# Title

Evolutionary drivers of group foraging: A new framework for investigating variance in food intake and reproduction

# Running Title

Variance reduction as driver of group foraging

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# Author Contributions

L.G. had the primary responsibility for designing the study, analysing the data and drafting the manuscript. L.G. and E.K.D. together were responsible for conducting field work and collecting data. M.J.T. assisted in data collection. Y.L. assisted in designing the study and drafting the manuscript. All authors were involved in revising the manuscript.

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# Data Accessibility Statement

All data generated and analysed during this study are [*will be*] deposited in Dryad online repository [*ref. number*].

# Abstract

A proposed fundamental driver of group living is more reliable, predictable foraging and reproduction, i.e. reduced variance in food intake and reproductive output. However, existing theories on variance reduction in group foraging are simplistic, refer to variance at the level of individuals and groups without linking the two, and do not spell out crucial underlying assumptions. We provide a new, widely applicable framework for identifying when variance reduction conveys fitness benefits of group foraging in a wide range of organisms. We discuss critical limitations of established theories, the Central Limit Theorem and Risk-Sensitive Foraging Theory applied to group foraging, and incorporate them into our framework while addressing the confusion over the levels of variance and identifying previously unaddressed assumptions. Through a field study on colonial spiders, *Cyrtophora citricola,* we demonstrate the importance of evaluating the level of food sharing as a critical first step, previously overlooked in the literature. We conclude that variance reduction provides selective advantages only under narrow conditions and does not provide a universal benefit to group foraging as previously proposed. Our framework provides an important tool for identifying evolutionary drivers of group foraging and understanding the role of fitness variance in the evolution of group living.

# Keywords

Sociality, cooperation, stochastic environments, feeding strategies, uncertainty, inequality

# Introduction

Numerous factors promote group living by increasing rates of feeding and reproduction. For example, a bird may discover more patches of food and reduce predation risk by flocking (Clark and Mangel 1984; Cresswell 1994), while a lion may catch larger prey, and her young have a better chance of survival due to cooperative hunting and breeding (Packer et al. 1990). Typically, an increase in mean food intake results in an increase in mean reproductive output, after a minimum level of nutritional intake is reached enabling an animal to reproduce (henceforth ‘the reproductive threshold’) (Schoener 1971; Poethke and Liebig 2008). However, selection acts not only on the mean but also on the variance in reproductive output, and variance in food intake may be linked with variance in reproduction (Gillespie 1977; Real 1980; Real and Caraco 1986). For example, high temporal variance in food acquisition could lead to periods of starvation, or missing out on a breeding season, which increases reproductive variance, severely affecting fitness (Real and Caraco 1986). Hence, selection may favour individuals that experience more reliable and predictable food intake, as these individuals will enjoy more predictable reproductive output (Gillespie 1977; Wenzel and Pickering 1991). Here, we focus on such variance reduction in food intake and in reproduction as an often-overlooked potential selective advantage favouring group foraging. Variance reduction may act in conjunction with other selective advantages of group living, such as the above-mentioned increases in mean foraging success, growth rate and survival rate, which we shall not review here. Importantly, the level of variance is expected to be independent of its mean whether applied to food intake or reproductive output.

We have three aims with this study. First, we argue that a new framework is needed to evaluate variance reduction as a potential selective advantage of group living. We substantiate this by critically reviewing established theories that apply to group foraging: the Central Limit Theorem and Risk-Sensitive Foraging Theory. While doing so, we reveal hitherto unexplored key assumptions and clear up the confusion over the level at which variance is measured. Second, we provide a new framework for investigating whether variance reduction offers a selective advantage relevant to any group foraging organism. Third, we apply our new framework in a field case study on the facultative colonial spider *Cyrtophora citricola*,while testing key predictions from these established theories.

## The Central Limit Theorem

In their seminal paper from 1991, Wenzel and Pickering argued that group foraging results in decreased variance in per-capita food intake, according to the fundamental statistical principle of the Central Limit Theorem (Wenzel and Pickering 1991). The Central Limit Theorem states that a set of many observations is less likely than a set of few observations to produce an extreme mean value. In other words, a higher sample size produces a more reliable mean value. When considering multiple sets of values, where each set has a mean value, the variance among such mean values will therefore decrease when more observations are included in each set. Imagine rolling two dice and taking the mean of the two observations. It would not be too surprising to roll a six twice and therefore obtain a mean of six. However, if rolling 30 dice, seeing six dots on each single die, thereby obtaining a mean of six, would be highly surprising. Just by increasing the sample size it becomes unlikely to see an extreme mean value from a set of dice, like a mean of one or six (Fig. 1). Hence, if rolling a set of dice many times, say 100 times, and calculating the variance among the mean values, we will experience reduced variance the more dice are in included in the set. At the same time, with more dice (i.e. more observations) per set, mean values become more normally distributed (Fig. 1).

The Central Limit Theorem applied to group foraging as proposed by Wenzel and Pickering (1991) (henceforth CLT) states that variance in per-capita food intake will decrease with group size due to this principle. This is because the number of group members, and thereby the number of foraging events, increases with group size. If food acquisition from a foraging trip is stochastic, just as the outcome of throwing a dice is stochastic, then the number of dice in Fig. 1 can be replaced by the number of foragers in a group. Larger groups will therefore experience less variable, i.e. more reliable, mean food intake values than smaller groups, simply because of the higher sample size of foraging events. Less variable mean (i.e. per-capita) food intake should then result in less variable, more predictable, per-capita reproductive outputs. Wenzel and Pickering proposed that this statistical property constitutes a universal and automatic benefit of group living even if mean values of food intake and reproduction are unaffected by – or even decrease with – group size. Indeed, the theory was developed as an attempt to explain how group living may evolve despite the apparent decrease in per-capita productivity with group size in some social insects (Michener 1964; Wenzel and Pickering 1991). They argue that the benefits of per-capita variance reduction may outweigh the costs of lower mean per-capita food intake and reproduction in larger groups (Wenzel and Pickering 1991).

The CLT focuses on per-capita values which, as described, refer to group means. Per-capita variance can be calculated in one of two ways: either as temporal variance in a given animal group, e.g. variance over time in a group’s daily mean food intake, or as between-group variance, e.g. variance between groups in their mean food intake over a specified time period. While the CLT fails to specify which of these two ways of calculating per-capita variance was used to develop the theory, these two ways are at least theoretically equivalent. This is because the CLT considers foraging trips to be stochastic events, just like rolling dice. For example, it should not matter whether we roll the same 30 dice 10 times, or 10 different sets of 30 dice. Now replacing dice with foragers in this example: variance across 10 average daily food intake values from the same group of 30 group members should be equivalent to the variance across daily averages from 10 different groups of 30 group members each, assuming no substantial differences in foraging behaviour among groups of similar sizes. For ease we here use between-group variance rather than temporal within-group variance. Henceforth we use ‘per-capita variance’ and ‘between-group variance’ interchangeably.

In either case, per-capita variance measures variance at the level of the group. However, crucially, as selection acts on individuals, group-level effects are important only if they affect the inclusive fitness of individuals (i.e. the direct and indirect fitness of an individual combined) (Hamilton 1964b, a; Marshall 2011; Grinsted et al. 2015). Group-level effects may increase an individual’s inclusive fitness only under specific conditions. For example, if all small groups of a certain species fall victim to predation while larger groups are less likely to perish, then this higher group-level survival of large groups may directly translate into higher survival for individuals in larger groups. However, group-level variance in either mean food intake or mean reproductive output may not be directly linked with variance at the individual level. This is because, as we will see below, group-level means may contain important variation among the individuals comprising the group.

