Group size and the resolution of insider–outsider conflict in animal societies

Sheng-Feng Shen [a],[*] , H. Kern Reeve [b] , Stephen T. Emlen [b] , Ming Liu [c] , Dustin Rubenstein [d]

[a] Biodiversity Research Center, Academia Sinica, Taipei, Taiwan
[b] Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, U.S.A.
[c] Department of Zoology, University of Oxford, Oxford, U.K.
[d] Department of Ecology, Evolution and Environmental Biology and Center for Integrative Animal Behavior, Columbia University, New York, NY, U.S.A.

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Although social group size and stability are key areas of interest for studying the evolution and maintenance of animal societies, the evolution of group membership control and how that affects the resulting group size have not been fully explored. Here we develop a game-theoretical model that considers how social and ecological factors jointly affect the resolution of conflict over group size between current group members (insiders) and potential joiners (outsiders). Our model predicts that group size will more closely approach the optimum for insiders when the potential conflict between insiders and outsiders is large, as well as when the cost of engaging in social conflict is high. We also show that the joining effort, repelling effort, cost of selfishness and genetic relatedness have interacting effects on conflict resolution between insiders and outsiders and, thus, on expected group size and structure. Our model further predicts that the expected group size will increase as genetic relatedness between insiders and an outsider increases, assuming that the direct fitness cost for insiders to accept an outsider is relatively large or that the benefit to the outsider joining is small. Ultimately, our model synthesizes previous insider–outsider conflict models to generate a framework for understanding the evolution of both group membership control and the size and structure of the resulting social groups.
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Group size is one of the defining traits of all animal societies (Wilson, 1975). Generally, the costs and benefits associated with different group sizes influence the optimal group size, or the size that maximizes the average direct fitness of group members (Alexander, 1974; Krause & Ruxton, 2002; Whitehead, 2008; Wilson, 1975). However, observed group sizes are often larger than the optimal size, suggesting that the optimal size may not actually be the most stable size (Pulliam & Caraco, 1984). As first proposed by Sibly (1983), a solitary, potential joiner (hereafter outsider) could benefit by joining a group even if doing so drives the group size to be larger than the optimum, as long as the fitness of joining is higher than that of remaining solitary. Similarly, the theory predicts that if floater intrusion pressure on a lone breeder (hereafter insider) is high, a solitary breeder may not repel outsiders from joining to form a group and breed, even if allowing them to join would lower the insider's fitness (Port & Johnstone, 2013). This

logic predicts that at the equilibrium group size, joining a social group provides little additional benefit over being solitary, raising the fundamental question of why grouping evolved in the first place (Giraldeaur, 1988; Higashi & Yamamura, 1993).

Despite the potential impacts on the evolution of group size if insiders could reject outsiders from joining social groups, most theoretical and empirical studies have focused on the 'dung fly model of sociality' (Dunbar & Shultz, 2010), which assumes that individuals freely distribute themselves in response to the shifting balance of the moment-by-moment costs and benefits of being in a group (Beauchamp & Fernandez-Juricic, 2005; Krause & Ruxton, 2002; Parravano & Reyes, 2008; Seno, 2006). The resulting associations are often called 'free-entry' groups because outsiders have little or no difficulty joining or moving among groups, and insiders can do little to prevent outsiders from joining. Biological examples of free-entry groups include many mating swarms of insects, schools of fishes, mixed-species foraging flocks of birds and herds of large herbivores in the East Africa savannah. Such 'free-entry' groups typically assume that either (1) potential joiners and group members both benefit from increased group

* Corresponding author.
 E-mail address: shensf@sinica.edu.tw (S. -F. Shen).

size or (2) group members do not benefit, but outsiders have control over joining.

In contrast to the free-entry groups that exist in species that form temporary associations, current group members actively control group membership (hereafter group membership control) in many highly social species that form more permanent social groups. Such groups typically have 'restricted entry' in the sense that current group members (insiders) can actively accept or repel potential joiners (outsiders), including offspring trying to recruit into their natal group. Insiders thus choose which outsiders will become new members (Zöttl et al., 2013). Additionally, once accepted, outsiders become insiders and typically interact repeatedly with a consistent set of individuals who are themselves fellow group members. Many studies have also shown that in highly cooperative societies, the signals that convey individual identity become more heterogeneous among group members as the social group becomes larger (Pollard & Blumstein, 2011). Consequently, members of these groups are better able to recognize different individuals within the group (Tibbetts et al., 2017), and therefore better able to control group membership. Since both partner choice and repeated interactions are considered to be important mechanisms promoting the evolution of cooperation (Johnstone & Bshary, 2008; McNamara et al., 2008; Trivers, 1971), the evolution of group membership control represents an important transition in the evolution of highly cooperative societies. Examples of societies exhibiting group membership control include nearly all eusocial insects (Choe & Crespi, 1997), most cooperatively breeding birds and mammals (Koenig & Dickinson, 2004; Solomon & French, 1997) and mammalian species that form cooperative hunting and foraging groups (Giraldeau & Caraco, 2000).

