Evolutionary Ecology Research, 2011, **13**: 253–267

Scarce resources, risk sensitivity, and egalitarian resource sharing

Emanuel A. Fronhofer[1], Henrik Pasurka[1], Oliver Mitesser[2]
and Hans Joachim Poethke[1]

[1]*Field Station Fabrikschleichach, University of Würzburg, Rauhenebrach, Germany and*
[2]*Universitäts- und Landesbibliothek, Technische Universität Darmstadt,*
Darmstadt, Germany

ABSTRACT

Background: Some recent findings in social spiders appear to be at odds with risk-sensitive foraging theory.

Question: Can egalitarian resource sharing be explained by a simple risk-sensitive foraging model that includes density dependence?

Mathematical method: A dynamic model of a population of individually foraging animals that breed in groups and share food for survival and reproduction. To derive conditions for egalitarian group formation, the model minimizes the amount of resources needed per capita at population-dynamic equilibrium. It combines density-dependent population growth with evolutionary dynamics, so extending classical models of risk-sensitive foraging.

Key assumptions: Fitness is a non-linear function of an animal's energy state. Egalitarian resource sharing reduces variance in foraging success. Population growth is density dependent. The model is designed to be general enough to apply to a wide range of organisms, from insects and arachnids to birds and mammals.

Predictions: Our model predicts optimal group sizes – which minimize the amount of resources needed per capita at population equilibrium – and yields a more complex evolutionary pattern than the simple dichotomy of risk-prone or risk-averse behaviour. Even in saturated environments with severe competition – and, consequently, low food availability – high variance in foraging success will favour group formation.

Keywords: egalitarian groups, resource sharing, risk-sensitive foraging, social spiders.

INTRODUCTION

Several explanations for group formation have been proposed (Sachs *et al.*, 2004; Nowak, 2006; Lehmann and Keller, 2006). Many of these explanations focus on inclusive fitness theory (Hamilton, 1964a, 1964b) and kin selection (Maynard Smith, 1964). Clearly, other, less restrictive paths to

---

Correspondence: E.A. Fronhofer, Field Station Fabrikschleichach, University of Würzburg, Glashüttenstr. 5, D-96181 Rauhenebrach, Germany. e-mail: fronhofer@biozentrum.uni-wuerzburg.de

cooperative behaviour should exist, since not all animal groups show sufficiently high levels of relatedness (Griffin and West, 2002; West *et al.*, 2002; Sachs *et al.*, 2004).

In recent years, multi-level selection (Okasha, 2006; Wilson and Wilson, 2007) has again become a hotly debated topic. Some researchers have proffered the idea that selective forces acting on whole groups favour the evolution of altruism and cooperation (Wilson and Hölldobler, 2005; Traulsen and Nowak, 2006; Hölldobler and Wilson, 2009). The importance of these and other factors remains highly controversial (Clutton-Brock *et al.*, 2009).

Game theory greatly increased our understanding of altruistic behaviours among unrelated individuals. Reciprocity (Trivers, 1971; Axelrod and Hamilton, 1981) in all its forms [i.e. direct, indirect, and in networks (Nowak, 2006)] is an important factor in the evolution of cooperation. Here, we develop a mathematical model for the evolution of egalitarian group formation emphasizing the importance of ecological factors (Hatchwell and Komdeur, 2000; Kikvidze and Callaway, 2009). We define egalitarian groups as containing identical members (i.e. egalitarian group formation is a self-interested mutualism). Group formation has three functional possibilities to enhance Darwinian fitness of group members and therefore to be adaptive: reproduction, foraging or survival, or any combination of these factors may be promoted (Whitehouse and Lubin, 2005). Foraging plays a central role in this triad of factors because reproduction and survival are usually functions of foraging success. Thus, we analyse the evolution of group formation in a foraging context.

In addition to the mean amount of food, the variance of a given resource influences foraging decisions (Caraco, 1980; Caraco *et al.*, 1980; Stephens, 1981; Real and Caraco, 1986; Schmitz and Ritchie, 1991). Risk-sensitive foraging theory (Bateson, 2002; Bednekoff, 1996; Kacelnik and Bateson, 1996; Smallwood, 1996) can be used to explain cooperative foraging and breeding (Poethke and Liebig, 2008), as in social spiders (Wenzel and Pickering, 1991; Caraco *et al.*, 1995; Avilés, 1997; Whitehouse and Lubin, 2005; Agnarsson, 2006). In the context of risk-sensitive foraging theory, group formation has been interpreted as a mechanism of risk avoidance (Caraco, 1981; Clark and Mangel, 1986; Wenzel and Pickering, 1991; Caraco *et al.*, 1995; Uetz, 1996; Uetz and Hieber, 1997). According to Jensen's inequality (Bednekoff, 1996), risk-averse behaviour can only evolve in environments where mean resource supply is high (concave-down part of the specific fitness function). This leads to the hypothesis that the formation of egalitarian (spider) groups should only occur in environments with high prey density (Uetz, 1992, 1996; Uetz and Hieber, 1997): intuitively, food sharing should only occur when food is not a limiting factor.

Recent fieldwork on different genera of social spiders (Fernández Campón, 2007, 2008; Powers and Avilés, 2007), however, does not support this hypothesis. Spider sociality was correlated with high resource variance but not necessarily with high resource availability. Risk-sensitive foraging theory predicts that, since cooperative foraging is a risk-averse foraging strategy, it should only evolve in environments with high resource mean. Thus, Powers and Avilés (2007) concluded that spider sociality cannot be readily explained by classical risk-sensitive foraging theory. This conclusion led to a wealth of new hypotheses (Avilés *et al.*, 2007; Powers and Avilés, 2007; Purcell and Avilés, 2008; Yip *et al.*, 2008).

In the following, we re-analyse risk sensitivity as a possible driving force for the evolution of cooperative foraging and present a dynamic model of a population of individually foraging animals that breed in groups and share food for survival and reproduction. This approach expands and generalizes previous work undertaken by Poethke and Liebig (2008). We model the influence of resource availability on mortality as well as on reproduction. Thus, our model accounts for the influence of foraging strategies on population growth, competition and, consequently, mean resource availability (Pen and Weissing, 2000). Similar notions can be found in Avilés (1999) and Trainor and Caraco (2006). These authors explore the influence of group size on population dynamics.