A key underlying assumption of the CLT is that group members share food. Such food sharing is expected to carry over variance reduction at the group-level to variance reduction at the individual level (Wenzel and Pickering 1991). However, food sharing can have multiple meanings and is not defined in previous literature on CLT. Importantly, food sharing does not necessarily reduce variance between individuals as is implicitly assumed in CLT. Different kinds of sharing include: 1) **Egalitarian Sharing**: All group members receive an equal share of pooled, group-level foraging. The mechanism behind such equal sharing may be either cooperation, whereby successful foragers share their food equally with unsuccessful- or non-foragers, or scramble competition, whereby all individuals stand an equal chance of obtaining food at each foraging bout, resulting in roughly equal between-individual food intake over time (Nicholson 1954), i.e. reduced between-individual variance; 2) **Sharing of Surpluses**: Successful foragers feed until satiation and unsuccessful foragers are allowed to eat – or not prevented from stealing – leftovers, as in producer-scrounger systems (Barnard and Sibly 1981), thereby equalising between-individual food intake over time, i.e. reducing between-individual variance; 3) **Skewed Sharing**: Dominant or reproductively superior individuals obtain larger shares of food from subordinate group members via cooperation or contest competition (Nicholson 1954). This common type of sharing in animal societies will increase rather than decrease variance between group members in food intake. Hence, determining the type of sharing is crucial – and yet previously unrecognised – for evaluating whether the CLT can provide fitness-benefits to individuals (Poethke and Liebig 2008). As we shall see in our proposed new framework, skewed sharing does not completely negate the possibility for per-capita variance reduction to provide fitness benefits to individual group members, but it does require a set of additional conditions to be met.

## Risk-Sensitive Foraging Theory

An alternative hypothesis, Risk-Sensitive Foraging Theory (RSF), focuses on temporal, within-individual food intake variance, i.e. the variance an individual experiences over time. It explains how animals, if given a choice, should choose a risk-averse strategy of foraging in patches that provide reliable, less variable food rewards if this provides sufficient food to meet the reproductive threshold (Caraco 1981; Real and Caraco 1986). However, if food abundance is generally low, animals would acquire too little food to reproduce via this strategy and should therefore prefer to forage on highly variable patches, adopting a risk-prone strategy. This way there is a small chance of locating high-food patches and reaching the reproductive threshold. The RSF was originally developed to predict optimal foraging strategies in solitary animals and was later applied to group foraging organisms. This was easily done as group foraging is thought to be a general mechanism of reducing within-individual variance (Clark and Mangel 1984; Uetz 1988; Poethke and Liebig 2008). Imagine an individual foraging in a stochastic environment. If food intake over time is highly variable there will always be a risk of repeatedly obtaining only small food rewards, but at the same time also a chance of obtaining large food rewards repeatedly. If foraging in a group reduces this temporal variance in food intake an individual would avoid the risk of low food intake but also forego the chance of higher-than average food intake. RSF predicts that when food is abundant, risk-averse group foraging should be favoured while risk-prone solitary living should give a selective advantage when food is limited as this would be the only strategy with at least a chance of obtaining enough food for reproduction (Fig. 2).

Hence, RSF predicts that the fitness-benefits of within-individual variance reduction depend critically on food abundance. An important and often overlooked detail, however, is that RSF does not refer to absolute food abundance but rather food abundance relative to the reproductive threshold (Poethke and Liebig 2008). This means that a risk-averse group-foraging strategy should be favoured not when food abundance is high per se, but when it is high as compared to the levels of food required to reach the reproductive threshold.

Group foraging is often simply assumed to reduce within-individual variance in food intake, yet the mechanism behind such variance reduction is rarely spelled out. Furthermore, empirical studies on RSF often report variance between individuals instead of within individuals, treating these two levels of variance as interchangeable (Uetz 1988; Rypstra 1989) (but see Uetz 1996). We argue that the only mechanism through which grouping can reduce within-individual variance is via a reduction in between-individual variance, i.e. via egalitarian or surplus sharing of food within groups, as described before. If group members share food more-or-less equally then variance between individuals is reduced and the variance an individual experiences over time will also decrease. Hence, while within- and between-individual variances are not interchangeable, between-individual variance reduction is a prerequisite for achieving the potentially beneficial within-individual variance reduction. In other words, egalitarian or surplus sharing is necessary for RSF to be relevant for a group foraging organism. This crucial assumption of more or less equal sharing within groups needs to be tested when investigating RSF in group foragers.

## The need for a new framework

We argue there is a need for a new framework for investigating potential selective benefits of variance reduction in group foragers. We will now highlight how existing theoretical frameworks in their simplicity fail to address several crucial factors. We incorporate these factors into a new framework for researchers to use when investigating variance reduction in food intake and reproductive output as a potential driver of group living, relevant for any group foraging organism.

Firstly, the CLT proposes that per-capita variance reduction provides a universal and automatic benefit of group living as long as group members share food (Wenzel and Pickering 1991). However, sharing can mean different things: sharing sometimes increases and sometimes decreases variance among individuals. Secondly, we have learned from RSF that the benefits of variance reduction depend on food abundance relative to the reproductive threshold (Real and Caraco 1986): indeed variance reduction is not always a selective advantage as proposed by the CLT. Thirdly, RSF assumes that group living reduces within-individual variance in food-intake but has yet to identify between-individual variance reduction, i.e. egalitarian or surplus food sharing, as the mechanism behind this important assumption (Clark and Mangel 1984; Uetz 1988; Poethke and Liebig 2008).

We argue that the level of sharing is the first, crucial element to evaluate when investigating whether variance reduction – at the group-level according to CLT or within individuals according to RSF – in food intake and reproduction may provide selective benefits of group living. If between-individual variance decreases with group size – reflecting more or less equal sharing of resources – variance in food intake and reproductive output is expected to decrease at both the group- and within-individual-level, producing fitness-benefits according to both CLT and RSF, providing that food abundance is high relative to the reproductive threshold. If group foraging concurrently increases mean food intake or reduces energy-related costs for an organism, e.g. associated with nest building or thermoregulation, the reproductive threshold will more easily be met, and the benefit of variance reduction is even greater.

However, if between-individual variance increases with group size – reflecting skewed sharing of resources – then the potential for variance reduction to provide selective advantages becomes dependent on a set of additional factors. An important theoretical contribution by Poethke and Liebig (2008) highlights how egalitarian versus skewed sharing of resources alters the assumptions behind the expected benefits of variance reduction (Poethke and Liebig 2008). They considered between-individual variance, making their findings relevant to both CLT and RSF. They find, consistent with RSF, that variance reduction based on egalitarian sharing of resources provides a selective advantage only if food availability is high relative to a low reproductive threshold. In contrast, with skewed sharing (high between-individual variance) they find that grouping may be favoured only when food availability is low relative to a high reproductive threshold. This is because sacrificing resources for a group member presents little cost if meeting the reproductive threshold alone is nearly impossible (Poethke and Liebig 2008). However, the evolution and maintenance of skewed sharing in animal groups requires either high genetic relatedness between group members or some chance for each individual to become the dominant reproducer (Hamilton 1964b; Poethke and Liebig 2008; Leadbeater et al. 2011). As group size increases, though, competition for the role of reproducer also increases, reducing an individual’s chance of obtaining direct fitness (Leadbeater et al. 2011). Unless relatedness is predictably very high, this likely confers a stronger, and opposite, selective force than variance reduction at any level when group size increases.

