Genetic relatedness and group size in an aggregation economy

LUC-ALAIN GIRALDEAU[1]* and THOMAS CARACO[2]

[1]*Department of Biology, Concordia University, 1455 ouest, Bd de Maisonneuve, Montréal, Québec, Canada H3G IM8*
[2]*Department of Biological Science, State University of New York, Albany, NY, USA*

Summary

We use Hamilton's Rule to investigate effects of genetic relatedness on the predicted size of social groups. We assume an aggregation economy; individual fitness initially increases with group size, but in sufficiently large groups each member's individual fitness declines with further increments in the size of the group. We model two processes of group formation, designated free entry and group-controlled entry. The first model assumes that solitary individuals decide to join groups or remain alone; group size equilibrates when solitaries no longer choose to join. The second model allows group members to regulate the size of the group, so that the predicted group size results from members' decisions to repel or accept intruding solitaries. Both the Nash equilibrium group size and any change in the equilibrium caused by varying the level of relatedness depend on the particular entry rule assumed. The largest equilibrium group size occurs when solitaries choose between joining or not joining and individuals are unrelated. Increasing genetic relatedness may reduce and can never increase, equilibrium group size when this entry rule applies. The smallest equilibrium group size occurs when group members choose between repelling or accepting intruders and individuals are unrelated. Under this entry rule, increasing genetic relatedness can increase and can never decrease, equilibrium group size. We extend the models' predictions to suggest when individuals should prefer kin vs non-kin as members of the same group.

Keywords: group size; inclusive fitness; Nash equilibrium; relatedness; sociality

Introduction

It has frequently been argued that genetic relatedness implies larger group sizes in social foragers. For instance, Rodman (1981) discussed groups composed of relatives and suggested that the group size maximizing each member's inclusive fitness always exceeds the associated group size where individual (i.e. direct) fitness attains a maximum. Smith (1981; 1985) proposed a similar argument for apparently supra-optimal hunting group sizes of the Inuit people inhabiting the Arctic. We examine the predicted positive effect of relatedness on group size because previous analyses share two questionable assumptions. First, proponents have assumed that group size should always maximize each member's fitness, that is, the prediction neglects stability considerations (reviewed by Giraldeau, 1988). Second, the prediction sometimes has been based on a common, but erroneous, definition of inclusive fitness: the 'simple weighted sum' (see Grafen, 1982). We consider each point in turn.

---

* To whom correspondence should be addressed.

Optimal and equilibrium group size

Let G represent group size. $\Omega(G)$ is the direct fitness of each of the G identical group members. To begin, we summarize models of equilibrium group size which treat G as a continuous variable (Sibly, 1983; Clark and Mangel, 1984; Pulliam and Caraco, 1984).

Sociality can be advantageous when $\Omega(G)$ defines an aggregation economy, implying that fitness initially increases with group size, that is, $(d\Omega/dG)_{G=1} > 0$. However, in a sufficiently large group, competition among the members ordinarily must cause fitness to decline with further increases in group size. Consequently, we restrict attention to 'peaked' fitness functions (Clark and Mangel, 1986), that is, we assume fitness is a non-negative quantity $(\Omega(G) \geq 0 \; \forall G)$ attaining a maximum at a unique $G = G^* \geq 2$. Therefore, $d\Omega/dG = 0$ and $d^2\Omega/dG^2 < 0$ only when $G = G^*$, so that G^* is an 'optimal' group size of two or more members.

Assume that groups form as solitary individuals decide to live socially and that an individual can enter any group at no cost (Sibly, 1983). Since $\Omega(G)$ is peaked, two cases are possible, but not equally probable. If

$$\lim_{G \to \infty} \Omega(G) > \Omega(G = 1) \tag{1}$$

every member of a model population could coalesce into a single group, since solitaries always increase their direct fitness by joining any group they encounter. Aggregation economies, however, will rarely be so beneficial; extremely large groups are more likely to form in response to spatial heterogeneity of resources than to benefits of sociality *per se* (Pulliam and Caraco, 1984). In the more probable case, Inequality 1 is reversed and we can predict a Nash equilibrium group size $G^\wedge$ where

$$\Omega(G^\wedge) = \Omega(G = 1) \tag{2}$$

Solitaries should join a group of size G as long as $\Omega(G + 1) > \Omega(1)$, since joining increases fitness. When group size has increased to $G^\wedge$ a solitary no longer gains fitness by joining that group. No group member is tempted to leave unilaterally, since departure does not offer a fitness increment. Therefore, $G^\wedge$ qualifies as a (neutrally stable) Nash equilibrium.