We analyse the simultaneous influences of mortality and natality in a risk-sensitive group-foraging context. Furthermore, the model presented here is not limited to dyads, but allows for groups of N-individuals.

MODEL DESCRIPTION

Resource distribution

In our model, we assume stochastic foraging and resource allocation. Thus, individual foraging success during a potential reproductive period (i.e. the time needed to raise offspring to weaning) follows a random distribution. The probability of collecting the amount x of food during one reproductive period can be described by a probability density function $P(x, \bar{x}, \sigma^2)$, with mean foraging success $\bar{x}$ and variance σ^2 (for a summary of all parameters, see Table 1). We assume that the amount of food collected is non-negative and continuous. Therefore, we define $P(x, \bar{x}, \sigma^2)$ as a gamma distribution Γ with shape parameter k and scale parameter θ:

$$P(x, \bar{x}, \sigma^2) = \Gamma(x, k, \theta) = x^{k-1}\,\frac{e^{-\frac{x}{\theta}}}{\theta^k \gamma(k)} \qquad (1)$$

with $\bar{x} = k\theta$ and $\sigma^2 = k\theta^2$. Note that θ can be interpreted as the mean (food) item size. γ is the gamma function with $\gamma(k) = \int_{y=0}^{\infty} e^{-y} y^{k-1} dy$ (see, for example, Otto and Day, 2007).

Table 1. Model parameters and meanings with fixed values

Parameter	Significance and fixed values
L_F	Life-history parameters of the fertility function ($F_{\max}$, s_F, and o_F)
$F_{\max}$	Maximal number of offspring
s_F	Slope of the fertility function, inversely related to the costs of offspring production
o_F	Offset of the fertility function (fixed to $o_F = 8$)
L_M	Life-history parameters of the mortality function (M_b, s_M, and o_M)
M_b	Baseline mortality (resource independent)
s_M	Slope of the mortality function (fixed to $s_M = -5$)
o_M	Offset of the mortality function (fixed to $o_M = 2$)
x	Resources available to an individual
$\bar{x}$	Mean per capita amount of resources available in population equilibrium, i.e. mean amount of resources required to balance natality and mortality
$\bar{X}$	Mean amount of resources available to a group of size N, i.e. group income
$\hat{x}$	Intersection of the mortality and fertility functions (see Fig. 2A)
θ	Mean item size; scale parameter of the gamma distribution
σ^2	Resource variance, determined by θ (see equation 1)
S^2	Variance in group income
σ_N^2	Variance experiences by a single individual in a group of size N
N	Group size

To obtain mean group income ($\bar{X}$), one can simply multiply mean individual foraging success ($\bar{x}$) by group size (N):

$$\bar{X} = N \cdot \bar{x}. \tag{2}$$

The same holds true for the variance (S^2) of group income when group members forage individually:

$$S^2 = N \cdot \sigma^2. \tag{3}$$

If food is shared equally among all members of a group of size N, the expected per capita mean is $\bar{x}$ and the resulting individual variance in the available amount of resources (σ_N^2) can be easily calculated. Using equation (3), the per capita standard deviation (σ_N) of the resource function for group members is

$$\sigma_N = \frac{S}{N} = \frac{\sqrt{N} \cdot \sigma}{N} = \frac{1}{\sqrt{N}} \cdot \sigma$$

and, accordingly,

$$\sigma_N^2 = \frac{1}{N} \cdot \sigma^2. \tag{4}$$

As described here, the formation of groups with egalitarian resource sharing reduces the variance of resources available to individuals. It thus is a risk-avoiding foraging strategy. Now, the amount of resources available to individuals in a group of size N follows a modified gamma distribution (see Fig. 1):

$$P_N(x, \bar{x}, \theta, N) = P\left(x, \bar{x}, \frac{1}{N}\sigma^2\right) = \Gamma\left(x, k, \frac{\theta}{N}\right). \tag{5}$$

From the above equations, the relation between mean item size (θ) and variance of the resource distribution (σ^2) is clear. Therefore, we use mean item size (θ) as a proxy for

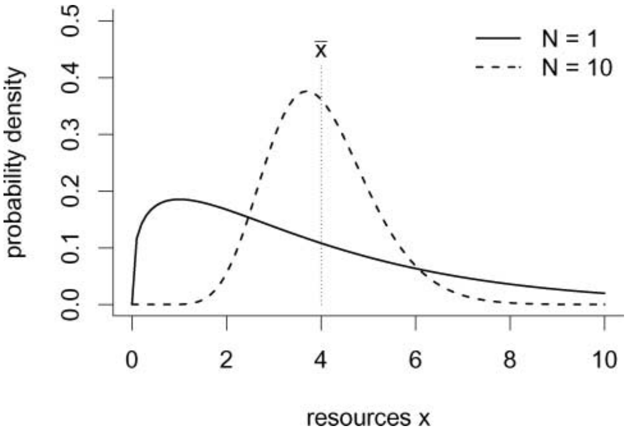

Fig. 1. Variance reduction by egalitarian resource sharing. Group formation reduces the variance of the resource distribution (dashed line; group size $N = 10$) compared with solitary individuals (solid line; see also equation 5). The dotted line represents the mean of both distributions ($\bar{x} = 4$), which does not change. The parameter θ can be interpreted as the mean item size of the foraged resource ($\theta = 3$).

variance. Note that our model assumes egalitarian resource sharing. Thus, we compare the advantages of egalitarian group formation to solitary living.

Fertility and mortality functions

Fitness is a non-linear function of an animal's energy state (Bednekoff, 1996; Smallwood, 1996). Here, fitness is divided into two components: fertility and mortality, which are functions of the amount of resources available. To allow for a broad spectrum of biologically plausible life histories, we assume sigmoid functions for fertility and mortality (see Fig. 2A). This is a common assumption in models of risk sensitivity, although the exact implementation may vary (Kuznar, 2002; Nevai *et al.*, 2007). Fertility (i.e. the number of offspring) is thus a function of the amount of resources (x) available to an individual:

$$F(x, L_F) = \frac{F_{\max}}{1 + e^{a_F \cdot x + b_F}} \tag{6}$$

with $a_F = -4 \cdot s_F / F_{\max}$ and $b_F = -a_F \cdot o_F$. Note that the model presented here operates with a fixed time span (i.e. one breeding season).