Two additional rarely discussed assumptions of both CLT and RSF further reduce the likelihood of them being applicable for societies with unequal sharing. Firstly, the number of foraging events must increase strongly and linearly with group size. However, social hierarchies or other demographic factors often influence foraging effort (Clutton-Brock 2002; Cant and Field 2005). If some group members contribute little or nothing to foraging, e.g. all males in lion prides (Scheel and Packer 1991), the higher-ranked group members in paper wasp colonies (Cant and Field 2005), and all individuals belonging to non-foraging castes in eusocial insects (Wilson 1953), then the number of foraging trips may be only a weakly increasing or a concave function of group size. Secondly, food returns from foraging trips must be stochastic, representing independent, random samples. This is not true in most social animals where experience, memory and communication systems direct foragers to rewarding feeding spots (Wilson 1975).

Taken together it is clear that the current literature on variance reduction as a selective benefit of group living can be confusing and appears incomplete. Here, we present a new and more complete framework for investigating the potential for variance reduction in food intake and reproduction to provide fitness benefits of group foraging. We further present results from a case study on colonial spiders using this new framework. Colonial spiders cooperate in building communal web structures, within which they maintain individual territories (Avilés 1997; Grinsted and Lubin 2019). Females feed and breed in groups but do so without direct cooperation (Bilde and Lubin 2011). Colonial spiders are highly suitable for this study because they have a simple group structure, akin to foraging flocks of birds, and lack confounding factors such as social hierarchies, castes, and reproductive skew (Grinsted and Lubin 2019). Furthermore, colonial spiders have been the focus of several previous studies on variance reduction as a driver of group living (Uetz 1988; Caraco et al. 1995; Uetz 1996). In a large field study, we recorded the frequency of feeding over multiple daily observations across multiple days, as an estimate of food intake, and the production of egg sacs, as an estimate of reproductive output, for 386 females from 144 spider colonies and 74 solitary webs over a month in southern Spain in May 2018.

# Materials and Methods

## Study organism

*Cyrtophora citricola* has a wide distribution across tropical and subtropical areas of the world where it can be found in colonies of up to thousands of individuals (Rypstra 1979). Our field site in southern Spain is one of its northernmost localities, where colony sizes are smaller, mostly <50 individuals, and solitary webs are common. Females reside in the centre of their long-lasting, three-dimensional capture web where they deposit a string of egg sacs. Individual capture webs are linked with neighbouring webs via common silk threads, but females aggressively defend their own territories within the colony.

All data was collected at field sites near Rota (Cádiz, Spain; 36°39'50.7"N 6°22'08.5"W) during spring 2018 (April-May). Here, *C. citricola* is almost exclusively associated with patches of prickly pear cactus (*Opuntia spp.*) that are commonly found bordering agricultural fields in rural areas of southern Spain.

## Experimental setup

We identified 14 suitable field sites with abundant spider colonies. At each site we marked and numbered focal spider colonies suitable for observations, including solitary webs, and counted all spiders within each colony. At the end of the observational period we again counted the spiders within all focal colonies to account for deaths and migration, and used the average (rounded up to nearest whole number) between the two counts as a measure of group size.

Spider colonies consist of clearly identifiable individual capture webs, within the larger communal frame. Juvenile group members may move about before settling in one location within a colony while older, larger females that have invested in a territory are less likely to relocate or to have their web usurped (Yip et al. 2017). Hence, we selected only larger females assumed to be sub-adult or adult as focal individuals for repeated observations. We did not capture focal individuals to inspect, measure and mark them as the capture process would destroy the web and the colony would collapse. Instead, we made sketches of the colonies so as to identify focal individuals repeatedly over time. Only a few females per colony judged to be easily recognisable within the colony web were selected as focal individuals to minimise the risk of misidentification. In total we selected 513 focal spiders in 259 colonies and solitary webs across the 14 field sites. Due to mortality during the observational period, our final sample size was 386 spiders from 218 colonies and solitary webs (median group size = 5, range: 1 to 34 group members).

As a proxy for focal spider body size we measured the diameter of the horizontal sheet within its capture web to the nearest cm using a measuring tape. To ensure that web diameter was a reliable estimate of spider body size, we correlated spider body size and web diameter of a set of 47 spiders from three nearby, unused field sites. Spider webs were measured as described above after which the spider was captured. We measured the body length (from the tip of the cephalothorax to the end of the abdomen) to nearest 0.1mm using digital callipers. A linear model revealed a highly significant, positive correlation between the two variables, confirming web diameter to be a reliable estimate of body size (*p* < 0.001; *R2* = 0.67).

### Estimating food intake and reproductive output

For each field site, we performed feeding observations on all focal individuals four times per day for nine separate days dispersed over the course of one month. Each field site was assayed by one of three different observers. Feeding observations were done on sunny days between 9:30 and 17:30 when flying prey were most active.

A feeding observation consisted of inspecting each focal spider for feeding behaviour. This resulted in four binary measures (feeding vs. not feeding) per day for each of nine days. We used the number of times observed feeding (out of the four observations) per day as an estimate of daily food intake. We included all spiders with a minimum of five full days of observations over the month for data analysis (*N* = 386 spiders, median number of observation days = 9). We then calculated the standard deviation across the 5-9 days in food intake for each individual as a measure of within-individual variation in food intake.

On each observation day, the number of egg sacs produced by each spider was also recorded. As an estimate of reproductive success we used the number of egg sacs produced per individual by the end of observations (ranging from 0-5 egg sacs; median = 1; excluding focal individuals that had perished early in the observational period, resulting in *N* = 354).

### Validation of food intake values

To ensure that our food intake values were a reliable estimate of actual daily food intake, we conducted an additional set of observations in October-November of 2018 with more extensive prey capture information. The procedure was identical to observations conducted in spring, with the following exceptions: We used a single field site (117 spiders from 57 colonies, including solitary webs), had a single observer, performed 10 feeding observations per day instead of four, and estimated the prey size for each feeding event. When a spider was found to be feeding, we estimated the body length of the prey to nearest 1mm and made a short description of it. In following observations, we judged whether the prey being consumed was the same as the one observed previously based on the prey descriptions. This way we had several different estimates of food intake per spider per day: Number of times seen feeding out of 10 observations, number of times seen feeding out of just four observations (similar times of day as in spring observations), length of prey caught, and estimated prey biomass consumed (see below for biomass calculations).

Mean number of times feeding out of four observations per day was found to be a reliable estimate of all other measures of food intake, as it correlated significantly with mean number of times feeding out of 10 observations (*p* < 0.001; *R2* = 0.71), mean prey length (*p* < 0.001; R2 = 0.52) and mean biomass (transformed to log(x+1)) (*p* < 0.001; *R2* = 0.37). Within-individual variation in food intake values (standard deviations) based on four observations per day also correlated significantly with those based on 10 observations per day (*p* < 0.001; *R2* = 0.59).

### Estimating food abundance

To test whether spiders tended to form larger groups when food was more abundant (Mestre and Lubin 2011), we determined the colony sizes for all colonies (focal and non-focal colonies and solitary webs) at defined sections of the cactus hedge (average 23.6m long stretches) at each of 12 out of the 14 field sites. In total we counted the number of female spiders in 383 colonies (including solitary webs, in total 1084 spiders) across the 12 sites. Sticky traps were used to estimate the availability of flying insect prey at each field site. Sticky traps were produced by smearing a thick layer of ultra-sticky insect glue (Temo Bi, Productos Impex Europa) on to an A4 sheet of transparent overhead projector film. The sheet was then tied between two bamboo sticks placed in the ground next to the cactus close to spider colonies and left in the field for 24h. We had two trapping events in spring, one in the beginning of the observational period and one towards the end. Each field site had two to three traps per site per trapping event depending on the size of the site (i.e. four to six traps in total per site).

