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Ecological Interactions Drive a Power-Law Relationship Between Group Size and Population Density in Social Foragers

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ABSTRACT

Past work has shown that group formation in foraging animals aids in resource acquisition and reduces the number of interactions with predators. However, group formation can also increase competition for resources among group members. Here, we model how the individual costs and benefits of group formation drive group size. Our model predicts that when competition for resources occurs within and between groups, forager group size will exhibit a one-third power-law relationship with population abundance. However, if groups form due to intragroup competition and predation, we predict either a one-half power-law relationship with population abundance or a constant group size depending on the coupling between predator and prey. Using empirical data on group foraging birds and ungulates, we found a scaling relationship consistent with the one-third power-law, suggesting that hierarchical competition drives the average group size. Our results support work highlighting the importance of density-dependent group formation in maintaining population stability.

1 | Introduction

Group foraging is a common phenomenon that has emerged in a range of ecological contexts (Rubenstein 1978). Known mechanisms that promote group foraging behaviour include the improved detection of spatially clustered resources, increased predator vigilance and increased time available to forage (Beauchamp 2019; Elgar 1989). However, increasing group size may also incur costs. The increased competition within groups and conspicuousness of larger groups negatively affect individual fitness (Elgar 1989; Hintz and Lonzarich 2018). The optimal group size should balance the costs and benefits of these interactions (Markham et al. 2015).

Early models of grouping behaviour used stochastic fusion-fission models to show how simple behavioural rules, for example, individuals leaving and joining groups randomly, drive the distribution of group sizes in a population. J. E. Cohen showed that these models can predict the distribution of group sizes in vervet monkeys (Cohen 1972) and play groups in primary school (Cohen 1971). Extensions of this modelling approach have shown that this approach can capture the basic patterns observed in the distributions of group sizes of static populations. Many of these models predict that these distributions follow fat-tailed distributions such as the truncated power-law distribution (Bonabeau et al. 1999; Bonabeau and Dagorn 1995; Sjöberg et al. 2000; Griesser et al. 2011; Vandermeer and Perfecto 2006) and the logarithmic distribution (Niwa 2003; Griesser et al. 2011) that have been hypothesised to arise due to similar fission and fusion forces across taxa (Bonabeau and Dagorn 1995).

Using a similar stochastic approach as Cohen (1971), Gueron and Levin (1995) extended these results to study populations with variable abundance. They showed that when individuals obey density-dependent fusion and fission rates, the average group size in a dynamic population is predicted to scale proportionally to the square-root of the population abundance. This modelling approach was extended by Niwa (1998), who incorporated more complex behaviours of schooling fish into these fusion and fission rates. Under this model, group sizes scale linearly with population size. Conversely, Viscido et al. (2005) used an individual-based simulation model with movement rules based on social cohesion forces to explore schooling behaviour in fish, finding that group size exhibits an asymptotic limit at high densities. Thus, theoretical models have made a wide range of predictions, but despite this discordance, there has not yet been a systematic assessment of whether group size exhibits density dependence or the nature of this dependence.

More recent efforts have focused on scaling up models of group dynamics to the population to determine how group dispersal mechanisms influence the stability of populations. Bateman et al. (2018) use detailed data on meerkat social groups to describe the annual change in the distribution of group sizes and population growth. Their model predicted that Allee effects were not present in meerkats, contrary to past work suggesting that social populations will have a higher propensity for these effects (Angulo et al. 2018). Lerch et al. (2018) further explored the link between group dynamics and population dynamics using an age-structured demographic model of the African wild dog. They showed that group-level Allee affects only scaled to the population level when a mechanism, such as density-dependent dispersal, coupled the group- and population-levels. This result was expanded on in Lerch and Abbott (2024), showing that the impact of group-level processes on population growth is determined by the interaction between within-group density dependence and its effect on the group size distribution. This work suggests that group-level Allee effects are not generally expected to scale to the populationevel, without a specific mechanism such as when group formation is stunted at low densities (Courchamp et al. 2000).