Since $\Omega(G)$ is peaked, it follows that $G^\wedge$ is unique and $(d\Omega/dG)_{G^\wedge} < 0$. Therefore, $G^\wedge > G^*$; free entry of solitaries predicts that group size will exceed the optimum G^* at competitive equilibrium (Sibly, 1983; Clark and Mangel, 1984; Pulliam and Caraco, 1984; see Giraldeau and Gillis, 1985). A similar approach should apply when a minimally required fitness value constrains the maximally sized group a solitary will join (see e.g. Caraco and Wolf, 1975).

Treating G as continuous is a simplifying convention. We can restrict G to positive integers and obtain the same results, that is, the first difference $\Delta\Omega(G)$, where $\Delta\Omega(G) = \Omega(G + 1) - \Omega(G)$, is positive for all $G < G^*$ and negative for all $G \geq G^*$. Hence, $\Delta\Omega(G) < 0$ around the Nash equilibrium $G^\wedge$.

Relatedness and group size

This section examines 'optimal' and equilibrium group size when members are genetically related, so that the economic analysis involves inclusive fitness. Inclusive fitness is often divided into a direct and an indirect component. The direct component encompasses benefits to self, while the indirect component refers to the net effect self exerts on benefits to its relatives, devalued by the coefficient of relatedness r. Grafen (1982) points out that some calculations of inclusive fitness have suffered from 'double-accounting', which inflates the indirect component of

inclusive fitness. Double-accounting consists of including all the benefits kin accrue, rather than only the extra portion that can be attributed to self's behaviour. In the context of group membership decisions, avoiding double-accounting implies that the indirect component should not include the benefits relatives already enjoyed before self joined the group (Grafen, 1982, 1991; Giraldeau, 1988; Giraldeau and Gillis, 1988). Our analysis will show that properly transforming the direct fitness function Ω into inclusive fitness changes the equilibrium (kin) group size in a manner that is dependent on the rules of entry.

Free entry assumes that solitaries can decide whether or not to join a group. Under group-controlled entry, group size is regulated by members deciding whether or not to repel joiners. Our results show that in the absence of genetic relatedness, equilibrium group size is usually larger (and never smaller) for free entry than for group-controlled entry. However, increasing genetic relatedness ordinarily decreases equilibrium group size under free entry and increases the equilibrium size under group-controlled entry.

To examine how relatedness between members of a population can affect group-membership decisions (and, hence, group size), we shall use Hamilton's Rule (see Grafen, 1991). Imagine a forager in an aggregation economy where all members of the population are genetically related by coefficient r. Hamilton's Rule proposes that an act can be selectively favoured when $rB - C > 0$, where B represents the net benefit of the act on all relatives at which it is directed and C is the cost of the action on self. The terms of Hamilton's rule refer to the evolution of altruism. Indeed, by definition, altruism must impose a cost on self and provide a benefit to others. However, Hamilton's Rule applies to the economics of any behaviour, once the effects of feasible actions on B and C are specified. With respect to group membership, the effect that joining (or leaving) a group has on self may be positive or negative, depending on group size. Similarly, the effects on others can also be positive or negative, depending on group size. In this context, therefore, it is better not to use the terms benefit and cost to refer to effects on relatives and self respectively. We replace B by E_R, the total effect on relatives and replace C by E_S, the effect on self. For decisions concerning membership in groups with free entry, Hamilton's Rule becomes as follows. Any individual encountering a group of relatives should join the group when