We wrapped each trap in cling film and took a photo of it using a flatbed scanner (Brother DCP-197C). From each photo we counted the number of insects within a rectangle of 12x20cm. We used the software ImageJ to measure the length of each insect from the tip of the head to the end of the abdomen, excluding appendages, to nearest 0.001mm. The majority of insects caught were dipterans. We estimated the biomass of each insect according to Hodar (1996, page 425) (Hodar 1996) using the equation for Hexapoda collected in south-eastern Spain:

*Biomass(mg) = 0.0315\*(BodyLength(mm)^2.492)*

We excluded insects <2mm as these are unlikely to be important prey for sub-adult and adult female *C. citricola* and calculated an average biomass (mg) of prey per trap per site as an estimate of food abundance. All statistical models gave qualitatively similar results when insects <2mm were included in the biomass estimate.

## Statistics

All statistical analyses were performed using R (R Core Team 2019). When models were fitted with a Gaussian error structure, we transformed the continuous response variable if necessary to meet assumptions of normality and homogeneity of residuals. When models were fitted with a Binomial, Poisson, or Negative Binomial, error structure models were tested for overdispersion. Collinearity of predictor variables in the models were checked using the vif-function from the R package car (Fox and Weisberg 2011).

### Evaluating between-individual variation with Lorenz Curves and Gini Coefficients

Lorenz curves were originally developed by economists to quantify inequality in wealth and income (Lorenz 1905) and later adopted by biologists to evaluate plant size inequalities (Weiner and Solbrig 1984). Individual food intake or egg sac production values are pooled and ranked within each group size category: Solitary and Small, Medium and Large colonies. Then the cumulative proportion of values are plotted against the cumulative proportion of individuals using the R package ineq (Zeileis 2014). If there was no variance within a category, i.e. all individuals have the same value, then it would create a diagonal line of equality. The further the plotted curve is from a diagonal line, the more variation exists among individuals. A Lorenz Curve is more informative than a single measure of variance, such as standard deviation or coefficient of variation, because the shape of the curve illustrates the skew of the distribution, e.g. whether high values are concentrated within a few individuals. The Gini Coefficient measures the degree of deviation of the Lorenz Curve from the diagonal line (Weiner and Solbrig 1984). Lorenz Curves and Gini Coefficients inform about variation in values relative to the mean and we can therefore compare variation in sets of values with different means or measured on different scales.

When including small group sizes and solitary individuals it is necessary to pool individual observed values within a group size category in order to calculate any measure of variation among individuals. This is because we cannot measure variation among a single or two values. Because of the necessity for data pooling, it is important that the set of values collected represent a random selection of individuals from the population and to exclude confounding variables. To do so, we excluded individuals with <9 feeding observations, and observations from one field site with food intake values significantly different from all the other field sites (Tukey, *p* < 0.05). Further, to remove the effect of a significant correlation between Web Diameter and Colony Size (*p* = 0.0095, *R2* = 0.019), we included only individuals of similar web diameters (median of 32cm +/- 4cm; new *p* = 0.43, *R2* = -0.0027).

This gave us a pool of 122 individual observations from 99 colonies (group size range: 1-33 spiders). We divided these observations into four group size categories: Solitary spiders (*N* = 31), Small colonies (2-4 group members, *N* = 34), Medium colonies (5-9 group members, *N* = 30) and Large colonies (10-33 group members, *N* = 27). These four data subsets were used for plotting Lorenz Curves and calculating Gini Coefficients (with 95% Confidence Intervals by bootstrapping using the R package boot (Canty and Ripley 2017)) for food intake values and egg sac production, and also for all re-sampling simulations described later.

### Individual-level data

We used GLMMs (Generalized Linear Mixed Models, R package lme4 (Bates et al. 2015)) to test the effects of colony size and prey availability, while controlling for web diameter (proxy for spider body size), on within-individual variation in food intake, and reproductive output (number of egg sacs produced).

The predictor variable Web Diameter was z-transformed to a mean of 0 and standard deviation of 1 and Insect Biomass was both log- and z-transformed. In all models we included Colony ID and Observer ID as random effects (i.e. random intercepts) as well as random slopes of the way the response variable might vary randomly with Colony size within Observer ID. Below, we describe both statistical models on individual-level data in detail.

#### Within-individual variation in food intake

This model tested the effect of various predictors on the within-individual variation in food intake. The response variable was calculated as the standard deviation of the number of times observed feeding per day across all days of observations. For data analysis we excluded 11 individuals for which sd = 0. Standard deviations were transformed to x1/3. Fixed effects included Colony Size, Insect Biomass, and Web Diameter as well as the two-way interaction terms between Colony Size and each of the other two predictors. This model was fitted with a Gaussian error structure and observations were weighted according to the number of days of observations (5-9 days).

#### Egg sacs produced

This model tested the effect of various predictors on the number of egg sacs produced. The response variable was the number of egg sacs an individual had produced by the end of the observational period (range 0 to 5 eggs sacs). Fixed effects included Colony Size, Insect Biomass, and Web Diameter as well as the two-way interaction terms between Colony Size and each of the other two predictors. This model was fitted with a Poisson error structure.

### Re-sampling simulations

Per-capita estimations of feeding success and egg sac production are expected to depend on the number of individuals sampled within colonies according to the CLT (Wenzel and Pickering 1991). We only sampled a fraction of spiders per colony in the field (usually 1-3 colony members) and so had to simulate fully-sampled groups to get reliable estimates of per-capita variation between groups. To do this, we pooled individual observations across colonies and field sites. To ensure that there were no confounding variables when pooling observations, we used the four data subsets described for evaluating between-group variation above for all simulations described below.

#### Per-capita variation

We resampled the observed individual feeding values (with replacement) to create 100 groups of each of the group sizes 1 to 30. The specified group size determined which of the four subsets we resampled from (e.g. to create 100 groups of a group size of 7 we used the Medium colonies data subset). Within each group we calculated the mean (i.e. per-capita) feeding success, and we then calculated the standard deviation of per-capita feeding values of each of the group sizes. We repeated this procedure 20 times in order to calculate mean values and plot these with error bars for each group size (1 to 30), in Fig. 1a. Finally, we repeated this resampling procedure for data on the number of egg sacs produced per individual, Fig. 1b.

#### Per-capita Lorenz curves and tests for normality

From each of the four data subsets we first resampled the observed group sizes to create 1000 group size-values of each group size category, e.g. for Medium colonies we created 1000 values that varied from 5-9. Within each data subset we then resampled the number of observed feeding values (with replacement) per group as specified according to the group size for each of the 1000 groups per subset, e.g. for a group of 6 we resampled 6 observed feeding values within the Medium colonies data subset. Within each group we then calculated the mean (i.e. per-capita) food intake. This allowed us to plot the distribution of 1000 per-capita food intake values within each group size category (Fig. 2a-d) and test for normality using the Shapiro-Wilk test. We drew Lorenz Curves using these resampled values and calculated Gini Coefficients (Fig. 1c). Finally, we repeated the resampling procedure for data on the number of egg sacs produced per individual (Fig. 1d, Fig. 2e-h).

### Correlations

#### Correlation between colony size and prey abundance

To test whether colony size correlated with prey abundance we used a GLM (Generalized Linear Model) with Colony Size as a response variable and log-transformed Insect Biomass as the sole predictor. The model was fitted with a Negative Binomial error structure to account for overdispersion.

#### Correlation between web diameter and spider body size

To test whether Web Diameter was a reliable estimate of spider size we used a Linear Model with a Gaussian error structure with Body Length as the response variable and Web Diameter as the sole predictor variable.