There is some evidence that group size in at least some taxa exhibits density dependence. Past empirical work on a number of Serengeti ungulates has shown that average group size tended to increase nonlinearly with forager abundance (Fryxell et al. 2022, 2007). Studies on the Pyrenean chamois (*Rupicapra pyrenaica*) (Pépin and Gerard 2008), common redshanks (*Tringa totanus*) (Cresswell and Quinn 2011) and a number of Atlantic seabirds (Beauchamp 2011) also found that average group size increased nonlinearly with population size. Theoretical work by Fryxell et al. 2022, 2007 found that density-dependent group formation can play an important role in stabilising predator–prey relationships by reducing encounter rates between predators and their prey. This reduced encounter rate lowers the total amount of prey predicted to be taken by predators relative to solitary animals, extending the space of coexistence. Thus, while density-dependent group size may be common in nature and have important ecological interactions, we still do not have a broad-scale assessment of whether populations follow past model predictions, or a sense of whether density-dependent group size is a general phenomenon.

Here, we examined how the risk of predation and intragroup competition influences the population growth rate when forming cooperative foraging groups. We used these models to predict how optimal group size depends on the density of foragers and their predators. We then tested model predictions using existing data on foraging birds' and ungulates' observed group- and population sizes and determined whether the observed patterns were consistent with model predictions.

2 | Materials and Methods

2.1 | Modelling Group Size in Foragers

We linked individual social behaviour to the population growth rate by determining how the decision to form groups affects the amount of time spent on interactions. We considered two state variables, forager (N) and predator (P) population abundances. A third variable, the average group size, γ, was an unknown function that may depend on N and P. We accounted for the time that an individual spends on intergroup interactions, intragroup interactions and time spent scanning for predators. We also included the number of individuals captured by predators.

For a population with average group size γ (corresponding to N/γ foraging groups), the amount of time taken on intragroup interactions within each foraging group is modelled as $\beta_W \gamma^2$. This term accounts for competition for resources within a foraging group or other factors such as the time spent maintaining within group bonds. The amount of time taken by each group to compete for resources between groups is modelled as $\beta_B N/\gamma$. Thus, the total time spent on competitive interactions is the sum of these terms multiplied by the number of groups (N/γ). The time an individual in a group of size γ spends on vigilance behaviour is modelled as $\beta_V P/\gamma$, an amount that increases with the number of predators and declines with group size. The total time spent being vigilant is this term multiplied by the number of individuals (N). As in past work on time budgets, we assume that time taken on these activities reduces the time available for foraging and thus reduces an individual's reproductive rate (Holling 1959). Additionally, we modelled the rate of predation as $\alpha PN/\gamma$, proportional to the time an individual spends being vigilant. Together with reproduction, we incorporated these factors into a model of population growth,

$$\frac{dN}{dt} = rN - \beta_W \left(\frac{N}{\gamma}\right)\gamma^2 - \beta_B \left(\frac{N}{\gamma}\right)^2 - \frac{NP}{\gamma}\left(\beta_V + \alpha\right) \qquad (1)$$

We found the group size function, denoted as $\gamma^*(N, P)$, that maximises the per-capita growth rate as a function of γ using analytical solutions when possible and numerical optimization otherwise under the constraints $\lfloor \gamma^* \rfloor = 1$ and $\lceil \gamma^* \rceil = N$. The dependence of each of the per-capita rates on group size are illustrated in Figure 1a. We considered four cases of equation (1), (i) competition with no predation ($\alpha = \beta_v = 0$), (ii) predation with