Animal groups vary greatly in the probability that potential joiners can successfully join or move between groups. What explains this diversity of outsider accessibility to social groups? Moreover, what role do ecological and social factors play in determining where a particular animal aggregation fits into the 'free entry' − 'restricted entry' continuum? And how does group membership control influence the expected size and composition of 'restricted entry' social groups? Although these questions are important for understanding how animal societies form, they are rarely asked in studies of social evolution. For example, most studies of cooperative breeding behaviour emphasize the decision of mature offspring to either disperse, float or remain on their natal territory (Ekman et al., 2004; Emlen, 1982; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2004; Koenig et al., 1992; Stacey & Koenig, 1990). However, by viewing offspring as outsiders, and parents as insiders, we can reformulate the key question to consider how different social and ecological conditions influence the probability that an offspring will successfully join its natal group. Although researchers often assume that animal social groups consist exclusively of kin, since many animal societies actually contain a mix of related and unrelated individuals (Riehl, 2013), there is often conflict among insiders and outsiders over group membership (i.e. insider-outsider conflict; Higashi & Yamamura, 1993). For example, the eviction of group members, which has been observed in several cooperatively breeding species (Bell et al., 2012; Kappeler & Fichtel, 2012; Rueger et al., 2018; Thompson et al., 2017), is a type of insider−outsider that alters the relationship between group size and fecundity. Thus, examining the factors, both ecological and social, that influence social conflict and group membership control is critical for understanding why social groups vary in size and structure and, more broadly, how animal societies evolve in the first place.

Here, we construct a game-theoretical model extended from the tug-of-war model of reproductive skew (Reeve et al., 1998; Reeve & Shen, 2006; Shen & Reeve, 2010) that allows us to explicitly calculate the inclusive fitness of insiders and outsiders in order to examine how social conflict and group membership control influence social group formation and structure. We consider a series of factors that influence group membership, including the joining effort, repelling effort and the personal cost of selfishness, that can be modelled within the framework of insider−outside conflict (Higashi & Yamamura, 1993). In addition, we examine the impact of relatedness between outsiders and insiders on the evolution of optimal joining and repelling efforts and joining probabilities. Finally, we compare the optimal group sizes for related outsiders and unrelated outsiders and generalize the previous predictions that the ratio of the joining and repelling benefits fundamentally affects the evolution of group size. Ultimately, our model presents a theoretical framework that elucidates the dynamics of conflict and resolution between insiders and outsiders during the social group formation process, which will help us better understand the dynamics of social group formation.

MODEL BACKGROUND

The concept of insider−outsider conflict constitutes the basic framework for studying group membership, size and structure in group-living species. Insider−outsider conflict models formally summarize the potential conflict over group size between current group members (insiders) and potential joiners (outsiders) (Giraldeau & Caraco, 1993, 2000; Higashi & Yamamura, 1993). Early models examined both free-entry systems where any individual can easily join a group, as well as insider-controlled systems where the ability of current group members to control entry was assumed. However, the assumption of complete control in these models does not account for the occurrence of actual social conflict between insiders and outsiders because, under complete control, the subordinate party can have no payoff for resisting control.

To better understand the conflict between insiders and outsiders, we must therefore distinguish between two important but not mutually exclusive meanings of 'control.' First, as has been explicitly assumed in previous insider-control models (Giraldeau & Caraco, 1993, 2000; Higashi & Yamamura, 1993), control may imply that one party (e.g. either one of the insiders or the outsider) has an inherent competitive advantage over the other because of differences in body condition or fighting ability. Alternatively, 'control' could refer to which party's interests are most realized when the conflict over group membership is resolved in an evolutionarily stable way. This second meaning of 'control' seeks the probability that potential joiners will successfully join a group when there is a conflict between insiders and outsiders over whether group size should increase. Although previous models of insider−outsider conflict have addressed conflict resolution (Higashi & Yamamura, 1993; Yamamura & Higashi, 1992), these models posited that resolution was contingent upon a fixed maximum competitive cost that competitively disadvantaged individuals could bear. In essence, the individual reaching this maximum cost threshold first (e.g. at which point joining a group or repelling an outsider no longer offers any inclusive fitness advantage) would be deemed the loser in the competition. However, this proposed mechanism lacks biological plausibility, as it relies on a maximum competitive cost that one party can withstand. Consequently, the competitively disadvantaged individual will consistently reach this threshold, resulting in minimal additional benefits from group membership.

A more biologically realistic approach to solving this problem of group membership is to view each party as strategically maximizing the benefit-to-cost ratio of pushing for its own optimum group size, something that will depend on the relative joining and repelling efforts of the two parties. This approach allows for evolutionarily stable continuous strategies of joining or repelling.

Port and Johnstone (2013) developed such a game-theoretical model and explicitly considered the influence of demographic factors (e.g. an individual's mortality rate and fecundity, as well as the resulting population density) on insider–outsider conflict and group formation. They found that when floater densities are high, other social factors such as power asymmetry and conflicts of interest between insiders and outsiders have little influence on the formation of social groups. However, since the focus of that paper was on the role of demographic factors on group formation, the authors modelled social structure in a relatively simple manner with groups containing only a solitary breeder. In other words, the authors did not consider the possibility of group members jointly defending group membership, something that is likely to be a common and important feature of most animal societies (Shen et al., 2017).