# Results

## New framework: Investigating fitness benefits from variance reduction in foraging and reproduction

The first step in our new framework (Fig. 3, first column) is to determine the type of sharing – if any – within groups. This is done by sorting all individual food intake values into categories of group size (e.g. solitary, small, medium, and large colonies) and plotting between-individual variation using Lorenz curves and Gini coefficients, after eliminating confounding factors that correlate with group size (see Methods for more detail). Lorenz curves plot the cumulative proportion of food intake or reproduction values against the cumulative proportion of individuals. The further a curve is from the diagonal line of equality, the higher the Gini coefficient, and the more variation exists between individuals. Lorenz curves and Gini coefficients were first developed by economists to quantify inequality in wealth and income (Lorenz 1905) and later adopted by biologists to evaluate plant size inequalities (Weiner and Solbrig 1984).

The second step of the framework (Fig. 3, second column) is to evaluate the abundance of food relative to the reproductive threshold. In the third step (Fig. 3, third column) temporal, within-individual variation is estimated according to RSF, and finally, in the fourth step (Fig. 3, fourth column) per-capita (between-group) variance is estimated according to CLT.

If egalitarian or surplus sharing occurs, as in groups with scramble competition (Fig. 3, top flow-chart), RSF is supported and within-individual variation is expected to decrease with group size. However, whether this variance reduction provides fitness benefits of group foraging depends on food abundance relative to the reproductive threshold: if food abundance is relatively high then variance reduction at both the individual and the group-level will favour grouping and there is also support for CLT. This benefit of variance reduction is even greater if group foraging at the same time increases mean food intake or reduces energy-related costs for an organism because the reproductive threshold would then more easily be met. Please note that there would be no support for CLT in an egalitarian or surplus sharing scenario if food was scarce relative to the reproductive threshold (Poethke and Liebig 2008).

If sharing is skewed, as in systems with contest competition or social hierarchies (Fig. 3, middle flow-chart), food abundance is expected to be low relative to the reproductive threshold and there is no support for traditional RSF. Although there might be support for the RSF prediction that within-individual variance decreases with group size, the disparity among individuals result in dominant individuals obtaining reliably high levels of food while subordinates obtain reliably low levels of food. Traditional risk-averse and risk-prone strategies in RSF do not apply to this type of group dynamics (Real and Caraco 1986; Uetz 1996). However, there might be support for CLT: group-level variance reduction might provide fitness benefits to individuals according to CLT if an additional set of assumptions are met: 1) all or most group members participate in food acquisition (Wenzel and Pickering 1991), 2) foraging is stochastic (Real and Caraco 1986), 3) genetic relatedness is high among group members *or* all group members have an equal chance of becoming reproducers (Poethke and Liebig 2008).

If there is no sharing (Fig. 3, bottom flow-chart) there will be support for neither RSF nor CLT: within-individual variance is not expected to vary consistently with group size and although group-level variance may decrease with group size, this variance reduction will not translate into fitness benefits of group foraging at the individual level.

## Case study: Colonial spiders

### Between-individual variance: the level of sharing

We first created four group size categories: Solitary individuals, Small colonies (2-4 group members), Medium colonies (5-9 group members) and Large colonies (10-33 group members), pooling individual food intake values and number of egg sacs produced within each category (after removing confounding factors, see Methods). We then explored whether between-individual variance varied with group size by plotting Lorenz curves for each group size category. This was done by ranking each food intake value (Fig. 4a) or egg sac production value (Fig. 4b) and plotting the cumulative proportion of values against the cumulative proportion of individuals within each category. Gini coefficients and their 95% Confidence Intervals (CIs) were calculated for each resulting Lorenz curve. We found no association between between-individual variance and group size: Gini coefficients did not consistently vary with group size and their CIs overlapped. Hence, we found no evidence for egalitarian, surplus or skewed sharing.

### Within-individual variance: Risk-Sensitive Foraging Theory

We tested three key predictions from RSF: 1) Groups are larger when food is more abundant; 2) Fewer individuals fail to reproduce in larger groups only when food is abundant; 3) Within-individual variance in food intake decreases with group size. We found support for the first prediction but not for the latter two: 1) Sites with higher abundance of insect prey supported larger spider colonies (*p* < 0.001; Fig. 5a); 2) The number of egg sacs produced was not influenced by prey availability, colony size, or their interaction (all terms: *p* > 0.50; Table 1; Fig. 5b-c); 3) Temporal, within-individual variance did not decrease with group size, in fact, it increased slightly for smaller spiders (interaction term between group size and spider size, indicated as web diameters, see Methods: *p* = 0.031, Table 2; Fig. 5d-f).

### Between-group variance: Central Limit Theorem applied to group foraging

We tested two key predictions from CLT: 1) Variance in per-capita food intake and reproductive output decreases with increasing group size; 2) Per-capita food intake and reproduction are more normally distributed in larger groups. We found support for both predictions: 1) Both per-capita food intake (Fig. 6a+c) and per-capita egg sac production (Fig. 6b+d) varied less in larger colonies: standard deviations (Fig. 6a-b), Lorenz curves and Gini coefficients (Fig. 6c-d) all showed a consistent negative association with group size and the CIs of Gini coefficients for the four group size categories did not overlap; 2) Values of both per-capita food intake (Fig. 7a+d) and per-capita egg sac production (Fig. 7e-h) tended more towards normal distributions in larger colonies (although all eight distributions deviated from normality; *p* < 0.01).

# Discussion

We document the need for a new framework for evaluating variance reduction in food intake and reproductive output as a potential selective advantage of group foraging. We provide such a new framework which is applicable for any group living organism. This framework highlights several important points: 1) The crucial first step when evaluating the effect of variance reduction on group foragers is to determine the level of food sharing within groups, i.e. between-individual variance, no matter whether within-individual or group-level variance is in focus according to RSF or CLT respectively; 2) Variance reduction (at any level) is not always a selective advantage: whether variance reduction presents a cost or a benefit to individuals depends on food abundance relative to the reproductive threshold (Real and Caraco 1986; Poethke and Liebig 2008); 3) Per-capita variance reduction, i.e. variance measured at the group-level, has the potential to provide selective benefits only if it increases the inclusive fitness of individual group members (Marshall 2011). This can be achieved either via egalitarian or surplus sharing of resources within a group, or in cases where most group members forage stochastically and group members are highly related or each group member has a chance of achieving direct reproduction (Poethke and Liebig 2008).

Our case study of colonial spiders demonstrates the importance of assessing the type of sharing in order to understand the effect of variance reduction on fitness. Indeed, we had to conclude that there was no support for CLT in this system despite finding support for both of its key predictions: Both per-capita food intake and per-capita reproduction varied less and were more normally distributed in larger colonies. Without taking between-individual variance into account, these results might have led to the mistaken conclusion that per-capita variance reduction provides selective benefits of group living in this system. However, we found that these group-level properties did not translate to fitness benefits for individual spiders. In colonial spiders, sharing of surpluses in the form of prey stealing is thought to reduce variance between group members: successful foragers may store surplus prey in their webs which may be stolen by less successful neighbours (Caraco et al. 1995; Uetz 1996). However, in *C. citricola* we found no evidence of variance reducing prey-stealing. Firstly, between-individual variance in both food intake and egg sac production did not decrease with group size. Secondly, out of 149 observed prey captures only one included prey stealing. Hence, a mechanism for reducing between-individual variance – crucial for translating group-level variance reduction to individual benefits – was lacking. This lack of food sharing also meant there was no mechanism for reducing within-individual variance in food intake in larger groups, resulting in a lack of support not only for CLT but also for RSF. Indeed, within-individual variance in food intake did not decrease with group size and the risk of failing to reproduce was not influenced by group size nor by prey availability. We did find support for the RSF prediction that groups were larger when food was more abundant, however, this finding is also consistent with other explanations. For example, more food might sustain higher densities of spiders which may lead to more grouping due to space constraints (Mestre and Lubin 2011).