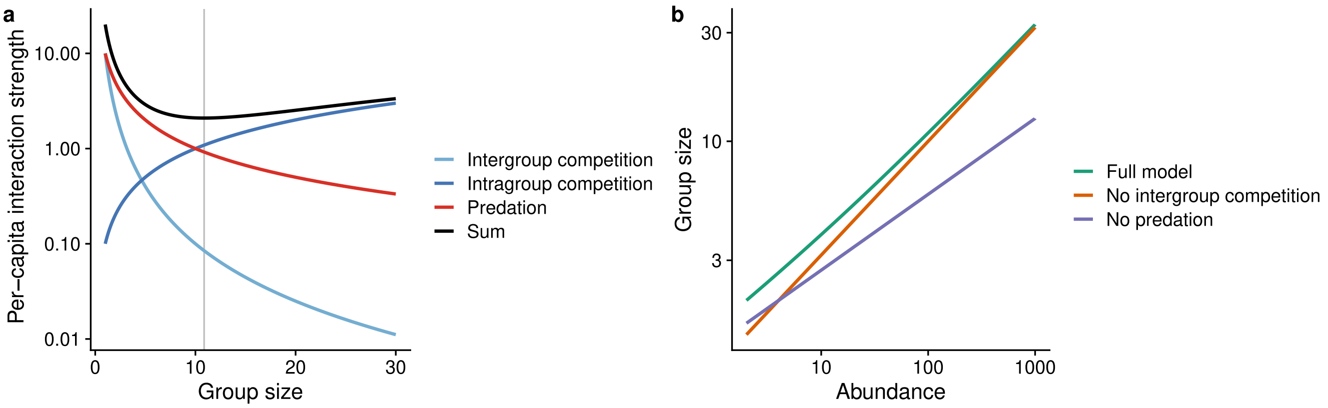

FIGURE 1 | The costs and optimal group size in forager populations. (a) The sum (black line) of the per-capita costs of competition and predation, lead to an optimal group size in a population of 100 of approximately 10 individuals per group (vertical grey line). (b) Optimal group size relationship with population abundance for a population of foragers exhibits a 1/3 power law when facing both intergroup and intragroup competition (purple line), a 1/2 power law when facing intragroup competition and predation (red line), and a more complex relationship that exhibits an asymptotic 1/2 power law when all terms are included in full model (green line). For both panels we set intergroup competition $\left(\beta_W\right) = 0.1$, intragroup competition $\left(\beta_B\right) = 0.1$, vigilance cost $\left(\beta_V\right) = 0$ and predation rate $(\alpha) = 0.1$, except when specific parameters are noted to be zero. We assumed that predator abundance was equal to prey abundance. Parameters used to simulate these groups were selected for illustrative purposes and the qualitative results are robust to the specific values used.

no intergroup competition ($\beta_B = 0$), (iii) predation with no intragroup competition ($\beta_W = 0$) (iv) the full model. For comparison, we also considered a model without hierarchical competition, $\frac{dN}{dt} = rN(1 - N/K) - \frac{NP}{\gamma}\left(\beta_V + \alpha\right)$.

To obtain solutions when analytical analysis was intractable, we used simulations across a range of values for N, α and the β's to explore numerical solutions to the optimal group size. For the model with no predation, we simulated population growth rates across a vector of values for the intergroup competition (β_B), intragroup competition (β_W) from 10^{-4} to 1 over 100 equally spaced values on the log scale and set the predation rate (α) to 0.001. We assumed that predator abundance was linearly dependent on prey abundance ($P = N$). We varied the forager population size, N, from 10^3 to 10^6 over 1000 equally spaced values on the log scale. The optimal group size was determined numerically for every set of parameter value combinations (β_W, β_B, α) by finding the maximum per capita growth rate using the optimise function in R (R Core Team 2022). For each set of parameter value combinations, the optimal group size and abundance were log-transformed to estimate the power-law exponent. We then fit a linear model to the simulated data of the form $\ln \gamma = a + b \ln N$ where the estimated slope, b, is the power-law exponent that determines the strength of the nonlinear relationship between group size and abundance, while the intercept, a, gives the average group size when $N = 1$. If $b = 0$, group size has no relationship to abundance, indicating that group size is not density-dependent, while if $b = 1$, the average group size is proportional to density.

2.2 | Empirical Data and Modelling

We used the following search terms on the Web of Science search service to search for papers on group foraging birds and ungulates. For birds, we used the following search terms (reported with the number of search results for each term): ‘“flock size” AND prey’ (857), ‘“flock size” AND population’ (248), ‘Prey AND “group size” AND scaling’ (89), ‘“population size” AND “group size” AND bird’ (16), ‘forag* AND “group size” AND scaling’ (12). We used the following search terms for ungulates: ‘“group size” AND “population size” AND “ungulate”’(16), ‘“group size” AND “density” AND “ungulate”’(99).

We read the abstract to determine taxon suitability and scanned figures and tables for available data. Papers that contained samples of group size (or group density or the number of groups) and population abundance (or population density) of birds or ungulates through time and/or space were used unless group size was clearly not related to foraging behaviour (e.g., nesting colonies). Datasets selected for analysis had a minimum of 4 observations of both group size (or number of groups or group density) and population abundance (or population density) through time and/or space. If papers did not have raw data available, they were digitised using the software web plot digitizer (Rohatgi 2022). When the number of groups and abundance were reported but not group size, we calculated the average group size by dividing the population abundance by the number of groups. When only group density and population density were available, we calculated average group size by dividing population density by group density. All reported population densities were converted to individuals per kilometer^2.