$$rE_R + E_S > 0 \tag{3}$$

To calculate the effect on relatives, E_R, resulting from the actions of self, we must subtract the direct fitness enjoyed by the relatives before self joins the group from the fitness resulting from the addition of self to the group. Suppose self joins a group of $(G-1)$ relatives and, thus, increases the group's size to G. The effect on each of self's $(G-1)$ relatives in the group is $\Omega(G) - \Omega(G-1) = \Delta\Omega(G-1)$. The total effect E_R on the $(G-1)$ relatives is

$$E_R = (G-1)\,\Delta\Omega(G-1) \tag{4}$$

E_S, the effect of joining the group on self, is given by the direct fitness of membership in a group of size G, $\Omega(G)$, minus the direct fitness of self in its alternate state, solitary foraging,

$$E_S = \Omega(G) - \Omega(1) \tag{5}$$

Assuming free entry of solitaries into groups, Inequality 3 implies that self should join a group when the resulting group size renders $rE_R + E_S > 0$. Since $\Omega(G)$ is peaked, the equilibrium group size for relatives should be the largest group where this inequality is not reversed (since reversal indicates decreased inclusive fitness). To specify how relatedness influences equilibrium group size, we simply substitute Equations 4 and 5 into Inequality 3; the result indicates that a solitary should join a group of size $(G-1)$ whenever

$$r(G-1) \; \Delta\Omega(G-1) + [\Omega(G) - \Omega(1)] > 0;$$
$$r(G-1) \; [\Omega(G) - \Omega(G-1)] + \Omega(G) > \Omega(1) \tag{6}$$

The left-hand side of Inequality 6 varies with both coefficient of relatedness and group size, but $\Omega(1)$ is a non-negative constant. We can rewrite Inequality 6 as:

$$H(r, G) > \Omega(1) \tag{7}$$

If $r = 0$, Inequalities 6 and 7 define $G\hat{}$ for the discrete case, that is, $H(r=0, G\hat{}) = \Omega(G\hat{} > \Omega(1) > \Omega(G\hat{} +1)$ when $G\hat{}$ is a stable equilibrium and $\Omega(G\hat{} = \Omega(1) > \Omega(G\hat{} +1)$ when $G\hat{}$ is neutrally stable.

We assume r is continuous on $[0, 1]$ and use Inequality 6 to emphasize that $H(r, G)$ depends linearly on the value of r:

$$H(r, G) = \Omega(G) + (G-1) \; \Delta\Omega(G-1) \; r \tag{8}$$

The slope of the line, for $0 < r \le 1$, will be positive or negative according to the sign of $\Delta\Omega(G-1)$

First, suppose that a solitary encounters a group that is smaller than the optimum, so that $2 \le G \le G^*$. For any such G, $\Omega(G) > \Omega(1)$. Since $\Delta\Omega(G-1) > 0$ for $G \le G^*$, we have

$$\partial H(r, 2 \le G \le G^*)/\partial r > 0 \tag{9}$$

Therefore, $H(0 \le r \le 1, 2 \le G \le G^*) > \Omega(1)$. Inequality 7 always holds, so that $rE_R + E_S > 0$ for every value of r. Thus a solitary, should always join any group of (G^*-1) or fewer members, independently of the degree of relatedness.

If a solitary encounters a group that is larger than $G\hat{}$ then $\Omega(G) < \Omega(1)$ and $\Delta\Omega(G) < 0$. Therefore, $H(0 \le r \le 1, G > G\hat{}) < \Omega(1)$. Inequality 7 can never hold and $rE_R + E_S < 0$ for every value of r. A solitary, therefore, will never be selected to join a group of $G\hat{}$ or more members, independently of the degree of relatedness. Since $G\hat{}$ is the equilibrium group size for $r = 0$, increasing relatedness apparently does not increase group size beyond $G\hat{}$ under free entry.

In combination, the two preceding paragraphs indicate that, independently of relatedness, the equilibrium group size must contain at least G^* members and no more than $G\hat{}$ members. Consequently, any influence of relatedness on the decision to join a group must involve $H(r, G^* < G \le G\hat{})$.

