Relatedness and conflict over optimal group size

Many animals live in groups during all or part of their lives. Some species forage primarily in groups, often on a transient basis, whereas others form semi-permanent breeding colonies. The selective factors promoting group living have been widely debated[1,2] and are likely to include both the direct advantages associated with avoiding predators or finding food[3], and the indirect effects of habitat heterogeneity in which sites differ in the number of individuals that can be supported by the available local resources[4]. Regardless of its cause, group living is also likely to have certain costs, such as increased ectoparasitism and competition for resources[3]. In most species, the costs and benefits associated with group living vary systematically with group size. The individual fitness of group members as a function of group size, which is determined by the costs and benefits associated with a particular group size, may either consistently increase, consistently decrease or have a maximum at an intermediate group size[5].

Models of group living

Theoretical studies of the evolution of group living have, for the most part, considered cases in which a fitness optimum exists at intermediate group sizes[6-8]. Although there is, at present, only limited empirical evidence for fitness functions with intermediate optimum group sizes, functions of this type are intuitively appealing and display some interesting theoretical properties. Intermediate optima may occur when the direct benefits of group living (such as enhanced predator avoidance or information transfer) increase rapidly in small groups but reach an asymptote in larger groups, while the direct costs (such as increased ectoparasitism and resource depletion) increase slowly in smaller groups, but rise rapidly in larger ones[9].

Given a peaked fitness function, group formation has generally been modeled as follows: solitary individuals sequentially choose groups to join, and group-living individuals switch among groups, so as to maximize their fitness, until an equilibrium is reached[7]. The fitness interests of solitary and group-living individuals may be at odds in some cases. A solitary individual might increase its fitness by joining a group that is at optimum size, for example, and at the same time decrease the fitness of other group members. Solitary individuals should always join a group if their fitness as a member will be higher than as a 'solitary'[6-8].

If solitary individuals can freely decide whether or not they join a group, the size of a group may be expected to increase (in a growing population) until the fitness of group-living individuals equals that of solitaries. In this case, group living is not an evolutionarily stable strategy (ESS), and the model does not adequately explain the evolution or maintenance of group living[10]. If conflicts between solitaries and group members occur, however, group-living individuals might often prevent solitaries from joining groups already at, or beyond, the optimum size[11], and the group-living individuals will have higher average fitness than solitaries (and group living will be an ESS).

Indirect (kin) selection might also influence group-joining decisions if solitaries are related to group members. Some studies[10,12] have considered individuals' choice of a group by taking into account inclusive fitness (IF). Decisions based on IF may be modeled from two perspectives: (1) that of solitaries who seek to join a group; and (2) that of the members of the group a solitary may seek to join[13]. Solitary individuals may, in certain cases, forgo joining a group whose size is already at, or above, the optimum since the benefit, in terms of an increase in the direct fitness of the solitary, will be offset by a net decrease in IF as a result of lowered direct fitness for its relatives in the group.

The precise point at which the effect of joining a group changes from being a net increase in inclusive fitness for the solitary to a net decrease depends on the average relatedness of the solitary to the group members and the nature of the fitness function. The group size at this point has been termed the 'stable' group size, since beyond this size the solitary may no longer be expected to join the group. In general, if the average relatedness, r, between a solitary and group members is greater than zero, the direct fitness of individuals living in groups of stable size will be greater than that of solitaries, and group living will be an ESS. From the opposite perspective, group members will readily accept related solitaries into a group that is at, or above, the optimal size if they increase their IF and offset the cost of the action (a decrease in their direct fitness) by doing so.

A new synthesis

Higashi and Yamamura[13] recently presented a synthesis of these two perspectives on inclusive fitness in the form of an IF model of the possible outcomes for conflicts over group-joining between solitary and group-living individuals. The region of conflict in this case is the parameter space, under an IF model, in which the fitness interests of the solitary and group-living individuals conflict. For example, it may be in the interest of a solitary individual to join a group (this increases its IF), but in the interest of group members to prevent a solitary from joining (thus maintaining a higher average IF for group members). In this case, a conflict will arise, and the 'benefit' of winning the conflict depends on the cost associated with a win.

Higashi and Yamamura[13] derive a function describing the outcome of such conflicts based on a model in which solitaries are at a cost disadvantage, by comparison with group-living individuals, in the event of a conflict. Group members each pay a cost, d, in any conflict, whereas solitaries pay a cost of knd, where k is the proportional advantage that group members have over solitaries in a conflict, and n is the group size. The authors define the function $f(n)$ to describe the outcome of any conflict under this model:

$$f(n) = [1 + r(n-1) + rkn]\phi_s + (kn + m)\phi_G$$

where r is the average relatedness between the solitary and the group members, ϕ_s describes the change in IF for a solitary that joins a group, and ϕ_G describes the change in IF for a group member if a solitary is allowed to join. For some value of n, the condition $f(n) \geq 0$ predicts that group members allow a solitary to join, whereas $f(n) < 0$ predicts that group members do not allow a solitary to join.