According to our new framework, egalitarian or surplus sharing of resources within groups is the most straightforward way to obtain fitness benefits from variance reduction. However, egalitarian food sharing is rare in group foraging societies. Perhaps it can be found in flocking birds that share patchily distributed, indivisible food, e.g. seeds (Mangel 1990), and in eastern tent caterpillars (*Malacosoma americanum*) that forage synchronously (Costa and Ross 2003). In colonial spiders, egalitarian or surplus sharing might exist in species that share prey too large for an individual to monopolise, such as *Parawixia bistriata* (Campon 2007), or in species where prey stealing is common, such as in *Meteperia spp.* (Uetz 1996), although prey stealing has the potential to disproportionally benefit larger, more competitive individuals, skewing rather than equalising food intake within colonies (Ventura et al. 2017). Egalitarian sharing may also occur in cooperatively breeding, social spiders, such as *Stegodyphus spp*. and *Anelosimus spp*., where successful foragers routinely share their prey with other group members (Grinsted et al. 2013; Settepani et al. 2013) with no apparent social hierarchy or contest competition (Grinsted and Bilde 2013) (but see Rypstra 1993). Although females in some mammals show nearly egalitarian cooperative breeding, food intake tends to be skewed towards dominant females, such as in banded mongooses (*Mungos mungo*) (De Luca and Ginsberg 2001), or towards males, such as in African lions (*Panthera leo*) (Packer et al. 2001). Indeed, in most types of group foraging societies food sharing is markedly skewed due to complex social hierarchies, caste systems, or contest competition (Wilson 1975). For example, dominance hierarchies and contest competition are common in cooperative breeders, such as chimpanzees (*Pan troglodytes verus*) and meerkats (*Suricata suricatta*), resulting in higher food intake and weight gain for dominants as compared to subordinates (Wittig and Boesch 2003; Clutton-Brock et al. 2006). In eusocial organisms, like social ants, bees and wasps, food is preferentially shared with the queen and her brood (Wilson 1975). As illustrated in our framework (Fig. 3) fitness benefits can still be gained from variance reduction in food intake in such skewed-sharing societies but a set of conditions must be met. First, food availability should be low compared to the reproductive threshold, otherwise individuals would benefit more from solitary foraging (Poethke and Liebig 2008). Second, the number of foraging events must increase strongly with group size (Wenzel and Pickering 1991) so the vast majority of group members should participate in foraging. Third, either the genetic relatedness among group members should be high, or all group members should have an equal chance to reproduce (Poethke and Liebig 2008). Finally, foraging events should be stochastic (Real and Caraco 1986).

The potential benefits from variance reduction may vary not only between species according to species-specific biology and behaviour, but also among different populations of a species. This is because, firstly, the level of sharing may differ among populations. For example, in baboons (*Papio spp.*) some populations have strong dominance relationships and competitive interactions that correlate with food intake rates (Barton and Whiten 1993), while other populations show inconsistent dominance relations, possibly due to more dispersed, less concentrated resources (Barton et al. 1996). Secondly, food availability or average genetic relatedness among group members may differ among populations, affecting whether variance-reduction is predicted to confer fitness benefits (Poethke and Liebig 2008).

We conclude that CLT does not provide a universal and automatic benefit of group living as previously suggested (Wenzel and Pickering 1991), and that group foraging will produce advantageous variance reduction only under narrow conditions. Fitness benefits from variance reduction will be conferred to individuals only in rare cases depending on food availability, reproductive threshold, level of sharing, participation in food acquisition, and genetic relatedness among group members. For clarity, we stress that we do not claim that group living can only be favoured in those scenarios described, but rather that variance reduction in food intake would be a selective advantage in only these specific scenarios. Many other benefits of group feeding and breeding may act instead of – or in conjunction with – variance reduction.

# Literature Cited

Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476-498 *in* J. C. Choe, and B. J. Crespi, eds. The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press Cambridge, United Kingdom.

Barnard, C. J. and R. M. Sibly. 1981. Producers and scroungers - a general-model and its application to captive flocks of house sparrows. Anim Behav 29:543-550.

Barton, R. A., R. W. Byrne, and A. Whiten. 1996. Ecology, feeding competition and social structure in baboons. Behavioral Ecology and Sociobiology 38:321-329.

Barton, R. A. and A. Whiten. 1993. Feeding Competition among Female Olive Baboons, *Papio-Anubis*. Anim Behav 46:777-789.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48.

Bilde, T. and Y. Lubin. 2011. Group living in spiders: cooperative breeding and coloniality. Pp. 275-306 *in* M. E. Herberstein, ed. Spider Behaviour, Flexibility and Versatility. Cambridge University Press, Cambridge.

Campon, F. F. 2007. Group foraging in the colonial spider *Parawixia bistriata* (Araneidae): effect of resource levels and prey size. Anim Behav 74:1551-1562.

Cant, M. A. and J. Field. 2005. Helping effort in a dominance hierarchy. Behav Ecol 16:708-715.

Canty, A. and B. Ripley. 2017. boot: Bootstrap R (S-Plus) Functions. R package version 1.3-20.

Caraco, T. 1981. Risk-Sensitivity and Foraging Groups. Ecology 62:527-531.

Caraco, T., G. W. Uetz, R. G. Gillespie, and L. A. Giraldeau. 1995. Resource consumption variance within and among individuals - on coloniality in spiders. Ecology 76:196-205.

Clark, C. W. and M. Mangel. 1984. Foraging and flocking strategies - information in an uncertain environment. American Naturalist 123:626-641.

Clutton-Brock, T. 2002. Behavioral ecology - Breeding together: Kin selection and mutualism in cooperative vertebrates. Science 296:69-72.

Clutton-Brock, T. H., S. J. Hodge, G. Spong, A. F. Russell, N. R. Jordan, N. C. Bennett, L. L. Sharpe, and M. B. Manser. 2006. Intrasexual competition and sexual selection in cooperative mammals. Nature 444:1065-1068.

Costa, J. T. and K. G. Ross. 2003. Fitness effects of group merging in a social insect. P Roy Soc B-Biol Sci 270:1697-1702.

Cresswell, W. 1994. Flocking Is an Effective Anti-Predation Strategy in Redshanks, *Tringa-Tetanus*. Anim Behav 47:433-442.

De Luca, D. W. and J. R. Ginsberg. 2001. Dominance, reproduction and survival in banded mongooses: towards an egalitarian social system? Anim Behav 61:17-30.

Fox, J. and S. Weisberg. 2011. An {R} Companion to Applied Regression. Sage, Thousand Oaks CA.

Gillespie, J. H. 1977. Natural-selection for variances in offspring numbers - new evolutionary principle. American Naturalist 111:1010-1014.

Grinsted, L. and T. Bilde. 2013. Effects of within-colony competition on body size asymmetries and reproductive skew in a social spider. J Evolution Biol 26:553-561.

Grinsted, L., T. Bilde, and J. D. J. Gilbert. 2015. Questioning evidence of group selection in spiders. Nature 524:E1-E3.

Grinsted, L. and Y. Lubin. 2019. Spiders: Evolution of Group Living and Social Behavior. Pp. 632-640 *in* J. C. Choe, ed. Encyclopedia of Animal Behavior. Elsevier, Academic Press.