Suppose $\Omega(G\hat{}) = \Omega(1)$. Then $G\hat{}$ cannot remain a Nash equilibrium for any $r > 0$. Above we assume that $G^* < G\hat{}$, implying that $\Delta\Omega(G\hat{} -1) < 0$. Applying Equation 8 to this case yields $H(0 < r \le 1, G\hat{}) < \Omega(1)$. Inequality 7 again cannot hold, so that $rE_R + E_S < 0$. Therefore, a solitary will not be selected to join a group of $(G\hat{} -1)$ members when $r > 0$. That is, $G\hat{}$ exceeds the equilibrium when individuals are related and the equilibrium group size must satisfy $G^* \le G < G\hat{}$. Relatedness cannot increase, but rather can decrease the equilibrium group size under free entry. This conclusion remains true for $\Omega(G\hat{}) \ge \Omega(1)$.

Continuing, recall that $\Omega(G) > \Omega(1)$ for $G^* < G < G\hat{}$. But $\Delta\Omega(G-1) < 0$ for each of these group sizes, so that

$$\partial H(r, G^* < G < G\hat{})/\partial r < 0 \tag{10}$$

$H(r, G)$ initially exceeds $\Omega(1)$, but declines as r increases. For at least the largest of these values of G (and possibly for all), $H(1, G) < \Omega(1)$, since there must be an equilibrium group size. For any such G, there is a critical level of relatedness r_G:

$$r_G = \frac{\Omega(G) - \Omega(1)}{(G-1) \; [\Omega(G-1) - \Omega(G)]} \tag{11}$$

Table 1. Numerical example of equilibrium group size when solitaries have free entry into groups of size $(G - 1)$

| | Group size (G) | | | | | | | |
	1	2	3	4	5	6	7	8
$\Omega(G)$	5	10	11	9	6	4	2	1
$E_S = \Omega(G) - \Omega(1)$	–	5	6	4	1	−1	−3	−4
$E_R = (G-1)\,[\Omega(G) - \Omega(G-1)\,]$	–	5	2	−6	−12	−10	−12	−7
$r\,E_R + E_S$								
$r = 0$	–	5	6	4	1[a]	−1	−3	−4
$r = 0.1$	–	5.5	6.2	3.4[a]	−0.2	−2	−4.2	−5
$r = 0.2$	–	6	6.4	2.8[a]	−1.4	−3	−5.4	−5
$r = 0.3$	–	6.5	6.6	2.2[a]	−2.6	−4	−6.6	−6
$r = 0.4$	–	7	6.8	1.6[a]	−3.8	−5	−7.8	−7
$r = 0.5$	–	7.5	7	1[a]	−5	−5	−9	−8
$r = 1.0$	–	10	8[a]	−2	−11	−11	−15	−11

[a] The equilibrium group size is the largest group for which $rE_R + E_S$ is positive for each level of r. When $r = 0$, the equilibrium group size is $G^{\wedge} = 5$. The equilibrium size decreases as r increases; the equilibrium is $G^* = 3$ when $r = 1.0$

If $r < r_G$, $H(r,\ G^*<G<G^{\wedge}) > \Omega(1)$. Equivalently, $rE_R + E_S > 0$, so that a solitary enhances its inclusive fitness by joining and therefore increasing the group size to G. Consequently, the equilibrium group size must be at least G. If $r > r_G$, $H(r,\ G^*<G<G^{\wedge}) < \Omega(1)$. In this case $rE_R + E_S < 0$. Now a solitary should not join the group and G must exceed the equilibrium size defined by the inclusive fitness criterion. For G between G^* and $G^{\wedge}$, greater relatedness can sometimes reduce the equilibrium group size. In fact, if $r > r_G$ evaluated at $G = (G^* + 1)$, the equilibrium group size will be as small as the 'optimal' group size G^*.