The shape of this function is determined by the maximum number of offspring per reproductive period ($F_{\max}$), the offset (o_F) of and the slope (s_F) in the inflexion point. The life-history parameters $L_F = \{F_{\max}, s_F, o_F\}$ are species specific and indicate how much energy has to be invested in offspring production: o_F is the amount of resources with which an animal is able to produce $F_{\max}/2$ offspring and s_F is inversely related to the costs of producing one offspring. The mortality function

$$M(x, L_M) = \frac{1 - M_b}{1 + e^{a_M \cdot x + b_M}} + M_b, \tag{7}$$

with $a_M = -4 \cdot s_M/(1 - M_b)$ and $b_M = -a_M \cdot o_M$, is completely described by the life-history parameters $L_M = \{M_b, s_M, o_M\}$. The parameters slope (s_M) and offset (o_M) are analogous to the corresponding parameters of the fertility function. In biological terms, this means that o_M represents the amount of resources needed to survive with a probability of 0.5. The slope (s_M) indicates how costly (in terms of resources) it is to reduce mortality. We assume that a constant, non-zero baseline mortality (M_b) exists. Note that here the slope (s_M) must be negative.

Population dynamics

To calculate offspring production $\phi(N, x, \bar{x}, \theta, L_F)$ of an individual in an egalitarian group of size N, we must integrate the fertility function (equation 6) weighted with the distribution of resources available to this individual (equation 5):

$$\phi(N, x, \bar{x}, \theta, L_F) = \int_0^\infty P_N(x, \bar{x}, \theta, N) \cdot F(x, L_F) \cdot dx. \tag{8}$$

The expected per capita loss of individuals due to mortality $\mu(N, x, \bar{x}, \theta, L_M)$ in such a group can be calculated similarly:

$$\mu(N, x, \bar{x}, \theta, L_M) = \int_0^\infty P_N(x, \bar{x}, \theta, N) \cdot M(x, L_M) \cdot dx. \tag{9}$$

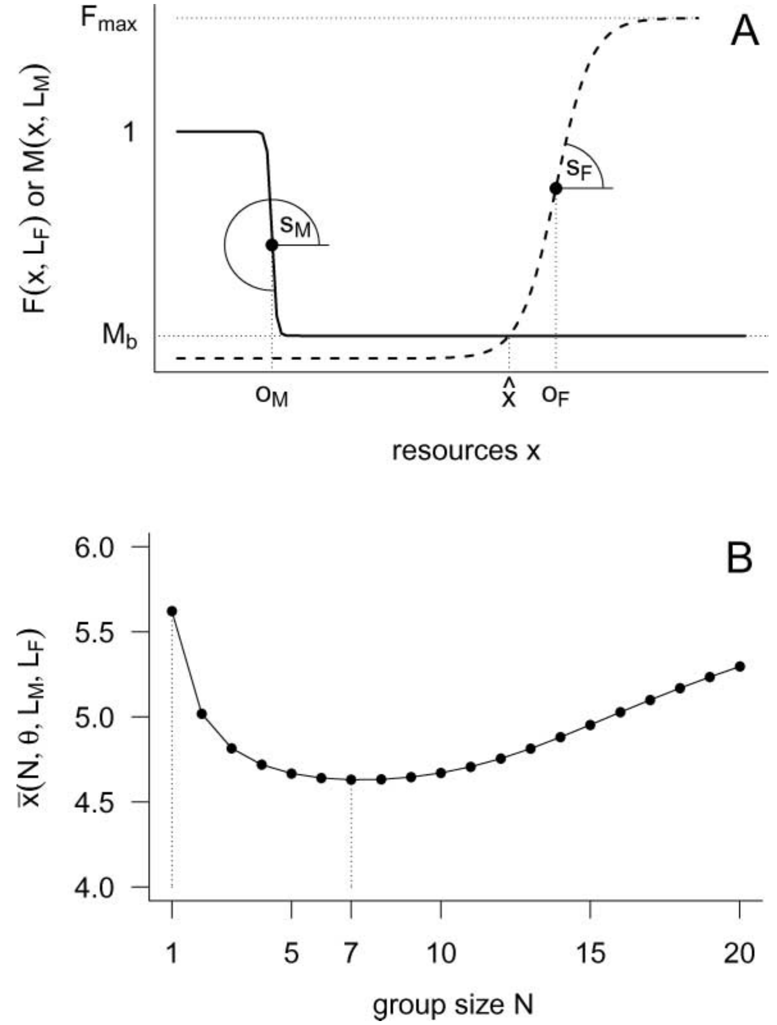

Fig. 2. Mortality and fertility functions, optimal group sizes. (A) The influence of the amount of resources (x) available to an individual on mortality and fertility. The mortality function $M(x, L_M)$ (equation 7) is characterized by the offset (o_M) of and the slope (s_M) in the inflexion point and by a lower limit, a baseline mortality (M_b). The parameters of the fertility function $F(x, L_F)$ (equation 6) are defined analogously. The intersection point of both functions ($\hat{x}$) determines the amount of resources needed in equilibrium when resource supply is constant (no variance). (B) A typical result for the numerical solution of equation (10) for the mean amount of resources required per capita in population equilibrium ($\bar{x}$) as a function of group size (N). For this specific parameter combination ($F_{\max} = 1$, $s_F = 3$, $o_F = 8$, $M_b = 0.01$, $o_M = 2$, $s_M = -5$, $\theta = 4$), the optimal group size (N_{opt}) would be 7 individuals. Of course, this function may have other runs. If the minimum is at $N = 1$, the function is increasing continuously and solitary living would be more advantageous than group formation.