The model presented by these authors resolves a number of theoretical and empirical problems. First, it provides an explanation for the evolution of group living since, if the relatedness between solitaries and group members is non-zero, the stable group size predicted under the IF–conflict model is always smaller than that under a direct-fitness model with no conflict (under a direct-fitness model, this is equal to the size at which the fitness of group members equals that of solitaries). Group-living individuals therefore always have greater direct fitness than solitaries under the IF–conflict model and group living is an ESS.

Second, the model explains why group size might exceed an expected optimum

size in nature. If the relatedness between solitaries and group members is non-zero, or *k* has a finite value, the stable group size will always be larger than the optimal group size. This result is similar to findings for other models of group formation[6-8]. The stable group size varies with *r*, and, when *k* is large, this increases with *r*.

Finally, the model explains why variation in group size may occur for some species[5], despite the existence of an optimal group size. The stable group size may vary in a range between the size at which the group members' direct fitness equals that of solitaries and the size at which it is maximized (the optimal group size), as a result of variations in *r* and *k* among groups. Consequently, Higashi and Yamamura's model[13] provides another possible explanation for the empirical observation of group-size variation that may be more accurate for some species of animals than existing explanations[5]. For example, black-tailed prairie dogs (*Cynomys ludovicianus*) probably use intra-group relatedness in their decisions to disperse from a coterie and to rejoin the same one after an absence[14].

Outstanding uncertainties

Despite the value of the approach taken by Higashi and Yamamura[13] in resolving some long-standing problems with explanations of the evolution and maintenance of group living, there are several conceptual difficulties for an IF-based, or IF–conflict-based, model of group formation. The first problem concerns the way in which individuals choose to join groups, or prevent others from joining, based on relatedness. There are three distinct steps in this process: (1) obtain an estimate of *n* (group size); (2) obtain an estimate of *r* (average relatedness between solitary and group-living individuals); (3) relate the estimated values of *r* and *n* to ϕ_s or ϕ_G and make a decision. If conflict is involved, two additional steps are necessary: (4) obtain an estimate of *k* (see previous definition); (5) relate the estimated value of *k* to *f(n)* and make a decision. The relative difficulty that individuals have in obtaining these estimates of *n*, *r* and *k* will generally differ between solitaries and group members. In principle, group members and solitaries may be capable of estimating group size accurately, although this will depend on the size of the group, time of year and the spatial distribution of group members[9]. Estimating relatedness may be easier for group members (who may often remain together from birth) than for solitaries, but this will again depend on the size of the group and the spatial distribution of members.

It is not known if animals assess relatedness in choosing groups, although relatedness probably does not figure in choices made by some species. In most eusocial insects, for example, individuals do not move among colonies and join groups based strictly on estimates of relatedness, but rather, the levels of relatedness within the group are primarily a result of the breeding structure and simultaneous natal dispersal by related co-foundresses[15,16]. If individuals of some species do assess relatedness in choosing groups, some degree of error is probably involved in this assessment process, and this will be particularly true as group size increases[17].

An uncertainty in the parameter *r* may be accounted for by modeling the estimate of *r* as having some distribution that depends on the true values of *r* and *n*. A related problem arises in estimating *k*. If *r* and *k* are statistical estimators that follow some error distribution, the expected outcomes for the model presented by Higashi and Yamamura[13] might be very different. In general, the cost of errors in the parameter estimate for a solitary will be a decrease in IF if an incorrect group-joining choice is the result. The actual cost of such errors will depend on the shape of the fitness function and the distribution of the group sizes. The authors' neglect of this important source of variability is a general outcome of their use of a deterministic model. A stochastic model that takes into account errors in estimates of *r* and *k* is likely to be more realistic, but also more complex, and may not yield a simple analytical solution.

Estimating the values of ϕ_s and ϕ_G, or *f(n)*, given estimates of *r*, *n* and *k* [steps (3) and (5)] is not straightforward. A human might use an approximate method (such as a Taylor-series expansion) to obtain expected values and variances for these functions, given estimates of *r*, *n* and *k*, but it is unclear how animals in nature will go about making such estimates in order to reach their decisions. If *r* and *k* are very nearly constant in some groups, certain patterns of behavior and decision making might evolve as fixed strategies that do not require the estimation of any parameter other than group size. In groups with highly variable values for *r* or *k*, however, this is unlikely.

One safe way that individuals could avoid the potential costs associated with errors in estimates of *r* and *k*, when these two parameters are highly variable, is to follow a fixed strategy for solitaries of only joining groups that are below the optimum group size (in terms of direct fitness), and for group members of only

allowing solitaries to join if the group is below the optimum size. In this case, the direct and indirect components of fitness for both solitary and group-living individuals are always increased, regardless of the values of *r* and *k*, so that a knowledge of these two parameters is unnecessary. An additional feature that increases the likelihood that animals may often use such a fixed strategy in choosing groups is that the optimal group size is, in general, easier for animals to evaluate than *r* or *k* since groups at, or near, optimum size may display obvious direct-fitness benefits. These apparent benefits could include increased amounts of food for members, or tolerable levels of ectoparasitism and disease. Such direct-fitness effects should be relatively easy for individuals to evaluate in nature and could lead them to correctly estimate optimal group size.