For free entry, group size increases as long as $rE_R + E_S > 0$. The minimal group size where adding an additional member reverses this inequality is the equilibrium group size. Suppose $r > 0$ and the equilibrium group size G exceeds G^*. Then G must satisfy $G^* < G < G^{\wedge}$, so that $\Delta\Omega(G) < 0$ for each G. Since G is the equilibrium

$$H(0<r\leq1,\ G) > \Omega(1) > H(0<r\leq1,\ G+1) \tag{12}$$

From Equation 8, the equilibrium group size is the maximal value of G where

$$\frac{\Omega(G+1) - \Omega(1)}{r[\Omega(G) - \Omega(G + 1)]} < G < 1 + \frac{\Omega(G) - \Omega(1)}{r[\Omega(G-1) - \Omega(G)]} \tag{13}$$

The general conclusion of the preceding analysis is that increasing relatedness will ordinarily decrease, and will never increase, equilibrium group size under free entry. Table 1 illustrates these results with a numerical example. Given the table's values for $\Omega(G)$, $G^* = 3$ and $G^{\wedge} = 5$. As r increases from 0 to 1.0, the inclusive fitness calculations show that the equilibrium group size for free entry decreases from 5 to 3.

Table 1 presents an example where the optimal group size G^* becomes the Nash equilibrium for $r = 1.0$. It might not be surprising that competitive and cooperative strategies can sometimes converge if individuals are genetically identical. Note, however, that the equilibrium group size does not always decrease as far as G^* when r increases to 1.0. For example, suppose that $\Omega(4)$ is increased from 9 to 10 in Table 1. The equilibrium group size for $r = 1.0$ is now $G = 4 > G^* = 3$. In this case a solitary encountering a group of G^* members increases its direct fitness (E_S) five

units by joining. The consequent collective effect on its genetically identical relatives (E_R) is a loss of three units. Then, $rE_R + E_S > 0$ and the equilibrium exceeds the optimum at $r=1.0$.

Group-controlled entry

The results in the previous section assume unrestricted access to group membership. Group members, however, will not always be indifferent to joiners (e.g. Vehrencamp, 1983). Therefore, we ask whether relatedness will also affect a group member's tendency to repel joiners. For simplicity we assume that all group members collectively expel the joiner when Hamilton's Rule favours preventing a solitary from increasing the size of the group. For this application the rule becomes: repel a solitary attempting to increase group size from G to $(G + 1)$ when $rE_R + E_S >$ 0. The terms E_R and E_S must be redefined to reflect the new decision being analysed. E_R is now the effect of repelling an intruding relative on the intruder:

$$E_R = \Omega(1) - \Omega(G+1) \tag{14}$$

Equivalently, the effect per group member is E_R/G. E_S is now the effect of repelling the intruder on self, where self is the entire group:

$$E_S = G[\Omega(G) - \Omega(G+1)] \tag{15}$$

Equivalently, the effect per group member is $-\Delta\Omega(G)$.

Each group member should choose to repel an intruder when $rE_R + E_S > 0$ and should accept an intruder when the inequality is reversed. Using Equations 14 and 15 repelling is favoured when

$$r[\Omega(1) - \Omega(G+1)] + G[\Omega(G) - \Omega(G+1)] > 0;$$
$$[\Omega(1) - \Omega(G+1)] (r/G) > \Delta\Omega(G) \tag{16}$$

We again assume $\Omega(G)$ is peaked and $\Omega(1) = \Omega(G^\wedge)$.

Initially, suppose that $1 \leq G \leq (G^* - 1)$. For any such G, $\Delta\Omega(G) > 0$ and $[\Omega(1) - \Omega(G+1)] < 0$, by the definition of G^*. Therefore, Inequality 16 cannot hold for any value of r and $rE_R + E_S < 0$. A group of (G^*-1) or fewer members should never repel a joiner, independently of the level of relatedness, since each addition to the group increases each group member's fitness.

For completeness, suppose $G \geq G^\wedge$. Then $\Delta\Omega(G) < 0$ and $[\Omega(1) - \Omega(G+1)] > 0$ by the definition of $G^\wedge$. Therefore, Inequality 16 always holds, so that $rE_R + E_S < 0$ for every value of r. Repelling joiners would be favoured, independently of relatedness.

Clearly, the equilibrium group size must contain at least G^* members and less than $G^\wedge$ members. The latter point shows that group-controlled entry, independently of the value of r, ordinarily will maintain each group member's fitness above $\Omega(G^\wedge)$, hence, above a solitary's fitness $\Omega(1)$.