We modelled the relationship between group size and population density using linear and nonlinear mixed effects models. First, we modelled log-group size using a power-law relationship with an interaction between log-population density and taxonomic class, an additive effect of data type (density or count) and a random slope and intercept that varied by taxa. We also considered several alternative descriptions of the data in addition to the power law. We tested an intercept model with fixed effects of taxonomic class and data type and random intercept that varied by taxa, a log-linear model where log-group size was regressed against population density interacting with taxonomic class, an additive effect of data type, and a random slope and intercept that varied by taxa, and a Monod model with additive effects of taxonomic class and data type on both the growth rate and half-saturation parameters (denoted as a and b in Table 1), and where each parameter had a random effect that varied by taxa. The Monod model tested whether group size stabilises at a fixed value at high population densities. The power-law, intercept and log-linear models were fit using the lme4 package (Bates et al. 2015), while the Monod model was fit using the nlme package (Pinheiro and Bates 2000). We used maximum likelihood estimates to perform model selection using the AICc, and reported parameters were estimated using restricted maximum likelihood.

The average group size may not accurately reflect the experience of a typical individual when the group size distribution is highly skewed. Alternative measures such as the mode or median group size may better characterise the experience of a typical individual. To determine when using the mean group size might be misleading for our analysis, we estimated the correlation between mean group size with median group size and with the herd fragmentation index (hereafter, HFI) a previously used measure of the spread in the distribution of group sizes (Haydon et al. 2008). We simulated group sizes from a Pareto distribution with a scaling parameter that varied from $\alpha = 1.05$ to $\alpha = 2$ over 20 equally spaced values. For each value of the scaling parameter, we simulated 10^6 realised group sizes, then calculated the mean group size, median group size and the HFI. We then calculated the correlation between these quantities on both the natural- and log-scales.

3 | Results

3.1 | Theoretical Relationships Between Group Size and Population Density

In the case of intergroup and intragroup competition, but no predation ($\beta_V = \alpha = 0$), the optimal groups size is predicted to follow

$$\gamma^*(N) = \left(N\frac{2\beta_B}{\beta_w}\right)^{1/3} \tag{2}$$

as illustrated in Figure 1b. Groups of size 1 ($\gamma^*(N) = 1$) occur when intragroup competition is much stronger than intergroup competition ($N < \beta_W / 2\beta_B$), while a single supergroup forms ($\gamma^*(N) = N$) when intergroup competition is much stronger than intragroup competition ($N < \sqrt{2\beta_B / \beta_W}$).

TABLE 1 | Models fit to group size data and their statistical support. Subtext denotes whether parameters varied by the predictors of taxonomic class (class), data type (type) or both.

Model name	Form of fixed effects	ΔAICc
Intercept	$\ln\gamma = a_{\text{class+type}}$	1079
Power-law	$\boldsymbol{\ln\gamma = a_{\text{class+type}} + b_{\text{class}}\ln(N)}$	**0**
Log-linear	$\ln\gamma = a_{\text{class+type}} + b_{\text{class}}\text{N}$	469
Monod model	$\ln\gamma = \ln\left(\frac{a_{\text{class+type}}\text{N}}{1+b_{\text{class+type}}\text{N}}\right)$	95

Note: Bold values indicate best overall model.

Incorporating predation with no intergroup interactions ($\beta_B = 0$) leads to group sizes proportional to predator abundance, $\gamma^*(P) = \left(P\frac{\alpha+\beta_V}{\beta_W}\right)^{1/2}$. In the case that predator abundances are independent of prey abundance average group size of the prey is predicted to be a constant, while if predators are linearly correlated with prey abundance then prey group size is predicted to follow a one-half scaling law (Figure 1b). Incorporating predation with intragroup interactions and no between group interactions ($\beta_W = 0$) and applying the boundary conditions ($1 \le \gamma^*(N) \le N$) gives $\gamma^*(N) = N$, predicting that individuals form a single supergroup.

Finally, we were not able to obtain analytical forms of γ^* in the full model. Numerical solutions indicated that when both competition terms and predation were present, the resulting dynamics are a mixture of the dynamics given by equations (2) and (3) (Figure 1b, Figure 2). This indicates that the strength of the power-law behaviour will change depending on the relative strength of competition and predation. For moderate levels of intergroup competition and low intragroup competition, population group formation was consistent with a population limited by predation and exhibited a 1/2 power law (Figure 2a). As the strength of intergroup and intragroup competition increased, the optimal group size exhibited a 1/3 power law (Figure 2b). The solution to our model without hierarchical competition is that the optimal group size should always be maximised so that $\gamma^*(N) = N$.