Grinsted, L., J. N. Pruitt, V. Settepani, and T. Bilde. 2013. Individual personalities shape task differentiation in a social spider. P Roy Soc B-Biol Sci 280.

Hamilton, W. D. 1964a. Genetical Evolution of Social Behaviour 2. Journal of Theoretical Biology 7:17-52.

Hamilton, W. D. 1964b. Genetical Evolution of Social Behaviour I. Journal of Theoretical Biology 7:1-16.

Hodar, J. A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecol 17:421-433.

Leadbeater, E., J. M. Carruthers, J. P. Green, N. S. Rosser, and J. Field. 2011. Nest inheritance is the missing source of direct fitness in a primitively eusocial insect. Science 333:874-876.

Lorenz, M. O. 1905. Methods of measuring the concentration of wealth Publications of the American Statistical Association 9:209-219.

Mangel, M. 1990. Resource divisibility, predation and group formation. Anim Behav 39:1163-1172.

Marshall, J. A. R. 2011. Group selection and kin selection: formally equivalent approaches. Trends in Ecology & Evolution 26:325-332.

Mestre, L. and Y. Lubin. 2011. Settling where the food is: prey abundance promotes colony formation and increases group size in a web-building spider. Anim Behav 81:741-748.

Michener, C. D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. Insect Soc 11:317-341.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Australian Journal of Zoology 2:9-65.

Packer, C., A. E. Pusey, and L. E. Eberly. 2001. Egalitarianism in female African lions. Science 293:690-693.

Packer, C., D. Scheel, and A. E. Pusey. 1990. Why Lions Form Groups - Food Is Not Enough. American Naturalist 136:1-19.

Poethke, H. J. and J. Liebig. 2008. Risk-sensitive foraging and the evolution of cooperative breeding and reproductive skew. BMC Ecol 8:2.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Real, L. and T. Caraco. 1986. Risk and foraging in stochastic environments. Annual Review of Ecology and Systematics 17:371-390.

Real, L. A. 1980. Fitness, uncertainty, and the role of diversification in evolution and behavior. American Naturalist 115:623-638.

Rypstra, A. L. 1979. Foraging flocks of spiders - study of aggregate behavior in *Cyrtophora-Citricola* Forskal (Araneae, Araneidae) in West-Africa. Behavioral Ecology and Sociobiology 5:291-300.

Rypstra, A. L. 1989. Foraging success of solitary and aggregated spiders - insights into flock formation. Anim Behav 37:274-281.

Rypstra, A. L. 1993. Prey Size, Social Competition, and the Development of Reproductive Division-of-Labor in Social Spider Groups. American Naturalist 142:868-880.

Scheel, D. and C. Packer. 1991. Group hunting behavior of lions - a search for cooperation. Anim Behav 41:697-709.

Schoener, T. W. 1971. Theory of feeding strategies. Annual review of ecology and systematics 2:369-404.

Settepani, V., L. Grinsted, J. Granfeldt, J. L. Jensen, and T. Bilde. 2013. Task specialization in two social spiders, *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius* (Theridiidae). J Evolution Biol 26:51-62.

Uetz, G. W. 1988. Group foraging in colonial web-building spiders - evidence for risk-sensitivity. Behavioral Ecology and Sociobiology 22:265-270.

Uetz, G. W. 1996. Risk sensitivity and the paradox of colonial web-building in spiders. American Zoologist 36:459-470.

Ventura, L., D. R. Smith, and Y. Lubin. 2017. Crowding leads to fitness benefits and reduced dispersal in a colonial spider. Behav Ecol 28:1384-1392.

Weiner, J. and O. T. Solbrig. 1984. The meaning and measurement of size hierarchies in plant-populations. Oecologia 61:334-336.

Wenzel, J. W. and J. Pickering. 1991. Cooperative foraging, productivity, and the central-limit-theorem. Proceedings of the National Academy of Sciences of the United States of America 88:36-38.

Wilson, E. O. 1953. The origin and evolution of polymorphism in ants. Quarterly Review of Biology 28:136-156.

Wilson, E. O. 1975. Sociobiology: The new synthesis. Harvard University Press, Masachusetts

Wittig, R. M. and C. Boesch. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. Int J Primatol 24:847-867.

Yip, E. C., T. Levy, and Y. Lubin. 2017. Bad neighbors: hunger and dominance drive spacing and position in an orb-weaving spider colony. Behavioral Ecology and Sociobiology 71.

Zeileis, A. 2014. ineq: Measuring Inequality, Concentration, and Poverty. R package version 0.2-13.

Tables

**Table 1:** Results from a GLMM on the number of egg sacs produced. Web diameter was used as a proxy for spider size (see Methods).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Response variable** |  | ***N spiders*** | ***N colonies*** | ***N field sites*** |
| Number of egg sacs |  | 305 | 187 | 14 |
| **Predictor variable***(transformation)* | ***Chi-Sq*** | ***d.f.*** | ***z-value*** | ***P-value*** |
| Colony size | 1.06 | 1 | 1.03 | 0.303 |
| Web diameter *(z)* | 28.01 | 1 | 5.29 | *<0.001* |
| Insect biomass *(z, log)* | 0.02 | 1 | 0.16 | 0.877 |
| Colony size \* Web diameter *(z)* | 0.26 | 1 | -0.51 | 0.611 |
| Colony size \* Insect biomass *(z, log)* | 0.00 | 1 | 0.03 | 0.974 |