THE MODEL

We construct a game-theoretical model that explicitly explores the evolutionarily stable levels of insiders repelling outsiders' joining efforts, which in turn determine the joining probability of a potential joiner seeking to join the group. In contrast to Higashi and Yamamura's model, which assumes that potential conflicts are resolved at the maximum cost that the weaker individual can bear (Higashi & Yamamura, 1993; Yamamura & Higashi, 1992), our model allows current group members to invest a continuous level of effort in cooperatively defending group membership. For simplicity, we assume no inherent asymmetries between insiders and outsiders. Instead, our model determines the probability that a potential joiner will successfully join a group when there is a conflict between insiders and outsiders over whether the group size should be increased. A lower value of the probability of successful joining indicates greater relative control (in the second sense above) of insiders over outsiders, even though we assume no differences in competitive ability between them. We then investigate the impact of critical social and ecological determinants (i.e. genetic relatedness, the group size–fecundity relationship, solitary breeding fecundity and personal costs of engaging in insider–outsider conflict) on the resolution of insider–outsider conflict. As a consequence, our model provides a framework for investigating insider–outsider conflict, the evolution of group membership control and the resulting social structure of animal societies.

To begin, consider a group of n current group members (the insiders, $n > 1$), where $f(n)$ denotes the mean direct fitness of each group member. For simplicity, we initially assume that groups are homogeneous in the sense that the direct fitness of all group members is the same (i.e. no reproductive skew). Assume further that if a potential joiner (an outsider) joins the group, then the mean direct fitness of each group member becomes $f(n + 1)$, whereas if the outsider does not join the group and instead remains solitary, then its direct fitness is $f(1)$.

No conflict over group membership is expected to occur if each individual has a higher direct interest in the larger group (i.e. $f(n + 1) > \max(f(n), f(1))$) or if no individual prefers to be in a larger group (i.e. $f(n + 1) < \min(f(1), f(n))$). The direct fitnesses of the insiders and the potential joiner (outsider) are all increased by the acceptance of the additional group member, which will also cause group size to increase. However, insider–outsider conflict over group membership (i.e. the 'battleground' of conflict; Cant, 2006; Godfray, 1995) is expected to occur when $f(n) > f(n + 1) > f(1)$. Under this condition, the outsider still gains fitness by joining the group because $f(n + 1) > f(1)$, but each insider loses fitness because $f(n) > f(n + 1)$. We then expect each individual to use its selfish

effort to achieve the best outcome (i.e. insiders in a repelling effort and outsiders in a joining effort). The probability that the outsider successfully joins the group will be determined by the relative magnitudes of the (combined) insiders' repelling efforts and the outsider's joining effort. Ultimately, the expected group size will then depend on this probability of joining, and the larger this probability, the larger the expected group size.

The group size–fitness functions (i.e. $f(1)$, $f(n)$ and $f(n + 1)$) can vary under different ecological conditions and also differ for the same species in different social contexts (e.g. foraging versus breeding). Thus, group size–fitness functions should be defined according to the organism's life history and the question of interest. Additionally, the number of insiders and outsiders also needs to be defined according to the question of interest. For example, in many cooperatively breeding vertebrates, mature offspring can be viewed as insiders in nonbreeding groups (Kleiber et al., 2007), but they become potential joiners at the beginning of the breeding season (Dickinson & McGowan, 2005). And since the group size–fitness functions are different in the two contexts, eviction can also be incorporated into our insider–outsider conflict framework. That is, the eviction of mature offspring from the breeding group is equivalent to the eviction of a related potential mate in the insider–outsider conflict model, as we described above.

Next, we let y represent the joining effort of the outsider, x the repelling effort of each insider, $y*$ the joiner's evolutionarily stable strategy (ESS) joining effort and $x*$ the ESS repelling effort of each of the insiders, where $0 < x$ and $y < 1$. We assume that each individual suffers a personal cost in terms of decreased future fitness with an increase in its selfish effort. The constant c, which we define as the cost exponent, measures how quickly future fitness declines as selfish effort increases (c is equivalent to the 'competitive intensity' in Reeve & Holldobler, 2007). Since the values of x and y must be between 0 and 1, the smaller the value of c, the greater the cost of selfish effort. Thus, the cost exponent for each insider is x^c, whereas the cost exponent for a potential joining outsider is y^c.

We also assume that a second exponent z controls the sensitivity to the outsider's probability of joining the group and is expressed as the ratio of its joining effort to the sum of the repelling efforts of the insiders. Said another way, z represents the effectiveness of cooperative repelling efforts among insiders. In particular, individuals' joining probabilities, p, are equal to $y^z/(y^z + nx^z)$ for outsider effort y and insider effort x (Cant, 2012; Reeve & Holldobler, 2007), which has been referred to as a contest success function in economics (see Hirshleifer, 1989). The 'effort component' is determined by the ecology of interest and the natural history of the organisms being studied. A large value of z indicates that the effect of an individual joining or repelling is relatively small (the larger z is, the smaller is x^z or y^z), but the cumulative effect of more individuals is relatively higher (nx^z). A higher value of z implies that the cumulative effects of eviction behaviours can be more efficient as more insiders perform them (i.e. the more insiders cooperate in chasing outsiders, the more effective they become). Conversely, a smaller z suggests that insiders are less likely to prevent outsiders from joining, for example when the distribution of resources is dispersed. As a result, the probability of an outsider joining is higher. Thus, the effort component measures the sensitivity of the probability of joining to the difference in selfish effort between insiders and outsiders.