3.2 | Empirical Relationship Between Group Size and Population Density

We obtained 41 total datasets containing samples of group size and population size through time and/or space. Twenty of these datasets contained bird data (average sample size in a dataset, $\overline{n} = 10.5$), and twenty-one contained ungulate data (average sample size in a dataset, $\overline{n} = 48.6$). The total number of observations used in the analysis was 1231 with a median number of 11 observations per taxa. The minimum number of observations in a dataset were 4 (*Corvus corax*, *Calcarius ornatus*, *Eremophila alpestris*) and the maximum was 112 (*Rupicapra pyrenaica*). The full dataset is available on Dryad.

We found that the power-law model fitted the data best, followed by the Monod model, the log-linear model and the intercept model. We estimated the relationship between group size and density to be (reported as mean [standard error] 0.33 [0.05] for the power law exponent of birds and 0.37 [0.07] for ungulates [Figure 3]). The 95% confidence interval of the estimated power-law exponent for birds was (0.22, 0.43), and ungulates was (0.27, 0.56). Thus, both estimates were consistent with the theoretical prediction of 1/3, while ungulates were also consistent with the prediction of 1/2. Residual plots indicated that two populations (waterbuck ($n = 80$) and Pyrenean chamois ($n = 112$)) displayed heteroskedastic residuals (Figure S1). Both populations exhibited an upper bound on group size due to the formation of single super groups, where all the individuals join a single group. We also found two populations (American pelican ($n = 8$) and grey-crowned crane ($n = 10$)) that had higher residual variation than the other

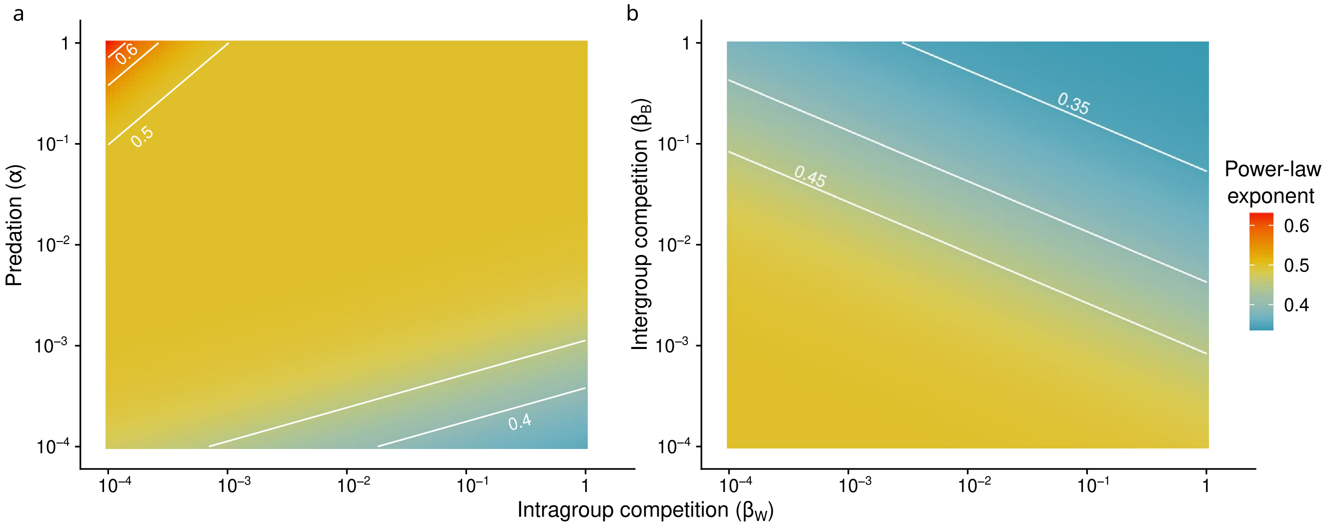

FIGURE 2 | The power-law exponents from the full model estimated from numerical simulations. (a) Illustrates exponents when predation rate is fixed at $\alpha = 0.001$ and competition strength is varied. When the strength of competition is weak relative to predation the exponent is $b = \frac{1}{2}$, while if competition is stronger than predation the exponent is $b = \frac{1}{3}$. (b) Illustrates power-law exponents when intergroup competition is fixed at $\beta_B = 0.001$. When predation is higher than competition the exponent is $b = \frac{1}{2}$, though at extreme values of predation the exponent starts to increase as the population starts to form a supergroup at low densities. For all simulations N was varied from 10^3 to 10^6 over 100 equally spaced values while the predation rate was $\alpha = 0.01$ and predator abundance was equal to prey abundance.