**Table 2:** Results from a GLMM on within-individual variation in food intake

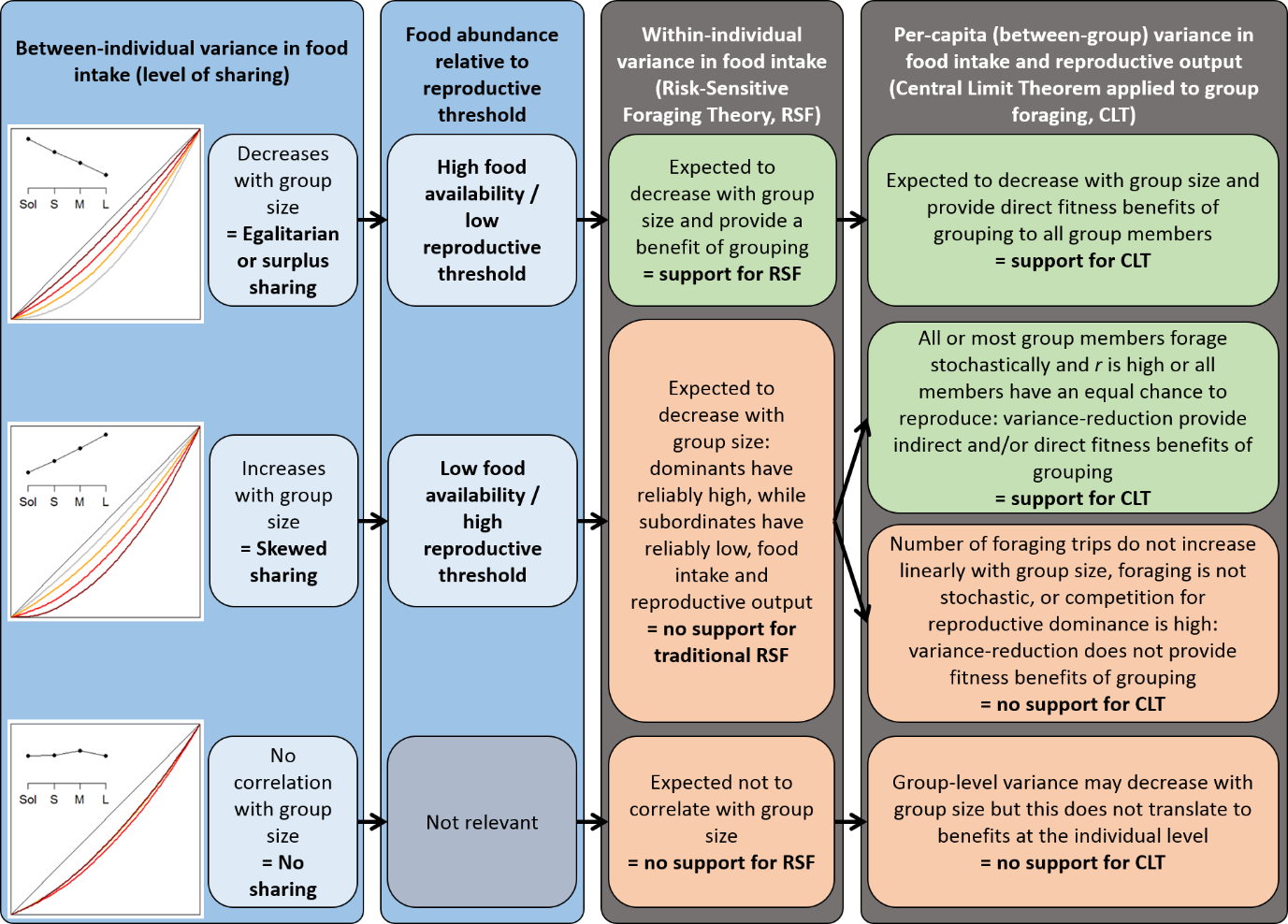
|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Response variable** *(transformation)* |  | ***N spiders*** | ***N colonies*** | ***N field sites*** |
| *S.D.* of the number of observations of feeding per day *(x1/3)* | | 379 | 215 | 14 |
| **Predictor variable***(transformation)* | ***Chi-Sq*** | ***d.f.*** | ***t-value*** | ***P-value*** |
| Colony size | 0.05 | 1 | 0.39 | 0.819 |
| Web diameter *(z)* | 14.43 | 1 | 4.21 | *<0.001* |
| Insect biomass *(z, log)* | 4.28 | 1 | -1.62 | *0.039* |
| Colony size \* Web diameter *(z)* | 4.67 | 1 | -2.16 | *0.031* |
| Colony size \* Insect biomass *(z, log)* | 0.04 | 1 | 0.20 | 0.845 |

Figures and figure legends

**Fig. 1:** The concept of the Central Limit Theorem explained with die rolls: A set of virtual dice are rolled 100 times. For each roll the mean value across the set of dice is calculated and stored, producing 100 mean values (i.e. 100 set means). Here, four histograms depict the distributions of mean values for N (the number of dice) of 1, 2, 5 and 30 respectively. According to the Central Limit Theorem, the grand mean in each histogram is unchanged by N (red lines, ~3.5) but the variance among set means become smaller as N increases (blue lines depict standard deviations around the grand mean). Furthermore, mean values also more normally distributed as N increases.

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**Fig. 2:** The concept of Risk-Sensitive Foraging Theory (RSF) applied to group foraging organisms: Six food intake values taken at different points in time, e.g. on six different days, are plotted for each of 10 imaginary individuals where each individual belongs to a group of 1-10 individuals (a group size of 1 means the individual is solitary). The underlying assumption of RSF is that the variance in within-individual food intake decreases with increasing group size, i.e. the spread of food intake values is smaller for individuals from larger groups as compared to individuals from smaller groups. For simplicity, mean feeding values per individual (large, red dots, also representing mean food availability) are not affected by group size. The blue line represents the reproductive threshold which is a certain amount of food the animal must consume each day in order to survive and reproduce. (a) Food availability is high relative to the reproductive threshold. In this case there should be selection for group foraging, as no single feeding observation lies below the reproductive threshold when belonging to a larger group. Hence, group living individuals minimise the risk of not obtaining enough food to reproduce. (b) Food availability is low relative to the reproductive threshold. In this case, group living individuals consistently obtain too little food to reproduce. Hence, solitary living is favoured because a high within-individual variance in food intake means at least a small chance of obtaining enough food to reproduce.



**Fig. 3:** New framework for investigating whether variance reduction in food intake and reproductive output provides fitness benefits of group foraging: The Lorenz curves and Gini coefficients in the first column are visual representations giving examples of how the different kinds of sharing could look like: the cumulative proportion of food intake or reproductive output values are plotted (y-axis) against the cumulative proportion of individuals (x-axis) after individuals have been ranked within their group size category. The further a curve is from the diagonal line of equality, the higher the Gini coefficient (shown as insets), and the more variation exists between individuals. Colour codes within the Lorenz curves: Grey = solitary spiders (Sol); Yellow = small colonies (S); Red = medium colonies (M); Dark-red = large colonies (L). In the third and fourth columns green indicates support for a theory while orange indicates no support. In the third column “traditional RSF” refers to within-individual variance reduction without predictable skew among individuals in their mean values. In the fourth column “*r”* refers to genetic relatedness among group members.

**Fig. 4:** Between-individual variance in food intake and production of egg sacs: Lorenz curves show the cumulative proportion of observed individual food intake values (a) and observed number of egg sacs produced (b) plotted against the cumulative proportion of individuals. The diagonal line is the line of equality. Data would follow this line if all individuals had identical values, i.e. with no variance among individuals. The further a curve is from the line of equality, the higher the Gini coefficient (depicted in the insets with 95% CIs as vertical lines), and the more variation exists between individuals. Colour codes: Grey = solitary spiders (Sol); Yellow = small colonies (S); Red = medium colonies (M); Dark-red = large colonies (L).

**Fig. 5:** Results from testing predictions from Risk-Sensitive Foraging Theory: a) Colony sizes at 12 field sites plotted against mean prey biomass at each site (mg/trap); b+c) Number of egg sacs produced per individual plotted against colony size (b) and against mean prey biomass at each site (mg/trap) (c); d-f) Standard deviation of food intake values per individual over time plotted against colony size. Due to a significant interaction effect between web diameter (as a proxy for spider size) and colony size (*p* = 0.031) the data were divided into small (web diameters 10-26cm), medium (web diameters 27-35cm) and large spiders (web diameters 36-54cm). In all plots (a-f) the depicted lines show simple regressions not based on the more comprehensive models used for statistics; full lines are drawn when an association was significant in the statistical model while dashed lines represent non-significant associations.

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**Fig. 6:** Per-capita variance in food intake and egg sac production: Standard deviations across colonies in per-capita food intake values (a) and per-capita egg sac production (b) plotted against group size. Dots are grand means and error bars are standard deviations. Lorenz curves show the cumulative proportion of colony mean food intake values (c) and number of egg sacs (d) plotted against the cumulative proportion of colonies and is an alternative way of depicting per-capita variance. The diagonal line in the Lorenz plots depicts the line of equality. Data would follow this line if all colonies had identical means, i.e. no variance among colonies. The further a curve is from the line of equality, the higher the Gini coefficient (depicted in the insets with 95% CIs as vertical lines), and the more variation exists among colonies. The depicted data are obtained from resampling observed values (see Methods). Colour codes: Grey = solitary spiders (Sol); Yellow = small colonies (S); Red = medium colonies (M); Dark-red = large colonies (L).



**Fig. 7:** Distribution of food intake and reproduction values: Histograms depicting the distribution of per-capita food intake values (a-d) and per-capita number of egg sacs (e-h) in solitary spiders (a+e), small colonies (b+f), medium colonies (c+g) and large colonies (d+h). The depicted data are obtained from resampling observed values (see Methods).