Using the direct fitness approach of Taylor and Frank (1996), which is equivalent to the neighbour-modulated fitness approach of Hamilton (1964), we seek the evolutionarily stable joining and repelling efforts of outsiders and insiders, respectively. The direct fitness payoffs to a potentially joining outsider, w_o, and to each insider, w_i, are given by the equations

$$w_i = \frac{y^z}{x^z + (n-1)\bar{x}^z + y^z}f(n+1) + \frac{x^z + (n-1)\bar{x}^z}{x^z + (n-1)\bar{x}^z + y^z}f(n) - ax^c \tag{1a}$$

and

$$w_o = \frac{y^z}{n\bar{x}^z + y^z}f(n+1) + \frac{n\bar{x}^z}{n\bar{x}^z + y^z}f(1) - ay^c \tag{1b}$$

where $\bar{x}$ denotes the mean levels of the nonfocal insiders' repelling efforts in the population (Parker & Maynard Smith, 1990) and a is a scaling factor for the costs of insiders' and an outsider's repelling effort. We solve for the evolutionarily stable joining and repelling efforts proposed by Taylor and Frank (1996) by finding the positive values of x^* and y^* to satisfy the equations

$$\frac{1}{n+1}\frac{\partial w_i}{\partial x} + r_i\frac{n-1}{n+1}\frac{\partial w_i}{\partial \bar{x}} + r_o\frac{1}{n+1}\frac{\partial w_i}{\partial y} = 0 \tag{2a}$$

for $x = \bar{x} = x^*$, $y = y^*$ and

$$\frac{1}{n+1}\frac{\partial w_o}{\partial y} + r_o\frac{n}{n+1}\frac{\partial w_o}{\partial \bar{x}} = 0 \tag{2b}$$

for $x = \bar{x} = x^*$, $y = y^*$, where r_i and r_o represent the average genetic relatedness among insiders and the relatedness between insiders and an outsider, respectively.

Importantly, we do not assume that each individual has the same relatedness to other individuals. Instead, when an outsider who is related to the current insider joins the group (e.g. an offspring recruiting into its natal group), the outsider becomes a member of the group (i.e. an insider), so there is a new average relatedness among the insiders. Then, when faced with another outsider, the insiders will exert their repelling effort according to the new r_i. Thus, the evolutionarily stable joining probability p^* of an outsider is

$$p^* = \frac{y^*}{n\,x^* + y^*} \tag{3}$$

and the expected group size $E(n)$ is simply

$$E(n) = (n+1)p^* + n(1-p^*) \tag{4}$$

where $(n+1)p^*$ describes the case when a potential joiner successfully joins the group, and $n(1-p^*)$ describes the case when insiders successfully repel the outsider. Although it is not possible to derive a general analytical solution to equations 2a and 2b, we can calculate solutions numerically for the general model with any values of z and c. Because we have made every effort to explore the parameter space that we believe to be biologically realistic, we believe that our results have a degree of generality. However, as with all model results obtained using numerical solutions, our results apply only to the parameter space that we have explored.

RESULTS

Insider−outsider conflict will occur whenever $f(n) > f(n+1) > f(1)$. Within this conflict parameter space, p^* represents the joining probability of an outsider, which is determined by both competitive ability and the expected payoff of winning the competition. In the general model, we find that the joining probability p^* decreases as the number of insiders increases in all cases within the parameter space that we examined (Fig. 1). However, an outsider will have a lower joining probability p^* when the effort exponent z is large (Fig. 1a and b) or when the cost exponent c is

small (Fig. 1c and d). The large effort component represents less efficient investment in selfish effort and small cost exponents represent higher personal costs of engaging in the selfish effort because the values of the selfish efforts, x and y, are between 0 and 1. Thus, an individual's selfish effort decreases with an increase in the effort component (Appendix Fig. A1a) and with a decrease in the cost component (Appendix Fig. A1b). Consequently, when the personal cost of engaging in the selfish effort is high, the numerical advantage of having more insiders engaging in such efforts causes the cumulative repelling effort of the group to increase as a multiple of group size (as nx^*). As a consequence, insiders will have an increasing influence on p^* as group size increases, and groups will become more membership controlled as they get larger. Finally, the general model also shows that different values of the effort exponent z and the cost exponent c do not qualitatively change the predictions in the parameter space that we examined. Thus, we use the specific model, in which $z = 1$ and $c = 2$, to explore the model predictions in greater detail below.