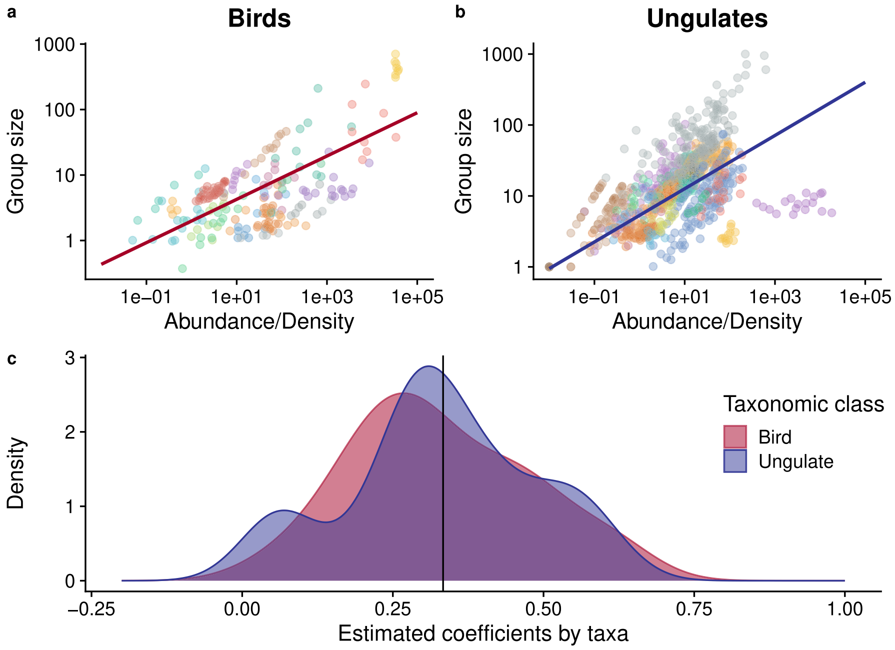

FIGURE 3 | Data for all taxa and the estimated relationships between density and group size from the mixed effects model. The lines in (a) and (b) correspond to the estimated power-law relationship at the level of taxonomic class. Colour distinguishes each population used in the analysis. In birds, the estimated slope is 0.33 (SE = 0.05), while for ungulates, it is 0.37 (SE = 0.07). The density plot (c) gives the distribution of estimated power-law exponents for each taxon. The vertical black line gives the 1/3 exponent predicted from the analytical model.

taxa (Figure S2). Both taxa were taken from studies that look at population density and group size across space (King and Michot 2002; Wamiti et al. 2021). It may be that the space-for-time substitution is more variable than repeated measures of the same population due to spatial variation in the forces driving group formation.

Our simulations testing the consistency between the mean, median and HFI statistics generated from the Pareto distribution found that on the log-scale these alternative statistics are consistent with the mean ($\hat{\rho}_{\mathrm{HFI}} = 0.82$ and $\hat{\rho}_{\mathrm{median}} = 1.00$) while on the natural scale the average group size had a strong correlation with the median ($\hat{\rho}_{\mathrm{median}} = 1.00$), but not the HFI ($\hat{\rho}_{\mathrm{HFI}} = 0.64$). This suggests that while the average group size can capture systematic changes in the central tendency of the group size distribution, it may not accurately capture changes in other properties of the distribution, for example when the spread of the group size distribution changes independently from the central tendency.