For every possible equilibrium group size G, where $G^* \leq G < G^\wedge$, $\Delta\Omega(G) < 0$. If $r = 0$, Inequality 16 must then always hold. Equivalently, repelling is favoured at each group size. For $r = 0$, the largest group to accept a joiner is $(G^* - 1)$; G^* is consequently the equilibrium group size when individuals are unrelated. Since $G^* < G^\wedge$, group-controlled entry results in a smaller equilibrium group size than does free entry when groups are composed of unrelated individuals.

If $0 < r \leq 1$, Inequality 16 might be reversed, so that the equilibrium group size increases as relatedness increases. For example, if $G = G^*$, Inequality 16 indicates that a joiner should be repelled unless r is large enough to satisfy

$$r[\Omega(1) - \Omega(G^*+1)] < G^*[\Omega(G^*+1) - \Omega(G^*)] < 0 \tag{17}$$

Table 2. Numerical example of equilibrium group size[a] when groups of size G can repel solitary joiners

	Group size (G)							
	1	2	3	4	5	6	7	8
$\Omega(G)$	5	10	11	10.5	10	8.5	6	4
$E_S = G[\Omega(G) - \Omega(G{+}1)]$	−5	−2	1.5	2	7.5	15	14	−
$E_R = \Omega(1) - \Omega(G{+}1)$	−5	−6	−5.5	−5	−3.5	−1	1	−
$r\,E_R + E_S$								
$r = 0$	−5	−2	1.5[b]	2	7.5	15	14	−
$r = 0.1$	−5.5	−2.6	0.9[b]	1.5	7.1	14.9	14.1	−
$r = 0.2$	−6	−3.2	0.4[b]	1	6.8	14.8	14.2	−
$r = 0.3$	−6.5	−3.8	−0.1	0.5[b]	6.45	14.7	14.3	−
$r = 0.4$	−7	−4.4	−0.7	0[b]	6.1	14.6	14.4	−
$r = 0.5$	−7.5	−5	−1.2	−0.5	5.7[b]	14.5	14.5	−
$r = 1.0$	−10	−8	−4	−3	4[b]	14	15	−

[a] The equilibrium group size is the smallest group for which $rE_R + E_S$ is positive.
[b] Equilibrium group size for each level of r.

If Inequality 17 holds, $rE_R + E_S < 0$ and the group of size G^* should not repel a joiner. If neither G^* nor $|\Delta\Omega(G^*)|$, is too large, a given value of r will be more likely to make Inequality 17 true. When there are few group members to incur a decline in fitness as group size increases (i.e. small G^*), it is less likely that a related intruder will be repelled. A small $|\Delta\Omega(G^*)|$ suggests that the effect on self is less likely to offset the indirect benefit to the related joiner. Increased relatedness can increase and will never decrease, the equilibrium group size under group-controlled entry.

For group-controlled entry, group size increases until $rE_R + E_S > 0$. The minimal group size satisfying this inequality is the equilibrium group size, since it is the smallest group to repel, rather than accept, a joiner. Suppose $r > 0$ and the equilibrium group size G exceeds G^*. Then $G^* < G < G^{\wedge}$ and $\Delta\Omega(G) < 0$ for each G. The equilibrium group size will be the maximal value of G where

$$\frac{r[\Omega(G{+}1) - \Omega(1)]}{\Omega(G) - \Omega(G{+}1)} < G < 1 + \frac{r[\Omega(G) - \Omega(1)]}{\Omega(G{-}1) - \Omega(G)} \tag{18}$$

Increasing relatedness can increase and will never decrease, equilibrium group size under group-controlled entry. Table 2 illustrates these results. The equilibrium group size is $G^* = 3$ for $r = 0$, but increases to 4 when $r = 0.3$ and then to 5 for $r \geq 0.5$. Note, however, that for the values of $\Omega(G)$ used in Table 1, the equilibrium group size under group control remains 3 for every r in $[0, 1]$.

Discussion

We begin this section by comparing the two models. Then we mention some implications of our results for free entry and for group-controlled entry. Finally, we comment on group size as an asymmetric game between a solitary and a group.

