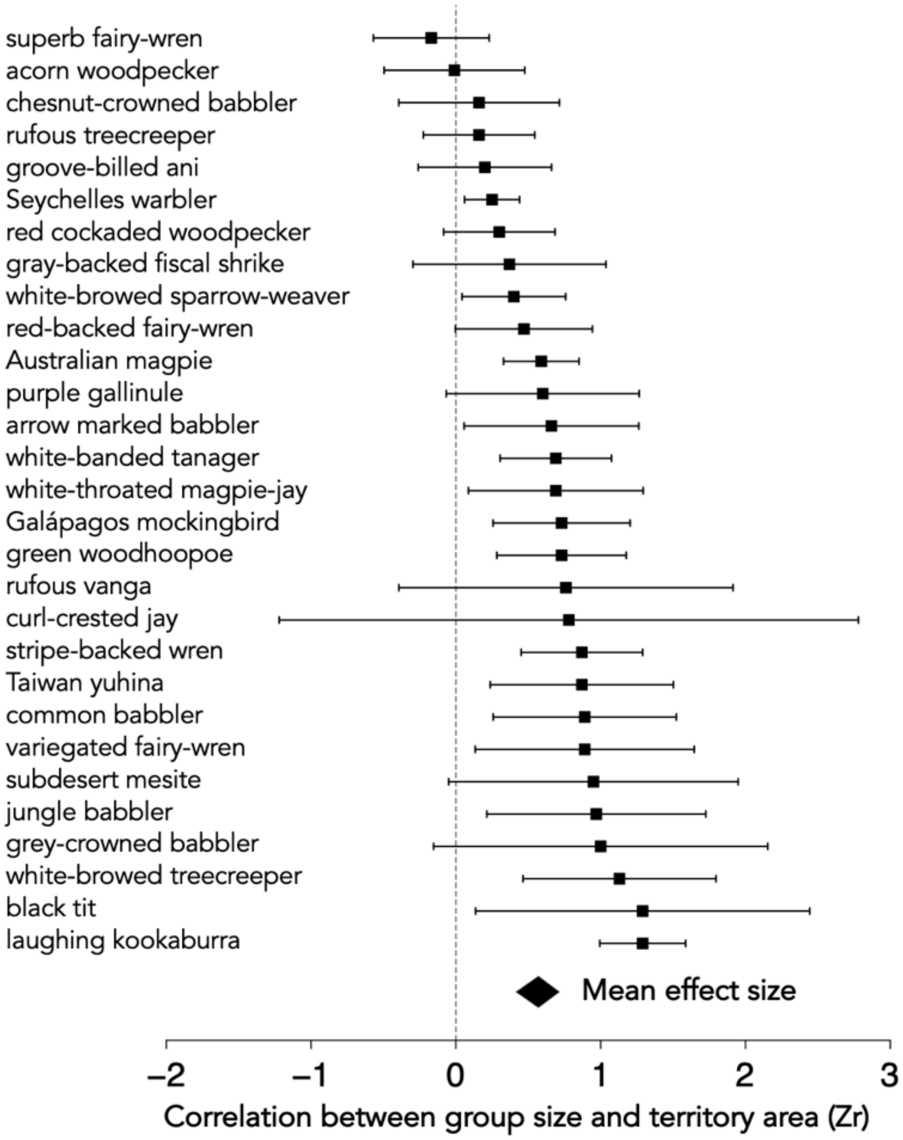


Figure 1. Forest plot showing the correlation (*Zr*) between group size and territory area for 29 cooperative birds. Each effect size is bracketed by its 95% CI. The mean effect size is the centre of the diamond whose left and right limits represent the 95% CI.

Five studies on four species measured how the sizes and territory areas of 34 different groups changed across breeding seasons. These were: jungle babbler, green woodhoopoe (two studies), grey-crowned babbler, and laughing kookaburra. The territories of groups that increased in size tended to expand while the territories of groups that decreased in size tended to contract (slope estimate = 5.87, 95% CI = 4.58 to 7.15; Figure 2). This relationship remained significant after removing one study on the green woodhoopoe which accounted for 65% of the data (slope estimate = 7.00, 95% CI = 5.08 to 8.92, N = 12 groups).

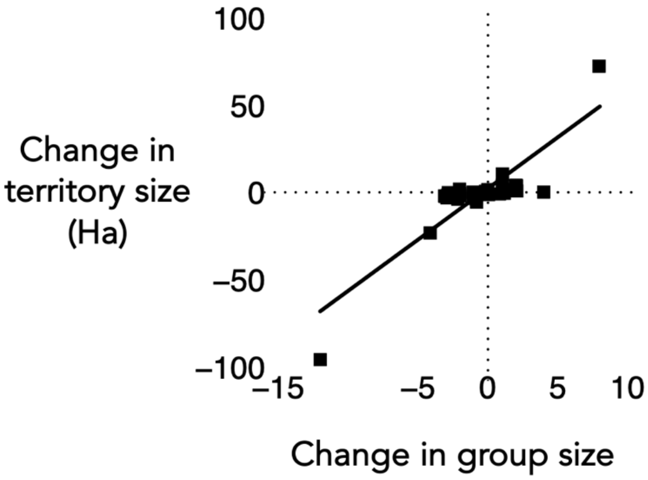


Figure 2. Within-group changes in group size and territory area for 34 different bird groups from five populations (four species). The slope (y = 5.87x + 2.26) is the estimate form our linear regression. Each datapoint is a different group.