4 | Discussion

We derived a scaling relationship between group size and abundance in foraging animals that emerges due to the trade-offs inherent in the group formation of many foraging animals. Past work has shown that sublinear power-law group formation can stabilise predator–prey dynamics (Fryxell et al. 2022). However, both the drivers of these laws and their general applicability were previously unclear. We found that the average bird and ungulate population exhibited power-law group formation consistent with the 1/3 exponent predicted by a model that includes hierarchical competition within and between groups, while the ungulate population was also consistent with a 1/2 power-law predicted by within-group competition and predation and a 1/2 power law predicted by random movement between groups (Gueron and Levin 1995). We did not consider the impacts of measurement error in the independent variable, population abundance, which is known to induce a negative bias in regression estimates of slopes (Riggs et al. 1978). Uncertainty in population abundance is present when studies use estimated abundance, rather than a censused abundance. Two of the studies used in our analysis reported uncertainty in estimates of population abundances; thus, the majority did not report standard errors and reported raw counts of population abundance which were presumably censused. However, in a few cases, reported counts appeared to be estimated based on the rounded numbers reported, though no uncertainty in estimates was reported. If measurement error is pervasive in this dataset, we would expect that the true exponent is higher than reported here.

Here, we took a strategic modelling approach (Levins 1966) that focused on key interactions, proposed here to be competition and predation, to understand broad scale empirical patterns in bird and ungulate group sizes. While this model-building approach can be useful for determining broad patterns, the simplified assumptions of the approach mean that applying the model to any individual taxa may be challenging. Thus, future work can build on these results by taking a more mechanistic approach to understanding how variation in life history, environment and social structure drives variation in group formation dynamics.

Past models of group dynamics have relied on approaches such as coagulation-fragmentation and individual-based models to account for the movement of individuals among groups. Our approach used a time-budget modelling framework that arises from an individual perspective but scales to the population-level model by assuming that individuals behave identically and averaging over any stochastic effects of demographic and environmental heterogeneity. While these effects have been shown to be an important component of some aspects of group dynamics, they were not required to explain the macroscopic-level patterns of group assembly examined here. A natural next step in model development would be to incorporate the group formation processes explored here with previously developed movement models. Such work may provide insights into when group formation is driven by ecological interactions and when stochastic forces dominate.

Our approach is in line with past work examining within- and between-group competition using game-theoretic formulations to model strategy tradeoffs. The consistency between model predictions and data suggests that this approach qualitatively captures the processes that determine group size in many forager populations. However, there was substantial variation across populations (Figure 3), suggesting that the factors that drive group formation vary widely across populations. This is reinforced by the dependency of our model predictions on the behaviour of the predator population and the potential dependence of group size scaling on how predators are coupled to their prey.

Our model predictions for the predation component assumed that predator abundance is proportional to prey abundance. This assumption will not hold when predator abundances are not regulated by their social prey or when more complex forms of dependency arise between predator and prey populations. Another form of predator–prey coupling not explored here is the ratio dependent model where predator abundance may be regulated by the number of prey per predator rather than the overall prey abundance (Arditi and Ginzburg 2012). This alternative coupling may lead to alternative forms of the group-abundance relationship.

We found that hierarchical interaction rates were necessary for density-dependent group formation to occur. Our model of hierarchical competition is similar in nature to other models that capture the effects of within- and between-group competition, including the nested tug-of-war model (Reeve and Hölldobler 2007), which has been used to predict the relative investment that ants should make in within-group and between-groupompetitive strategies. Models of cooperation in humans have also been proposed to arise from differentials of within- and between-group competition (Puurtinen and Mappes 2008) and empirical evidence has documented effects of hierarchical competition in primates (Stevenson and Castellanos 2001; Lemoine et al. 2020). Hierarchy of competition can be facilitated by factors including relatedness (Ruch et al. 2009), access to prey (MacNulty et al. 2014; Yip et al. 2008), habitat quality (García et al. 2022; Radford and Fawcett 2014) or access to mates (McDonald et al. 2012).

Our model predicts a sudden shift from populations exhibiting group size power-laws to the dissolution of groups (when the power-law exponent switches to 0) or the fusion of all groups into a single supergroup (when the exponent switches to 1) with changes in abundance, or when the strength of ecological interactions changes. Empirical examples of animals moving across these critical boundaries include the swarming of desert locusts (*Schistocerca gergaria*) when abundances increase (Despland et al. 2000), the formation of regional supergroups of rorqual whales in response to increased resources (Cade et al. 2021), the formation of heterospecific winter flocks in birds due to increased predation risk (Herrera 1979), and increased social grouping in moose (*Alces alces gigas*) with increases in predation risk (Molvar and Bowyer 1994).