We scaled the logic of our models so that a 'decision' taken because $(rE_R + E_S)$ is positive results in a group of G members. The two models are more similar than the resulting expressions for effects on the relative(s) and on self might suggest. For example, a solitary deciding to join another solitary (a group of one) is essentially identical to a group of one choosing not to repel a

joiner. More generally, suppose a group increases from m to $(m + 1)$ members. Let $E_R(f)$ and $E_S(f)$ represent the free-entry model's components of inclusive fitness, each evaluated at $G = (m + 1)$. Similarly, let $E_R(g)$ and $E_S(g)$ represent the group-controlled model's components of inclusive fitness, each evaluated at $G = m$. From the equations in the text we have $E_R(f) = -E_S(g)$ and $E_S(f) = -E_R(g)$. If the given increase in group size means that a group of m does not repel a joiner, then $rE_R(g) + E_S(g) < 0$. In terms of the free-entry model's elements, this expression is:

$$rE_S(f) + E_R(f) > 0 \tag{19}$$

Inequality 19 shows that the models predict group size changes in an economically symmetric manner, despite the important behavioural difference between free entry and group-controlled entry.

Group-controlled entry begins with the assumption that a solitary individual attempts to establish membership in the group. Free entry asks whether a solitary should or should not prefer group membership. Consequently, the model for free entry has a certain logical precedence over the group-controlled model; a group cannot repel unless a solitary tries to join. However, the group-controlled model may apply quite appropriately to questions concerning eviction of an individual from its natal unit or when social dominance relationships govern group composition. Group control may additionally prove important when changing ecological conditions, such as temporal variation in food availability, change the relationship between group size and fitness, so that the equilibrium group size becomes smaller.

The argument concerning the effect of genetic relatedness on the decision to join others is not new. For instance, Grafen (1986) reanalysed Noonan's (1981) data on the decision of female brown paper wasp (*Polistes fuscatus*) whether to join a nest and become a worker, establish a nest of her own as a solitary queen or simply die. He pointed out that the decision depended on the effect that joining had on relatives. In situations where relatedness is high, Grafen (1986) predicted that females would either join unrelated females or even prefer to die rather that be solitary queens. We apply the argument to a more general aggregation economy and consider the effects of group-entry rules.

Suppose the free-entry model applies. Then solitaries about to make a group-membership decision should respond to the extent of their genetic relatedness to group members. Many animals apparently act as if they recognize genetic relatives, based on preferences for kin as associates (Blaustein *et al.*, 1991). When such discrimination is possible, we can envisage certain patterns in group-membership decisions. First, assume that $G < G^*$. Individuals should prefer joining groups of relatives. Joining enhances inclusive fitness through both benefits to relatives and benefits to self. As relatedness between group members and the joiner increases, the indirect contribution to self's inclusive fitness increases. Thus, for a given E_R, solitaries should prefer joining groups with their closest relatives. A similar prediction arises for group-controlled entry when $G < G^*$. The members of the group always enhance direct fitness by not repelling a solitary, but the increase in inclusive fitness is greater when a more closely related individual joins the group.

Now assume free entry with $G \geq G^*$. Individuals might prefer to join groups of non-relatives. This would avoid the negative effect imposed upon relatives (hence, upon the decision-maker's inclusive fitness) when a solitary joins a group and inflates its size beyond G^*. Joining non-relatives could offer the opportunity to avert this effect. However, the prediction differs for group-controlled entry. When $G \geq G^*$, not repelling a new group member amounts to kin-selected altruism. Hence, the group should repel an intruder unless that individual is related so closely that the benefit to the relative overcomes the loss of direct fitness. It is important to realize

that these predictions involve G^*, not because it is the expected size of groups of relatives, but because it is the pivotal group size around which group-membership decisions are based. The analysis suggests that kin recognition occurs not only so that relatives can assort positively, but also so that relatives may (under different ecological conditions) avoid each other during group formation.

This note has two explicit purposes.

(1) To specify how relatedness enters the elements of decision rules that in turn influence group size in an aggregation economy.

(2) To emphasize that the inclusive fitness of every group member need not always attain a maximum at the equilibrium group size.