Joining/Repelling Benefits and Genetic Relatedness

We found that the average genetic relatedness between insiders and the outsider (r_o), as well as the average insider's decrease in fecundity from accepting an outsider ($f(n) − f(n+1)$), referred to hereafter as the 'repelling benefit', have interacting effects on an outsider's joining probability p^*. The outsider's joining probability p^*, and thus the expected group size, decreases as r_o increases when the repelling benefit is small (when the insider's decrease in fecundity is small, e.g. $f(n+1) = 1.8$), but p^* increases as r_o increases when the repelling benefit is large (when the insider's decrease in fecundity is large, e.g. $f(n+1) = 1$; Fig. 2a and b). This intriguing nonlinear effect of relatedness on the joining probability results from the resolution of conflict between insiders and outsiders. From the insiders' perspective, as the repelling benefit decreases, the negative effect of accepting the outsider decreases (i.e. the benefit of repelling an outsider decreases) and the insiders' repelling efforts will also decrease (Fig. 2c, represented by the case of $r_o = 0.5$). Importantly, the results are qualitatively similar no matter which value of relatedness we choose. However, when the repelling benefit is large (i.e. when the average insider's decrease in fecundity from accepting an outsider is large), there is little incentive for an outsider to join a group. As $(f(n+1) − f(1))$, referred to hereafter as the 'joining benefit,' increases, the incentive for an outsider to join increases (i.e. the benefit of joining, denoted by the joining benefit increases) and an outsider will fight harder by expending more selfish effort to gain entry (Fig. 2d), while keeping $f(n)$ and $f(1)$ constant. However, if the genetic relatedness between insiders and an outsider is high, both insiders and the outsider invest lower levels of joining or repelling efforts because their genetic interests are more aligned (Fig. 2c and d, Appendix Fig. A1c). Similarly, if average genetic