These equations allow us to calculate – as a function of group size – the mean amount of resources $\bar{x}$ needed per individual to balance reproduction and mortality, i.e. when

$$\mu(N, x, \bar{x}, \theta, L_M) = \phi(N, x, \bar{x}, \theta, L_F). \qquad (10)$$

We thus assume population equilibrium and our results are only valid for this specific case (i.e. saturated habitats). The implications of this assumption will be discussed below.

Resource mean as a function of group size

Depending on the extrinsic variance of the resource distribution (i.e. the mean item size, θ) and on life-history parameters L_M and L_F (i.e. the form of the mortality and fertility functions: equations 6 and 7), the mean amount of resources required in population equilibrium ($\bar{x}$) is a function of group size (N; see Fig. 2B).

$$\bar{x} = f(N, \theta, L_M, L_F) \tag{11}$$

Note that for egalitarian groups variance is minimal ($\sigma_N^2 \to 0$) when group size is very large ($N \to \infty$). Then, $\bar{x}$ equals $\hat{x}$, which is the intersection point of the mortality and fertility functions (see Fig. 2A). Our model is based on the interaction between behavioural strategy (group size) and population size. It allows us to predict the influence of group size on the mean amount of resources needed per individual to balance mortality and natality (Fig. 2B). Evidently, an evolutionary minimization of this amount of resources needed per capita should be greatly advantageous in an environment with limited resources. Minimizing the amount of resources needed per capita boosts carrying capacity and in saturated environments the behavioural type with highest carrying capacity should out-compete any other strategy. Selective forces favouring an increase in carrying capacity are known to act in constant environments, i.e. K-selection (MacArthur, 1962; MacArthur and Wilson, 1967; Boyce, 1984; Lande *et al.*, 2009). However, it should be noted that in an age-structured population, for example, this assumption does not hold (Roff, 2002). Then the appropriate quantity to maximize is the size of the age group affected by density dependence (Charlesworth, 1972; Benton and Grant, 2000; Caswell *et al.*, 2004). Note that when evolutionary and population dynamics are brought together, usually an adaptive dynamics approach is appropriate. Yet, the optimization approach is much simpler and since our model does not include any frequency-dependent effects, the optimization approach presented above is sufficient.

We treat group size as a fixed life-time strategy. As a consequence, our model cannot be applied to taxa with highly flexible group-forming strategies. Our model operates on an evolutionary time scale that is, of course, longer and slower than the ecological time scale of population dynamics. We do not explicitly model population dynamics, but assume that the focal population has saturated its habitat. Therefore, our model will hold as long as this is true or population equilibrium is reached within a very short period. In disturbed habitats (strong r-selection) without resource limitation, selection on group formation may be less important (E.A. Fronhofer *et al.*, in preparation).

In summary, since we neither assume a changing environment nor an age structure or any frequency-dependent effects, it is correct to maximize carrying capacity, i.e. minimize $\bar{x}(N, \theta, L_M, L_F)$. Therefore, we assume that the group size $N_{\mathbf{opt}}$ minimizing $\bar{x}(N, \theta, L_M, L_F)$ for a set of given environmental and life-history parameters is an evolutionarily stable optimal group size that can range from $N_{\mathbf{opt}} = 1$ (i.e. solitary individuals) to $N_{\mathbf{opt}} \to \infty$ (i.e. large groups).

In general, equation (10) cannot be solved analytically for $\bar{x}$. To analyse the influence of group size on $\bar{x}(N, \theta, L_M, L_F)$, we solved it numerically for different values of the environmental parameters θ (mean item size, i.e. resource variance) and M_b (resource-independent baseline mortality), and of the life-history parameters $F_{\mathbf{max}}$ (maximal number of offspring) and s_F (i.e. costs per offspring) using the programming language R v.2.9.2 (R Development Core Team, 2009). All other parameters were fixed: $o_F = 8$, $o_M = 2$, and $s_M = -5$.

The relative benefit of group formation was quantified as the relative influence of cooperation on the equilibrium food supply ($\bar{x}$):

$$\text{relative benefit} = 1 - \frac{\bar{x}(N_{\text{opt}}, \theta, L_M, L_F)}{\bar{x}(1, \theta, L_M, L_F)}. \tag{12}$$

RESULTS

For the broad spectrum of environmental conditions [i.e. resource variance (or item size θ) and resource-independent baseline mortality (M_b)] and life-history parameters (L_F, L_M) used in our numerical solutions, environmental conditions were found to have the most important effect on the evolution of cooperatively foraging groups (Figs. 3 and 4). These factors predominantly determine the optimal size of groups.

As group formation with egalitarian resource sharing is a risk-reducing strategy, it should be most common in risky environments. As predicted, variance in resource availability generally promoted group formation (high values for θ; Fig. 3A, B, C) and the relative effect of group formation on equilibrium food supply and carrying capacity was highest in variable environments (Fig. 4A).

Increasing baseline mortality (M_b), on the other hand, results in a decrease in carrying capacity and consequently an increase in the amount of resources available to individuals in equilibrium. Thus, with increasing baseline mortality, resource-dependent mortality becomes less and resource-dependent fertility more important for population dynamics. In this situation, it is attractive to stay solitary and keep variance in resource availability high (white areas in Fig. 3C, F, I). This allows individuals to profit from high fertility when food is abundant, while low food rarely results in severely increased mortality risk.

Evidently, the opposite holds when maximum fertility ($F_{\max}$) is only marginally larger than baseline mortality ($F_{\max} < 2 \cdot M_b$): it becomes more and more difficult for individuals to compensate high baseline mortality with sufficient offspring production. For such life-history traits, individuals produce as many offspring as they can and are thus very close to their maximum fertility ($F_{\max}$). As a consequence, in population equilibrium they do not profit from an increase in resource variability, because fertility cannot be increased further. In contrast, an increase in variance would lead to a severe increase in mortality. In such cases, a reduction in variance by group formation is indicated (black areas in Fig. 3C, F, I).