We analysed free entry and group-controlled entry separately since different processes will govern group formation in different social systems. Earlier analyses of equilibrium group size have uniformly assumed free entry. Our model suggests that predicted group sizes depend on the explicit assumptions concerning group entry. Groups of primates and social carnivores, for instance, might often control the entry of solitaries (Jansson, 1985), while free entry might often describe group formation in granivorous birds.

We could weaken assumptions about entry rules and model changes in group size as the outcome of an asymmetric game between a solitary and the group. Suppose, for example, that $G^* < G < G^{\wedge}$, $\Omega(G+1) > \Omega(1)$ and $r = 0$. A solitary's fitness would increase if it joined the group, but every current group member's fitness would decline. The interaction of the competing objectives can be portrayed by modifying the fitnesses to consider the cost of entry for the solitary and the cost of repelling an intruder for the group. The solution to the game, for different levels of relatedness, would indicate when changes in group size follow the free-entry rule and when group-controlled entry applies. Our arguments assume that relatedness does not affect the shape of the fitness function. Increased relatedness could, however, allow the evolution of qualitatively different social behaviour that alters group size effects on fitness and, consequently, influences the equilibrium group size.

Acknowledgements

Note added in proof

A different analysis of the group size problem has led to analogous conclusions concerning the effect of relatedness on group size (Higashi and Yanamura, 1993).

References

Blaustein, A.R., Bekoff, M., Byers, J.A. and Daniels, T.J. (1991) Kin recognition in vertebrates: what do we really know about adaptive value? *Anim. Behav.* **41**, 1079–83.

Caraco, T. and Wolf, L.L. (1975) Ecological determinants of group sizes of foraging lions. *Am. Nat.* **109**, 343–52.

Clark, C.W. and Mangel, M. (1984) Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.* **123**, 626–41.

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

Giraldeau, L.-A. (1988) The stable group and the determinants of foraging group size. In *The Ecology of Social Behavior* (C.N. Slobodchikoff, ed.), pp 33–53. Academic Press, NY, USA.

Giraldeau, L.-A. and Gillis, D. (1985) Optimal group size can be stable: a reply to Sibly. *Anim. Behav.* **33**, 666–7.

Giraldeau, L.-A. and Gillis, D. (1988) Do lions hunt in group sizes that maximize hunters' daily food returns? *Anim. Behav.* **36**, 611–3.

Grafen, A. (1982) How not to measure inclusive fitness. *Nature* **298**, 425–6.

Grafen A. (1986) Natural selection, kin selection and group selection. In *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs and N.B. Davies, eds), 2nd edn, pp. 62–84. Blackwell, Oxford, UK.

Grafen, A. (1991) Modelling in behavioural ecology. In *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs and N.B. Davies, eds), 3rd edn, pp. 5–31. Blackwell, Oxford, UK.

Higashi, M. and Yanamura, N. (1993) What determines the animal group size: insider–outsider conflict and its resolution. *Am. Nat.*, (in press).

Jansson, C.H. (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus appella*). *Behav. Ecol. Sociobiol.* **18**, 125–38.

Noonan, K.M. (1981) Individual strategies of inclusive-fitness-maximizing in *Polistes fuscatus* foundresses. In *Natural Selection and Social Behavior: Recent Research and New Theory* (R.D. Alexander and D.W. Tinkle, eds), pp. 18–44. Chiron Press, NY, USA.

Pulliam, H.R. and Caraco, T. (1984) Living in groups: is there an optimal group size? In *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs and N.B. Davies, eds), 3rd edn, pp. 122–47. Blackwell, Oxford, UK.

Rodman, P.S. (1981) Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. *Am. Nat.* **118**, 275–83.

Sibly, R.M. (1983) Optimal group size is unstable. *Anim. Behav.* **31**, 947–8.

Smith, E.A. (1981) The application of optimal foraging theory to the analysis of hunter–gatherer group size. In *Hunter–Gatherer Foraging Strategies* (B. Winterhalder and E.A. Smith eds), pp. 36–65. Chicago University Press, Chicago, USA.

Smith, E.A. (1985) Inuit foraging groups: some simple models incorporating conflicts of interest, relatedness, and central-place sharing. *Ethol. Sociobiol.* **6**, 27–47.

Vehrencamp, S.L. (1983) A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **31**, 667–82.