relatedness between insiders is high, the repelling effort of an insider will be higher and the joining effort of an outsider will be lower (Appendix Fig. A1d). In other words, the joining probability p^* becomes relatively less sensitive to $f(n+1)$ when the genetic relatedness between insiders and an outsider is high (Fig. 2).

Outsider Fecundity and Genetic Relatedness

The fecundity of a solitary outsider ($f(1)$) and r_o also have interacting effects on the joining probability p^*. An unrelated outsider has a higher joining probability p^* than a related outsider if $f(1)$ is lower, but a more closely related outsider has a higher joining probability p^* if $f(1)$ is higher (Fig. 3a). These intriguing predictions can be understood by inspecting the relationship
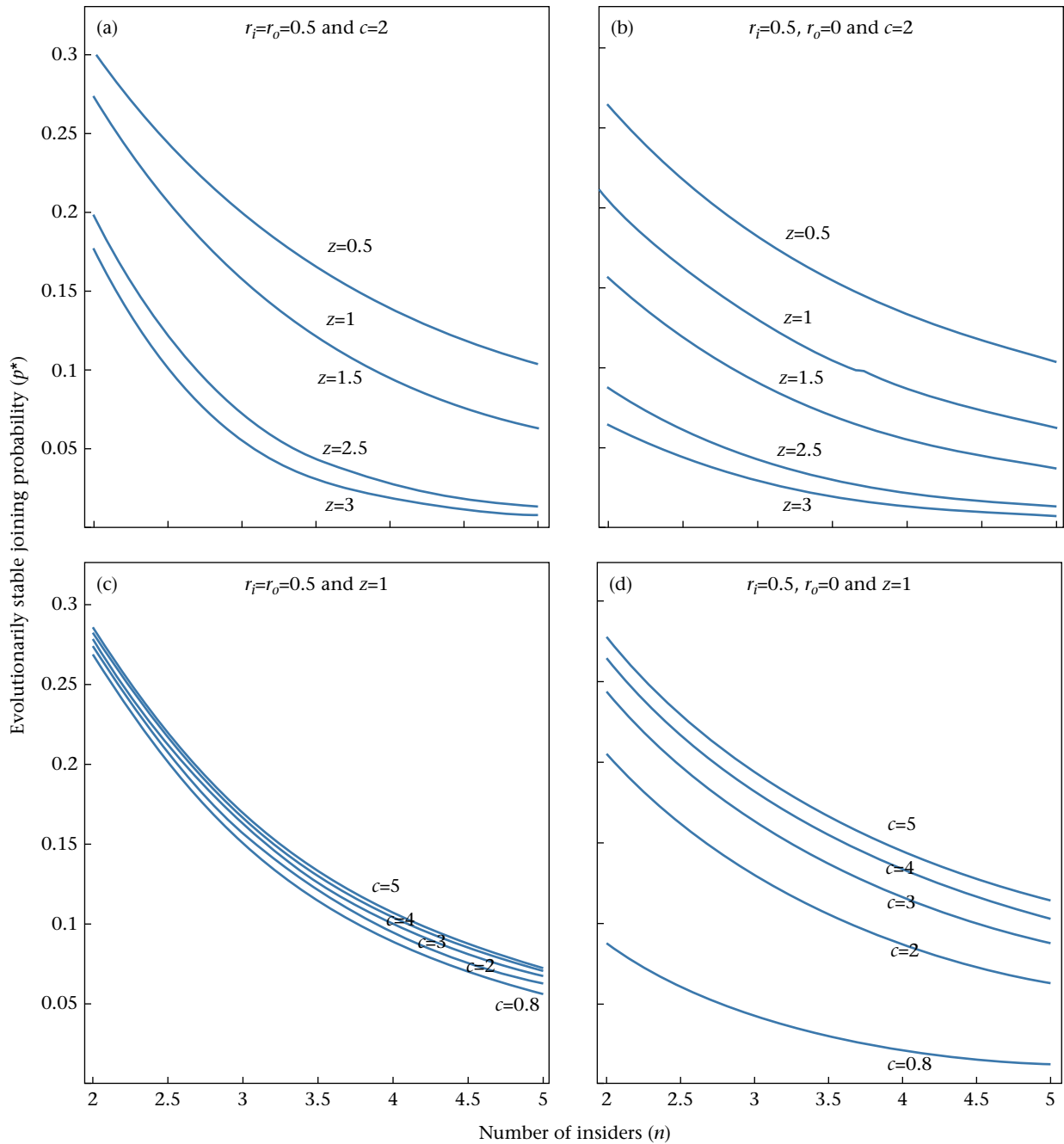
Figure 1. The joining probability $p*$ of an outsider in relation to the number of insiders n and (a) different values of the effort exponent z, at $c = 2$, $r_i = r_o = 0.5$, (b) different values of the effort exponent z, at $c = 2$, $r_i = 0.5$ and $r_o = 0$, (c) different values of the cost exponent c, at $z = 1$ and $r_i = r_o = 0.5$ and (d) different values of the cost exponent c, at $z = 1$, $r_i = 0.5$ and $r_o = 0$. Parameter values used in (a) to (d) are $f(n) = 2$, $f(1) = 0.8$, $f(n+1) = 1$ and $a = 0.5$. In the model, 'r_i' refers to the average genetic relatedness among the current group members, also known as insiders, and 'r_o' denotes the genetic relatedness between these insiders and a potential joiner, labelled as an outsider. The term '$f(n)$' describes the mean direct fitness of insiders when the group consists of 'n' current members. If the outsider remains solitary and does not join the group, its direct fitness is represented by '$f(1)$'. However, if the outsider decides to join, the resulting group size increases to '$n+1$', and its mean direct fitness is described by '$f(n+1)$'. Lastly, 'a' serves as a scaling factor that determines the repelling effort costs for both the insiders and the outsiders.