Life-history parameters become important both when maximum fertility of individuals is extremely low compared with baseline mortality ($F_{\max} < 2 \cdot M_b$) and, if baseline mortality (M_b) is low, when offspring production is very costly (i.e. low values of s_F). Group formation was found to be largely independent of the costs of offspring production, except when life-history parameters indicated the production of high numbers of very costly offspring ($s_F < 2$). In this case, group formation was advantageous, especially when baseline mortality was low (Fig. 3A, D, G). When egalitarian group formation was favoured (i.e. in variable environments), group sizes were found to increase with a decreasing maximal number of offspring.

To assess the evolutionary relevance of the results presented above, we quantified the relative benefit of group formation (see equation 12). This effect could be as high as 0.57, i.e. individuals in groups of optimal size reduced $\bar{x}(N_{\text{opt}}, \theta, L_M, L_F)$ – their mean amount

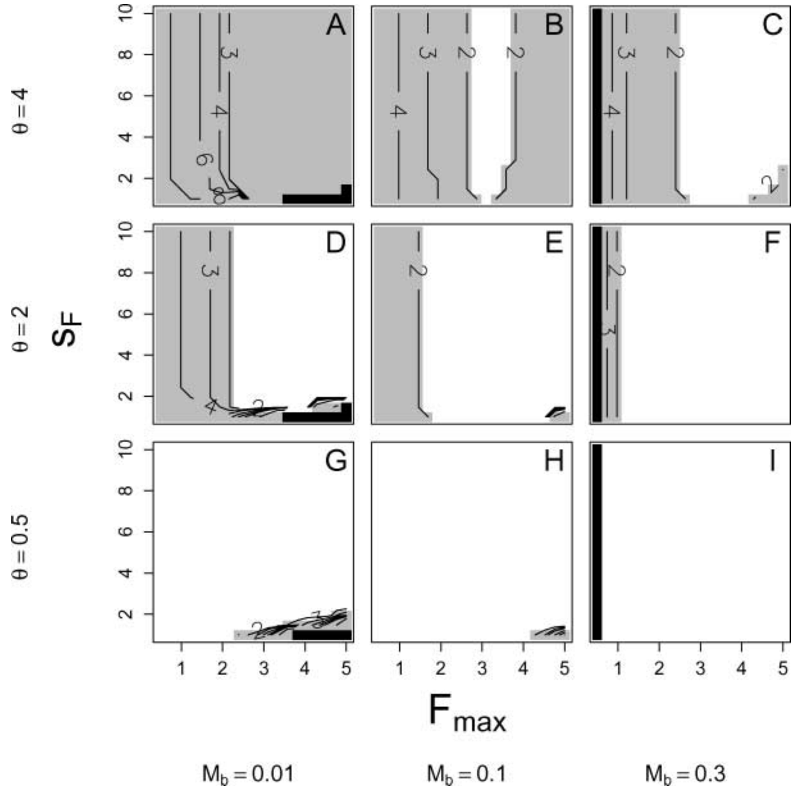

Fig. 3. Group formation dependent on environmental and life-history parameters. Item size (θ) increases from the bottom to the top row. Baseline mortality (M_b) increases from left to right. The slope of the fertility function (s_F) is always represented on the vertical axis and the maximum number of offspring possible ($F_{\max}$) can be found on the horizontal axis. Contour lines indicate optimal group sizes. Shading highlights certain special cases: white areas indicate solitary individuals, grey areas groups of an intermediate optimal size, and black areas very large groups ($N \to \infty$).

of resources required in equilibrium – compared with solitary individuals under the same conditions by 57%. This effect was examined separately for each model parameter of interest (Fig. 4).

Variance in food supply had the most dramatic effect on the reduction of $\bar{x}(N_{\text{opt}}, \theta, L_M, L_F)$ (mean item size θ; Fig. 4A). The relative benefit of group formation increased quasi-exponentially with θ: larger food items favoured group formation strongly. The opposite effect could be seen for baseline mortality (M_b; Fig. 4B). Egalitarian groups were very weakly favoured for small resource-independent mortalities. A similar trend could be observed for the cost of offspring production (s_F; Fig. 4C) and for maximal fertility ($F_{\max}$). Egalitarian group formation was slightly advantageous when offspring were expensive (small s_F). At higher values of s_F, this parameter had no influence on model results. Small values of the maximal number of offspring possible ($F_{\max}$; Fig. 4D) favoured group formation strongly. The inter-quartile range for high values of $F_{\max}$ indicates that at least for some parameter combinations, very high numbers of maximal offspring production may have a positive effect on group formation.

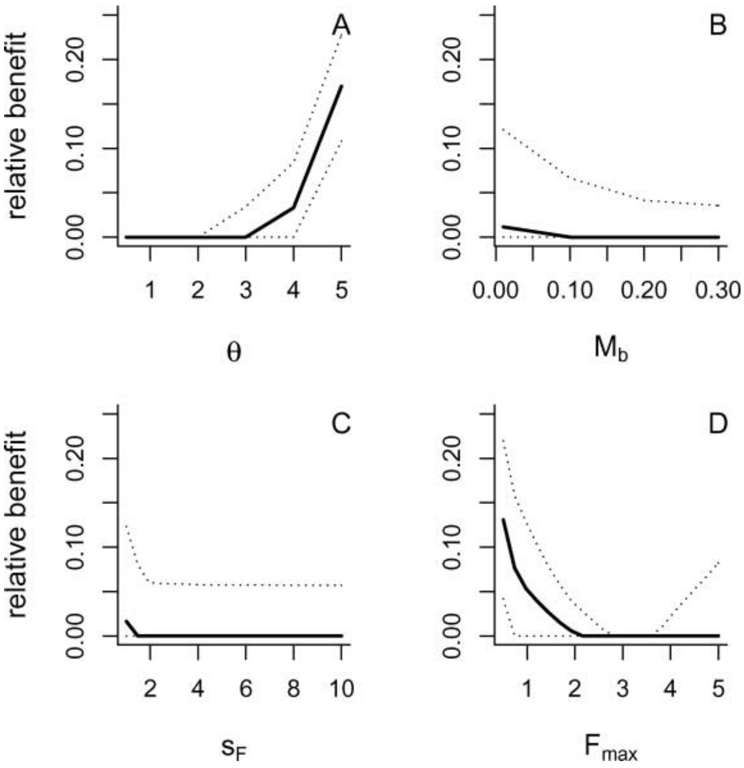

Fig. 4. Relative benefit of group formation (see equation 12), i.e. the reduction of the mean amount of resources needed per capita in groups of optimal size compared with the mean amount of resources needed by solitary individuals. For each model parameter, the median (solid lines) and the inter-quartile range (dotted lines) of the relative benefit are shown. The inter-quartile range indicates the effect of the other parameters (e.g. for panel A – with focal parameter θ – the effect of M_b, s_F, and $F_{\max}$).