DISCUSSION

How local competition affects cooperative group size has rarely been considered in theoretical or empirical work. If cooperative groups cannot increase their resource base, it seems logical that their sizes should be limited. Our finding that group size and territory area are positively correlated in most cooperative bird species (Figure 1) supports this, indicating that resource availability and group size go hand in hand. When specific groups increased or decreased in size, their territory expanded or contracted respectively (Figure 2), further supporting the idea that large groups need extra resources to avoid local competition.

We assumed that territory area is a good proxy for resource availability. Territory area in our case corresponds to space use during the breeding season. This is appropriate because the cooperative behaviour we are interested in, feeding offspring produced by others, takes place during this period and more space should mean more food. There are other 'critical' resources which affect the survival and reproduction of cooperative breeders which also correlate with group size. In our sample of studies these include: mast storage holes in acorn woodpeckers (Zr = 0.30), blackberry bramble in superb fairywrens (*Zr* = 0.79), bull-horn acacia in white-throated magpie jays (*Zr* = 0.59), and Eucalyptus canopy trees (*Zr* = 0.83) and hollow-bearing logs (*Zr* = 0.55) in the rufous treecreeper. Territory area has the advantage of being comparable between species. An alternative is to use a composite 'territory quality' measure, but this has only been done in three species: Seychelles warbler (*Zr* = 0.60), rufous treecreeper (*Zr* = 0.50), red-cockaded woodpecker (*Zr* = 0.30).

Group size and territory area were negatively correlated in the acorn woodpecker and the superb fairywren. These appear to be outliers. The effect size we used for the superb fairywren is the weighted mean of two effect sizes in opposite directions: *Zr* = -0.51 and 0.56. It is negative overall (*Zr* = -0.17) because of the difference in sample size between studies (N = 19 vs 9 respectively). For the acorn woodpecker, we excluded one study whose group size measure included juveniles (MacRoberts and MacRoberts 1976). This study reported an extremely strong correlation between group size and territory area (*Zr* = 1.22) which would have resulted in a positive weighted mean effect size for this species (*Zr* = 0.59).

A potential confounding variable which was not controlled for in any study is breeder quality (Rowley 1965; Downing et al. 2020). High quality breeders may have larger territories and more offspring than poor quality breeders. This would create a positive correlation between group size and territory area in species in which groups grow via natal philopatry, independently of resource availability. Three lines of evidence suggest that group size is adjusted to resources, however, and does not simply reflect breeder quality. First, within-group changes in size are tracked by changes in territory area (Figure 2). This is unlikely to be the case if territory area is determined by breeder quality alone. Second, in 22/25 species territorial displays between groups were reported (Table 1, four species were missing data) and group size influences the outcome of such displays (eg. MacRoberts and MacRoberts 1976; Ligon and Ligon 1978; Radford 2003; Hale et al. 2003; Seddon and Tobias 2003). In just three species was there movement between groups and no displays were reported. Third, experimental manipulations in several species show that territory quality influences dispersal, and hence group size, independently of breeder quality (Komdeur 1992; Walters et al. 1992; Covas 2004; Dickinson and McGowan 2005; Baglione et al. 2006), complementing the findings of multiple long-term field studies (e.g., Stacey and Ligon 1987; Koenig et al. 1992; Pasinelli and Walters 2002; Nelson-Flower et al. 2018; Suh et al. 2020; Cousseau et al. 2020).

An expanding resource base can alleviate local competition, enabling group sizes to increase, seemingly without harmful effects. Two unknowns, however, are how resource expansion affects a group's total reproductive output and reproductive skew within the group. Territory expansions could increase the output of the dominant breeders, akin to "resource enhancement" altruism where cooperation is selected because it increases the resource supply (Van Dyken and Wade 2012), but the extra resources may allow more individuals to reproduce (e.g. Stacey and Koenig 1990; Koenig and Dickinson 2016), destabilising cooperation. More work is needed to better understand the social consequences of resource enhancement for cooperative groups.

The problem of local competition does not go away once cooperation has evolved. It probably gets worse as groups become larger, even if groups can expand their resource base. Although the theoretical literature is replete with ideas on how to avoid local competition (Rodrigues and Gardner 2013), these typically do not deal with group size evolution. This leaves us with an opportunity to develop and test new theory on how extremely large cooperative groups evolved. In superorganisms, for example, public goods production in the form of agriculture, and legionary behaviour, where colonies do not have permanent nests but continuously roam, both ease local competition. In addition to microbial systems, these provide a promising avenue for future empirical work.

DATA AVAILABILITY

Data, code, and supplementary information currently available here: https://github.com/pipdowning/Birds_Local_Competition/tree/main

AUTHOR CONTRIBUTIONS

PAD: conceptualization, methodology, formal analysis, investigation, data curation, visualisation, writing – original draft, writing – review and editing; HH: conceptualization, project administration, writing – original draft, writing – review and editing

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CONFLICT OF INTEREST We declare no conflict of interest

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