between the joining effort of an outsider and the repelling effort of insiders and $f(1)$ under different values of r_o. Both repelling effort and joining effort decrease as $f(1)$ increases (Fig. 3b and c, represented by the case of $r_o = 0.5$). However, the repelling efforts of the insiders decrease relatively more slowly than the joining effort until $f(1)$ is close to $f(n)$ when insiders are less related to the outsider, and vice versa (Fig. 3b and c). Nevertheless, in all cases, the joining probability will be smaller if the relatedness among insiders is higher (Figs 2 and 3).

Ecology, Genetic Relatedness and Expected Group Size

The expected group size is determined by the joining probability $p*$ of an outsider: the higher the joining probability, the larger the expected group size (Fig. 2). Given the insider—outsider conflict scenarios described above, our model predicts that the expected group size will decrease as relatedness between insiders and a potential joiner increases, provided that the negative impact of accepting an outsider's fecundity is low (Fig. 2b). However,
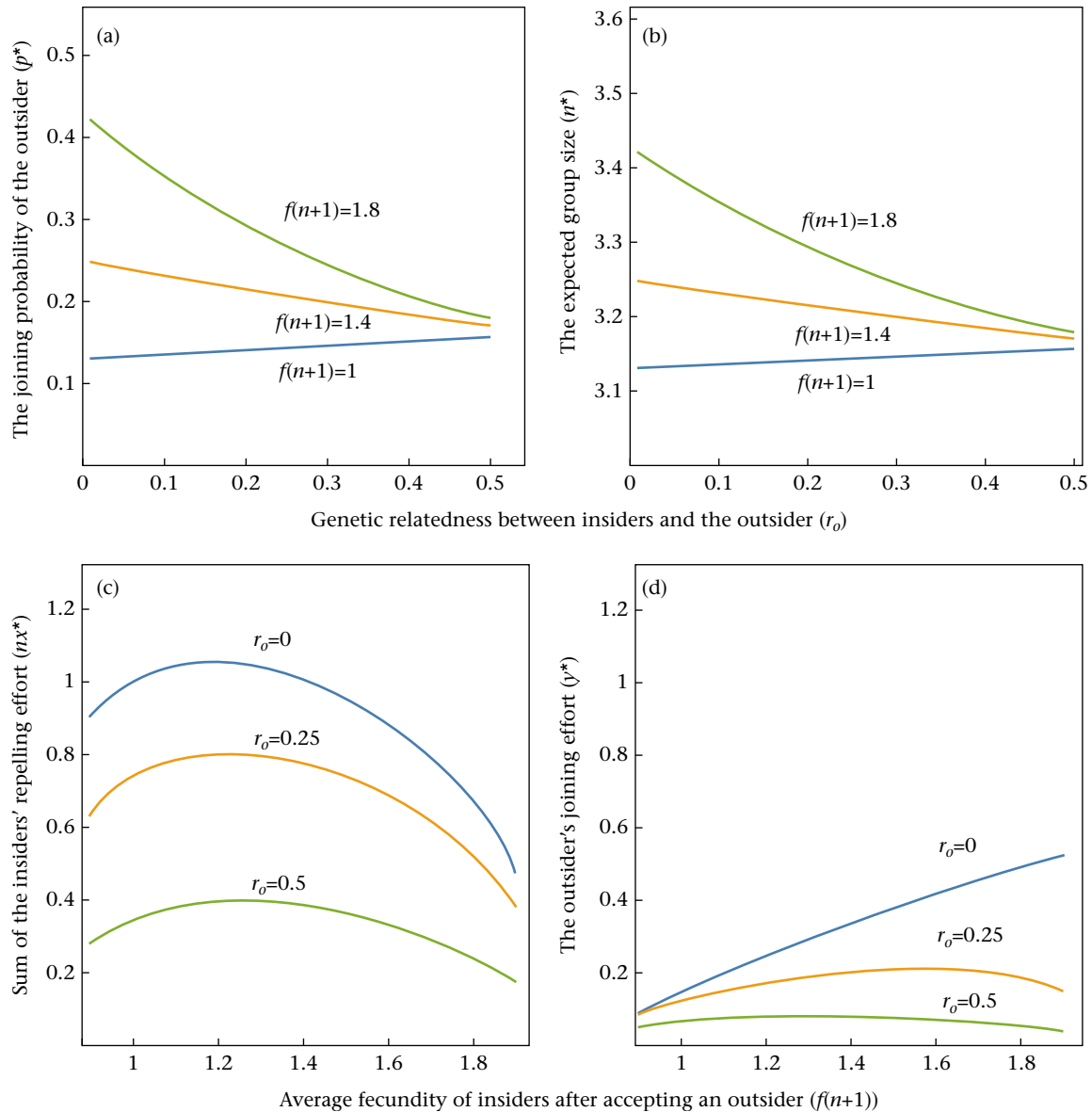
Figure 2. The (a) joining probability and (b) expected group size and insider–outsider conflict in relation to the average genetic relatedness r_o between insiders and an outsider and the average decrease in the insiders' direct fitness from accepting an outsider $f(n+1)$ at $f(1) = 0.8$, $f(n) = 2$ and $a = 0.5$ when genetic relatedness among insiders is $r_i = 0.5$. (c) The sum of the insiders' repelling effort and (d) an outsider's joining effort in relation to the average genetic relatedness r_o between insiders and the outsider and the average insiders' fecundity after accepting an outsider at $f(1) = 0.8$, $f(n) = 2$, $n = 3$ and $a = 0.5$, when genetic relatedness among insiders is $r_i = 0.5$.

expected group size will increase as relatedness between insiders and an outsider increases if the negative impact of accepting is high (Fig. 2b). For the same reason, the fecundity of a potential joiner also affects the expected group size: the lower the solitary joiner's fecundity, the larger the expected group size.

Finally, we explore the relationship among the expected group size, the joining benefit and the repelling benefit. We find that the lower the relatedness between outsiders and insiders, the more the group size is affected by the difference between the joining and repelling benefits (Fig. 4a). Surprisingly, group size is relatively stable when the relatedness between outsiders and insiders is high (Fig. 4a). Related outsiders are less likely to join when the joining benefit is greater than the insiders' per capita repelling benefit because, in this case, joining the group hurts the insider's direct fitness more, and therefore hurts the related outsider's inclusive fitness. Consequently, this region is called the 'region of sacrifice'

(see also Higashi & Yamamura, 1993), which represents cases in which the related outsiders sacrifice their direct interests to avoid harming relatives (Fig. 4b). Conversely, when the per capita repelling benefit is larger than the joining benefit, more closely related outsiders have a higher probability of joining than less related outsiders. Therefore, this parameter space, which we call the 'region of tolerance' after Higashi and Yamamura (1993), represents the region where insiders tolerate related outsiders because of their inclusive fitness, even though their direct interests are harmed (Fig. 4c).