DISCUSSION

Risk-sensitive foraging theory predicts that animals should be risk-averse when resources are abundant and risk-prone when the opposite holds (Bateson, 2002). Since group formation with egalitarian food sharing is a risk-averse strategy (i.e. diminishes variance), it is thus assumed that species should form groups when living in habitats where food supply is highly variable and the mean amount of food available per individual is high (Uetz, 1992, 1996; Uetz and Hieber, 1997). On the other hand, solitary living is predicted when mean food availability is low. Models that take energy budgets into account further predict that increasing baseline mortality makes solitary living more attractive (Kacelnik and Bateson, 1996; Bateson, 2002).

These general statements may be true for species with highly flexible group-forming behaviours. Such animals may decide from one reproductive period to the next whether it is better to join a group or to stay solitary. Yet, whenever the species-specific strategy is fixed, it will itself have an influence on population dynamics and on the amount of resources available. Density regulation will feed back on the specific fitness assigned to a behavioural strategy. Pen and Weissing (2000) have previously shown that incorporating density regulation may have important consequences for model predictions concerning the evolution of cooperative breeding. In contrast to our model of egalitarian group formation, these authors focus on communal breeding with highly skewed reproduction.

Our model results generally support the idea that variance reduction by group formation may be evolutionarily advantageous by increasing individual fitness. This is particularly true in environments with high variance in food supply. Our model also confirms the prediction of McNamara *et al.* (1991) that high baseline mortality (M_b) leads to risk-prone behaviour (Figs. 3, 4B). However, we have pointed out that increasing baseline mortality does not necessarily favour solitary individuals (Fig. 3C, F, I). As soon as baseline mortality is lower than a critical threshold value, which is determined by the maximum reproductive output of individuals, group formation (i.e. risk-aversion) is promoted. For our specific choice of fertility function, this threshold is given by the inflexion point of the fertility function ($F_{\max}/2$). This will hold for all sigmoid fertility functions, although the value of the threshold will depend on the specific type of function.

Life histories with small maximal numbers of offspring favour group formation (Fig. 3A or D). Under such conditions, group formation (i.e. variance reduction) predominantly leads to a reduction in mortality. This is necessary for the population to remain in equilibrium because mortality has to be as low as offspring production. All other things being equal, slightly higher maximal numbers of offspring logically result in solitary individuals (Fig. 3B, C). High maximal numbers of offspring promote group formation again (Fig. 3B, C). This effect occurs because in this case variance reduction leads to a reduction in natality. This again is due to density dependence and to the fact that in population equilibrium natality and mortality have to be balanced (equation 10). This is achieved by variance manipulation (i.e. the formation of specific group sizes), which may either reduce mortality or natality.

The cost of offspring production has a similar effect on group formation as maximum fertility. Groups are favoured when offspring are expensive, i.e. when the slope of the fertility function (s_F, equation 6) is shallow (Figs. 3, 4C).

Note that the overall relatively small optimal group sizes in Fig. 3 are due to the low values assumed for fixed model parameters (especially o_M and o_F). Increasing these values leads to larger optimal group sizes (data not shown). Changing the difference between o_M and o_F will only influence optimal group sizes quantitatively over a wide portion of the parameter space. The effect of the difference between o_M and o_F is comparable to s_F: a larger difference indicates that offspring production is proportionally more expensive, which favours egalitarian group formation. In summary, varying the values of the fixed parameters does not have any qualitative effect on the results.

Our model results clearly demonstrate that the benefit of group formation is not restricted to high mean food supply. Here, we assume competition for food. Thus, food is the limiting resource that is always scarce when populations have reached their equilibrium size. Nevertheless, we predict that group formation should be frequent when resources are sufficiently variable (Fig. 3A, B, C, Fig. 4). Thus, for example, sociality in spider species like *Anelosimus eximius* and *A. domingo* (Powers and Avilés, 2007) may readily be explained by our model of risk-sensitive foraging. In contrast to subsocial spider species like *A. baeza*, which lives at high elevations where resource variance is low and mean resource supply is high, *A. eximius* and *A. domingo* are typically found in lowland tropical rainforest habitats (Costa, 2006) where average insect sizes are significantly higher, and insect density and biomass are significantly lower than in high-elevation habitats (Powers and Avilés, 2007). In other words, spider sociality evolves when resource mean is low and variance is high. Similar results have been reported for the neotropical genus *Parawixia* that inhabits wet and dry forests in South America (Fernández Campón, 2007, 2008). Compared with wet sites, dry ones are associated with larger and fewer potential prey items.

Our findings contradict previous models of risk-sensitive foraging theory that do not incorporate density dependence, and as a consequence predict risk-averse behaviour for the case of high food levels only. We assume that the modelled population has reached its equilibrium size and, therefore, that resources are limited. Of course, our results do not hold for situations in which resources are not a limiting factor. In such cases, solitary living would be more advantageous than egalitarian group formation over a wide range of parameter space. Here, we show that colony size can be readily explained as a risk-sensitive foraging strategy as long as density dependence is taken into account. Large spider colonies, for example, evolve as a strategy to minimize variance, which allows them to dominate in habitats with higher resource variance (i.e. larger prey). The occurrence of other solitary species in, for example, tropical lowlands is not at odds with our predictions, since life-history parameters like the number of offspring or energetic investment per offspring must be accounted for. Our model does not include such spider-specific aspects as three-dimensional webs or maternal care, issues that are known to be important for the evolution of social groups (Avilés, 1997; Agnarsson, 2006).