Since any indication of conflict would suggest that the group is already at, or above, the optimal size, solitaries might also use conflict with group members as a means to assess whether the group is near optimal size. Solitary individuals could use an additional fixed strategy to choose groups in this case: if a conflict occurs with a group member, do not join the group. Such a strategy could prove highly effective if group members are generally better able than solitaries to assess the direct benefits of group size. This is likely to be the case, since they have already been living in the group.

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Hares and tortoises in *Drosophila* community ecology

The sprint speed of a tortoise will seldom approach that of a gently strolling hare. Nevertheless, in Æsop's famous fable the slow tortoise won a race because the fast hare, presumptuous of success, foolishly took a nap before completing the course, thus inadvertently allowing the more persistent tortoise to catch up and overtake. So Æsop illustrated that 'competitive ability' can depend on both speed and persistence. In a recent pair of papers on *Drosophila* community ecology, Sevenster and van Alphen[1,2] lend theoretical and empirical support to Æsop's illustration. They show that a 'fast' strategy can win, lose or tie against a 'slow' strategy, depending on the nature of the environment. The take-home message of these papers is that coexistence of competing species in spatially homogeneous environments can be promoted by life-history differences.

The life histories of co-occurring *Drosophila* species can be relatively 'fast', with rapid larval development, or 'slow', with slow larval development. Moreover, the juvenile developmental period is mirrored by the adult longevity: the faster the development, the shorter the adult life expectancy. Since *Drosophila* develop in limited and ephemeral resources, fast development is advantageous to larvae since it increases their ability to compete for resources and complete development before the resources are exhausted. The catch is that the consequently short adult lifespan reduces the likelihood of finding fresh resources for progeny production. Adults of relatively slowly developing species, however, have better chances of finding new breeding opportunities because their greater longevity allows them to persist longer in the environment. 'Slow' species are thus expected to fare relatively better than their 'fast' counterparts when breeding opportunities are scarce and competition between larvae is weak.

Model simulations

In the first paper of the pair, Sevenster and van Alphen[1] explore this idea using a model to simulate the population dynamics of a 'fast' and a 'slow' species competing for limited resources. The model is aimed at understanding the influence of the frequency of breeding opportunities on the relative advantages of the two species types. Breeding opportunities occur with a given probability each day, and, if a breeding opportunity occurs, the adults of each species reproduce, resulting in future recruits to the respective adult populations. The numbers and timing of the recruits joining the population depends on many biological factors such as the developmental period and the intensity of competition: Sevenster and van Alphen use estimates of these derived from their own experimental data[2] and from the literature. They then employ the model to examine the consequences of varying average time intervals between breeding opportunities. Their simulations confirm the expectation that 'fast' species become dominant when the average interval is short, while 'slow' species dominate when opportunities are less frequent. A sensitivity analysis revealed that this result is robust against realistic changes in the parameter values used in the initial simulations.

Having shown that the relative advantages of 'fast' and 'slow' life-histories are dependent on the daily probability of breeding opportunities, Sevenster and van Alphen go on to ask whether there are circumstances under which the two strategies can stably coexist. They note that species will coexist if each is able to invade a system where the other is established. Thus, they used the model to allow one species to become established in the absence of the other, then they introduced one adult of the other species and ran the simulation further. Simulations were repeated, for each species as potential invader, at various average intervals between reproductive opportunities. These simulations reveal that, at intermediate average intervals of about five days, the 'fast' and 'slow' species can coexist.

Laboratory and field tests

Sevenster and van Alphen's modelling[1] is closely integrated with the empirical work on 22 species of frugivorous *Drosophila* from the neotropics presented in the second of their two papers[2]. They perform the necessary experiments on these species to derive estimates of the life-history parameters included in their model, and show that the species they study have a range of developmental periods and that these are positively correlated with adult lifespan in the absence of food. They then go on to test the predictions of the model in these species. Population cage experiments[2] with a 'fast' species and a 'slow' species showed that the outcome of the interaction is influenced by the interval between the provision of new oviposition substrate. In these experiments, new substrate was added on regular fixed schedules but the outcome matched the predictions of the model[1], with parameters set for the species used and with the stochastic element removed.

In addition to their empirical laboratory work, Sevenster and van Alphen take the important step of examining whether the predictions of their model are supported by field evidence. By simultaneously collecting adult and juvenile populations and comparing the species composition of the sampled adults with the juveniles, when these emerged, they tested the idea that 'slow' species are more abundant among adults than among recruits, since the adults of 'slow' species persist longer. The data confirmed this expectation. They also showed that the slow species are more common, relative to fast species, when breeding opportunities occur less frequently in the field. A further prediction is that specialist species (which can only develop on a narrow range of resource types) will be 'slower' than more-generalist species, since specialists perceive a lower frequency of breeding opportunities. Comparison of 15 species from the community showed that species with longer developmental periods were indeed more specialized than fast-developing species.

This field evidence only provides circumstantial support to the model since, whereas Sevenster and van Alphen's modelling and laboratory experiments contained limited, or no, spatial and temporal variability, such variability is omnipresent in the field. Heterogeneity in

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