While the empirical power-law relationship was supported by our modelling work, past theoretical work incorporating more detailed individual-level interactions between group members has shown that group size can also exhibit linear (Niwa 1998) or saturating functions (Viscido et al. 2005) with respect to population abundance. We did not find support for these hypotheses in this dataset, though future work exploring taxa-specific or environmentally mediated deviations away from our proposed power-law relationship may focus on how and when sublinear power-law relationships are poor approximations of the processes driving group formation. Recent work highlights how within-group processes such as dispersal can decouple population processes from group-level dynamics (Bateman et al. 2018; Lerch and Abbott 2024), thus understanding the drivers of dispersal among taxa may be a fruitful approach for identifying deviations from the proposed power-laws. The localised movement of individuals between groups may also be a driver of increased local relatedness.

Classic work on the evolution of cooperation suggests that kinship has played a primary role in the evolution of cooperative groups (Hamilton 1964; Queller 1992; Kelly 1994). For example, Packer et al. (1990) suggest kinship could explain why observed lion groups tend to be larger than optimal (Caraco and Wolf 1975). Future work assessing the group size–abundance relationships in high-fecundity taxa such as insects, where it may not be necessary to admit non-kin to groups, may provide important clues about the role of kinship on these scaling relationships. However, kinship alone may limit group sizes to suboptimal levels in many species and create potential issues with finding suitable mates. A middle ground to assuming that group membership is not strictly enforced or strictly kin is to structure the probability of accepting new members as a function of relatedness (Avilés et al. 2004). It has been proposed that this approach can explain how group sizes grow beyond the limitations of fecundity and direct kin, important for the long-lived taxa explored here.

Several additional known drivers of forager group size that were not explicitly incorporated into our models may introduce heterogeneity in group size, a factor thought to play an important role in driving emergent population-level effects (Angulo et al. 2018). For example, relaxing the assumption that individuals have knowledge of overall population densities, rather than local densities (Halloway et al. 2020), incorporating the impact of habitat heterogeneity on optimal group size (Brown et al. 2002a, 2002b; Fortin et al. 2009), or variation in the strength of interactions over time or space due to behaviour and habitat (Smith et al. 2020) would all potentially drive variation in group size. Other key processes may deviate systematically away from the optimum explored here. Incorporating advantages in resource detection with group size (Hake and Ekman 1988), increases in disease transmission with group size (Brandell et al. 2020), and increases in group conspicuousness with group size (Elgar 1989; Hebblewhite and Pletscher 2002; Hintz and Lonzarich 2018) may shift groups away from the optimum found here. Finally, we did not find suitable data to explore group-abundance scaling in mixed species groups, which arise in birds and ungulates (Sridhar et al. 2009; Stensland et al. 2003), likely because assessing population size in this case is more complex.

Power-law models are scale-free, an especially striking relationship in Ecology where many processes are contingent on scale (Chave 2013). Studying these relationships has allowed ecologists to identify key organising processes and link patterns across scales (Brown et al. 2002a, 2002b). Power-laws have been identified across ecology, including relationships between population density and body size (Marquet et al. 2005), population density and species per unit area (Cohen 2020), and predator and prey biomass (Hatton et al. 2015; Salahshour 2023). While both our models and the data suggest that the exact exponent that scales group size may be contextual, not a fundamental constant, we did find strong evidence for sublinear scaling across these taxa. Our study reveals that hierarchical competition is likely to be driving the observed patterns in group formation in many populations of social birds and ungulates. Our results suggest that density-dependence in group formation occurs in nature; these aggregations may stabilise predator–prey interactions. However, additional work is needed to better understand the factors that drive hierarchical competition and how density-dependence in animal behaviour drives population- and community dynamics. Because group formation of foragers is common across a wide range of taxa and trophic levels beyond those considered here, including microbes (West et al. 2007), fish (Foster 1985), primates (Dunbar et al. 2018), cetaceans (Conner 2000) and insects (Lin and Michener 1972; Sumpter and Pratt 2003), our results suggest that the stabilising effects of group formation may be common in nature.

Author Contributions

A.R. acquired the data, conducted the statistical analysis, and wrote the first draft of the manuscript. A.N.W. provided feedback on the data acquisition, statistical analysis and subsequent manuscript drafts. J.M.F. conducted the analytical modelling and provided feedback on the data acquisition and subsequent manuscript drafts.

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Data Availability Statement

Data and code have been deposited on Dryad (https://doi.org/10.5061/dryad.6hdr7sr83).

Peer Review

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