CONCLUSIONS

We have demonstrated the enormous potential of variance reduction as a driving force for the evolution of cooperatively foraging egalitarian animal societies. Our approach highlights the importance of ecological factors for the evolution of cooperation. At the same time, the role of life-history parameters is clarified. Crucially, the influence of density dependence is taken into account. Since our model does not include relatedness, it can be applied to other phenomena involving egalitarian animal groups such as the formation of mixed species groups in spiders (Hodge and Uetz, 1996), in birds (Sridhar *et al.*, 2009), or in terrestrial and marine mammals (Stensland *et al.*, 2003; Quérouil *et al.*, 2008).

Of course, foraging is only one aspect influencing group living and, depending on further environmental settings or specific life histories, other advantages and costs of cooperation (Krause and Ruxton, 2002) have to be considered. Egalitarian groups are extreme examples from a continuum of cooperative behaviours. Note that even in some of the above cited spider species, it is not clear whether a perfectly egalitarian system is attained (Rypstra, 1993). Repeated interactions, future pay-off (Kokko and Johnstone, 1999), and other mechanisms mentioned above are well-known factors promoting cooperation. Our model assumes a saturated habitat. The colonization of empty habitat patches might strongly favour smaller optimal group sizes or even solitary living. All these factors – and many more not listed here – have been ignored in the above model. Yet, as Kokko (2005) points out, there are useful ways of being wrong.

ACKNOWLEDGEMENTS

The authors would like to thank Thomas Caraco for very useful and constructive comments that helped to improve the manuscript. Financial support for this research was provided to H.J.P. by the German Research Foundation, DFG (SFB 554, TP C6). E.A.F. was supported by a grant of the German Excellence Initiative to the Graduate School of Life Sciences, University of Würzburg.

REFERENCES

Agnarsson, I. 2006. A revision of the new world *eximius* lineage of *Anelosimus* (Araneae, Theridiidae) and a phylogenetic analysis using worldwide exemplars. *Zool. J. Linn. Soc.*, **146**: 453–593.

Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. In *The Evolution of Social Behavior in Insects and Arachnids* (J.C. Choe and B.J. Crespi, eds.), pp. 476–498. Cambridge: Cambridge University Press.

Avilés, L. 1999. Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. *Evol. Ecol. Res.*, **1**: 459–477.

Avilés, L., Agnarsson, I., Salazar, P.A., Purcell, J., Iturralde, G., Yip, E.C. *et al.* 2007. Altitudinal patterns of spider sociality and the biology of a new midelevation social *Anelosimus* species in Ecuador. *Am. Nat.*, **170**: 783–792.

Axelrod, R. and Hamilton, W.D. 1981. The evolution of cooperation. *Science*, **211**: 1390–1396.

Bateson, M. 2002. Recent advances in our understanding of risk-sensitive foraging preferences. *Proc. Nutr. Soc.*, **61**: 509–516.

Bednekoff, P.A. 1996. Risk-sensitive foraging, fitness, and life histories: where does reproduction fit into the big picture? *Am. Zool.*, **36**: 471–483.

Benton, T.G. and Grant, A. 2000. Evolutionary fitness in ecology: comparing measures of fitness in stochastic, density-dependent environments. *Evol. Ecol. Res.*, **2**: 769–789.

Boyce, M.S. 1984. Restitution of *r*- and *K*-selection as a model of density-dependent natural selection. *Annu. Rev. Ecol. Syst.*, **15**: 427–447.

Caraco, T. 1980. On foraging time allocation in a stochastic environment. *Ecology*, **61**: 119–128.

Caraco, T. 1981. Risk-sensitivity and foraging groups. *Ecology*, **62**: 527–531.

Caraco, T., Martindale, S. and Whittam, T.S. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Anim. Behav.*, **28**: 820–830.

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

Caswell, H., Takada, T. and Hunter, C.M. 2004. Sensitivity analysis of equilibrium in density-dependent matrix population models. *Ecol. Lett.*, **7**: 380–387.

Charlesworth, B. 1972. Selection in populations with overlapping generations. III. Conditions for genetic equilibrium. *Theor. Popul. Biol.*, **3**: 377–395.

Clark, C.W. and Mangel, M. 1986. The evolutionary advantages of group foraging. *Theor. Popul. Biol.*, **30**: 45–75.

Clutton-Brock, T., West, S.A., Ratnieks, F.L.W. and Foley, R. 2009. The evolution of society. *Phil. Trans. R. Soc. Lond. B*, **364**: 3127–3133.

Costa, J.T. 2006. *The Other Insect Societies*. Cambridge, MA: The Belknap Press of Harvard University Press.

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

Fernández Campón, F. 2008. More sharing when there is less: insights on spider sociality from an orb-weaver's perspective. *Anim. Behav.*, **75**: 1063–1073.

Griffin, A.S. and West, S.A. 2002. Kin selection: fact and fiction. *Trends Ecol. Evol.*, **17**: 15–21.

Hamilton, W.D. 1964a. Genetical evolution of social behaviour I. *J. Theor. Biol.*, **7**: 1–16.

Hamilton, W.D. 1964b. Genetical evolution of social behaviour II. *J. Theor. Biol.*, **7**: 17–52.

Hatchwell, B.J. and Komdeur, J. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.*, **59**: 1079–1086.

Hodge, M.A. and Uetz, G.W. 1996. Foraging advantages of mixed-species association between solitary and colonial orb-weaving spiders. *Oecologia*, **107**: 578–587.

Hölldobler, B. and Wilson, E.O. 2009. *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies*. New York: W.W. Norton.

Kacelnik, A. and Bateson, M. 1996. Risky theories – the effects of variance on foraging decisions. *Am. Zool.*, **36**: 402–434.

Kikvidze, Z. and Callaway, R.M. 2009. Ecological facilitation may drive major evolutionary transitions. *BioScience*, **59**: 399–404.

Kokko, H. 2005. Useful ways of being wrong. *J. Evol. Biol.*, **18**: 1155–1157.

Kokko, H. and Johnstone, R.A. 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proc. R. Soc. Lond. B*, **266**: 571–578.

Krause, J. and Ruxton, G.D. 2002. *Living in Groups*. Oxford: Oxford University Press.

Kuznar, L.A. 2002. Evolutionary applications of risk sensitivity models to socially stratified species: comparison of sigmoid, concave, and linear functions. *Evol. Human Behav.*, **23**: 265–280.

Lande, R., Engen, S. and Saether, B.E. 2009. An evolutionary maximum principle for density-dependent population dynamics in a fluctuating environment. *Phil. Trans. R. Soc. Lond. B*, **364**: 1511–1518.

Lehmann, L. and Keller, L. 2006. The evolution of cooperation and altruism – a general framework and a classification of models. *J. Evol. Biol.*, **19**: 1365–1376.

MacArthur, R.H. 1962. Some generalized theorems of natural selection. *Proc. Natl. Acad. Sci. USA*, **48**: 1893–1897.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Maynard Smith, J. 1964. Group selection and kin selection. *Nature*, **201**: 1145–1147.

McNamara, J.M., Merad, S. and Houston, A.I. 1991. A model of risk-sensitive foraging for a reproducing animal. *Anim. Behav.*, **41**: 787–792.

Nevai, A.L., Waite, T.A. and Passino, K.M. 2007. State-dependent choice and ecological rationality. *J. Theor. Biol.*, **247**: 471–479.

Nowak, M.A. 2006. Five rules for the evolution of cooperation. *Science*, **314**: 1560–1563.

Okasha, S. 2006. *Evolution and the Levels of Selection*. Oxford: Oxford University Press.

Otto, S.P. and Day, T. 2007. *A Biologist's Guide to Mathematical Modelling in Ecology and Evolution*. Princeton, NJ: Princeton University Press.

Pen, I. and Weissing, F.J. 2000. Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. *Proc. R. Soc. Lond. B*, **267**: 2411–2418.

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

Powers, K.S. and Avilés, L. 2007. The role of prey size and abundance in the geographical distribution of spider sociality. *J. Anim. Ecol.*, **76**: 995–1003.

Purcell, J. and Avilés, L. 2008. Gradients of precipitation and ant abundance may contribute to the altitudinal range limit of subsocial spiders: insights from a transplant experiment. *Proc. R. Soc. Lond. B*, **275**: 2617–2625.

Quérouil, S., Silva, M.A., Cascão, I., Magalhães, S., Seabra, M.I., Machete, M.A. *et al.* 2008. Why do dolphins form mixed-species associations in the Azores? *Ethology*, **114**: 1183–1194.

R Development Core Team. 2009. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ranta, E., Rita, H. and Lindström, K. 1993. Competition versus cooperation: success of individuals foraging alone and in groups. *Am. Nat.*, **142**: 42–58.

Real, L. and Caraco, T. 1986. Risk and foraging in stochastic environments. *Annu. Rev. Ecol. Syst.*, **17**: 371–390.

Roff, D.A. 2002. *Life-History Evolution*. Sunderland, MA: Sinauer Associates.

Rypstra, A.L. 1993. Prey size, social competition, and the development of reproductive division-of-labor in social spider groups. *Am. Nat.*, **142**: 868–880.

Sachs, J.L., Mueller, U.G., Wilcox, T.P. and Bull, J.J. 2004. The evolution of cooperation. *Q. Rev. Biol.*, **79**: 135–160.

Schmitz, O.J. and Ritchie, M.E. 1991. Optimal diet selection with variable nutrient intake – balancing reproduction with risk of starvation. *Theor. Popul. Biol.*, **39**: 100–114.

Smallwood, P.D. 1996. An introduction to risk sensitivity: the use of Jensen's inequality to clarify evolutionary arguments of adaptation and constraint. *Am. Zool.*, **36**: 392–401.

Sridhar, H., Beauchamp, G. and Shanker, K. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.*, **78**: 337–347.

Stensland, E., Angerbjörn, A. and Berggren, P. 2003. Mixed species groups in mammals. *Mammal Rev.*, **33**: 205–223.

Stephens, D.W. 1981. The logic of risk-sensitive foraging preferences. *Anim. Behav.*, **29**: 628–629.

Trainor, K.E. and Caraco, T. 2006. Group size, energy budgets, and population dynamic complexity. *Evol. Ecol. Res.*, **8**: 1173–1192.

Traulsen, A. and Nowak, M.A. 2006. Evolution of cooperation by multilevel selection. *Proc. Natl. Acad. Sci. USA*, **103**: 10952–10955.

Trivers, R.L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.*, **46**: 35–57.

Uetz, G.W. 1992. Foraging strategies of spiders. *Trends Ecol. Evol.*, **7**: 155–159.

Uetz, G.W. 1996. Risk sensitivity and the paradox of colonial web-building in spiders. *Am. Zool.*, **36**: 459–470.

Uetz, G.W. and Hieber, C.S. 1997. Colonial web-builiding spiders: balancing the costs and benefits of group-living. In *The Evolution of Social Behavior in Insects and Arachnids* (J.C. Choe and B.J. Crespi, eds.), pp. 458–475. Cambridge: Cambridge University Press.

Wenzel, J.W. and Pickering, J. 1991. Cooperative foraging, productivity, and the central limit theorem. *Proc. Natl. Acad. Sci. USA*, **88**: 36–38.

West, S.A., Pen, I. and Griffin, A.S. 2002. Conflict and cooperation – cooperation and competition between relatives. *Science*, **296**: 72–75.

Whitehouse, M.E.A. and Lubin, Y. 2005. The functions of societies and the evolution of group living: spider societies as a test case. *Biol. Rev.*, **80**: 347–361.

Wilson, D.S. and Wilson, E.O. 2007. Rethinking the theoretical foundation of sociobiology. *Q. Rev. Biol.*, **82**: 327–348.

Wilson, E.O. and Hölldobler, B. 2005. Eusociality: origin and consequences. *Proc. Natl. Acad. Sci. USA*, **102**: 13367–13371.

Yip, E.C., Powers, K.S. and Avilés, L. 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. *Proc. Natl. Acad. Sci. USA*, **105**: 11818–11822.