DISCUSSION

The importance of group membership control for group size and structure has long been acknowledged (Giraldeau & Caraco, 1993, 2000; Giraldeaur, 1988; Higashi & Yamamura, 1993; Shen et al.,
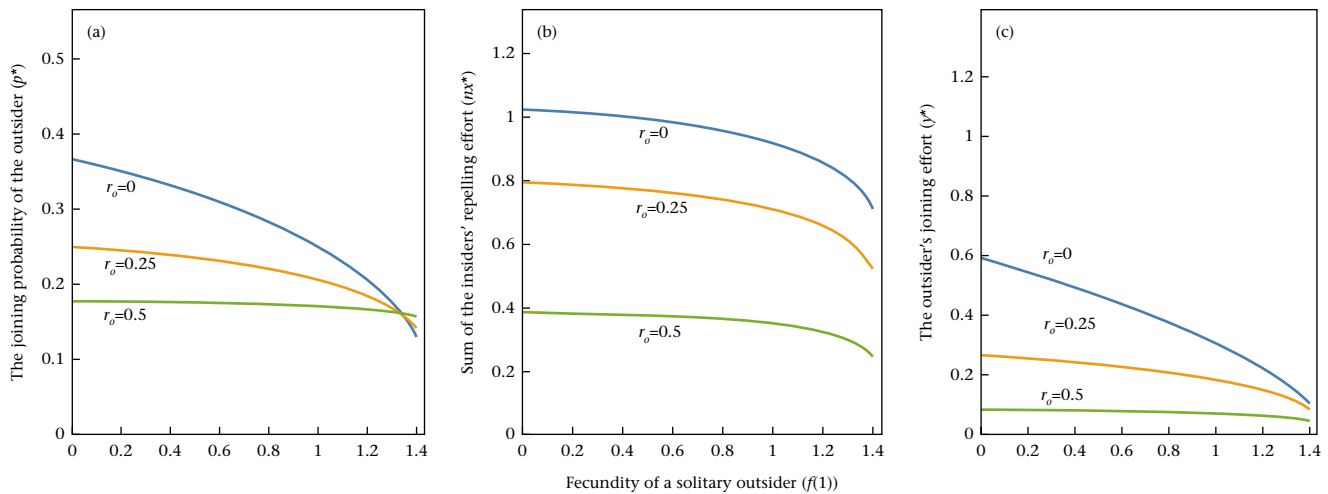
Figure 3. The joining probability and level of insider–outsider conflict in relation to the average genetic relatedness r_o between insiders and an outsider and the fecundity of a solitary outsider $f(1)$ at $f(n + 1) = 1.5$, $f(n) = 2$ and $a = 0.5$ when (a) genetic relatedness among insiders is $r_i = 0.5$. (b) The sum of the insiders' repelling effort and (c) an outsider's joining effort in relation to the average genetic relatedness between insiders and an outsider and the fecundity of a solitary outsider at $f(n + 1) = 1.5$, $f(n) = 2$, $n = 3$ and $a = 0.5$, when genetic relatedness among insiders is $r_i = 0.5$.

2017; Sibly, 1983). However, most previous theoretical models assumed that insiders had either complete control or no control over group membership (Giraldeau & Caraco, 1993, 2000), or that conflict was resolved at the maximum cost (Higashi & Yamamura, 1993; Yamamura & Higashi, 1992). By explicitly modelling the insiders' repelling effort and an outsider's joining effort as continuous strategies in a tug-of-war model framework (Reeve et al., 1998), we provide a game-theoretical model to generate novel predictions about levels of actual conflict ($y* + nx*$) and joining probabilities ($p*$) during the formation and maintenance of a social group. Thus, we are able not only to provide a theoretical framework for understanding the continuum in the degrees of group membership control found within and among social species (from 'free entry' to complete 'insider group membership control'), but also to explain why expected group size may either predictably increase or decrease as relatedness between insiders and outsiders increases, and predict actual levels of insider–outsider conflict during group formation. We discuss each of these results in greater detail below.

A Continuum in the Degree of Group Membership Control

Our results show that ecology and genetic relatedness have important interacting effects on the evolution of group membership control. Within the region of conflict (which is largely determined by ecological factors, since the payoffs of solitary breeding and group size–productivity relationships are both affected by ecology), an outsider's joining probability will always decrease as current group size increases because of the numerical advantage that insiders have for repelling a potential joiner. In addition, more closely related insiders will invest higher levels of repelling effort than less related insiders, resulting in membership control by insiders being more likely to evolve in kin groups. The relative cost of engaging in social conflict also has a critical effect on the resolution of conflict over group size. Our model predicts that if the cost of engaging in conflict is high (i.e. high-cost exponent or low-effort exponent), the ESS joining probability of an outsider will be lower. This result is important because it has been argued previously that the opposite was true (Beauchamp & Fernandez-Juricic, 2005). Thus, the numerical advantage of insiders will result in stable, restricted-access groups. In contrast, if there is little cost of engaging in social conflict, then free-entry groups are expected to

form. Thus, our model generates novel predictions for understanding interspecific and intraspecific variation in the degree of insider membership control in animal societies.

Group Size and Relatedness

Our model also emphasizes the need to study the effect of relatedness on expected group size. Although kinship has been the central focus in studying social behaviour since Hamilton (1964), there have been surprisingly few theoretical or empirical papers specifically addressing how kinship affects group size. Interestingly, our model predicts that the expected group size will decrease as genetic relatedness between insiders and an outsider (r_o) increases, if the insider benefits of repelling the outsider are small or the outsider benefits of joining are large. However, the expected group size will increase as r_o increases if the insider benefits of repelling the outsider are large or the outsider benefits of joining are small (Fig. 4). Previous insider–outsider conflict models (Giraldeau & Caraco, 1993, 2000; Higashi & Yamamura, 1993) predicted that the expected group size would decrease with an increase in genetic relatedness when outsiders have control of the group membership, which corresponds to the small joining benefit or large repelling benefit scenario in our model, and would increase with an increase in genetic relatedness when insiders have control over group membership, which corresponds to the large joining benefit or small repelling benefit scenario. Thus, without externally assumed membership control, our model essentially synthesizes these previous insider–outsider conflict models and provides a more general framework for understanding the important interacting effects of ecology and genetic relatedness on expected group size and group composition.

In addition to making novel predictions about the size and composition of kin groups, our model offers an alternative explanation for the evolution of nonkin groups, which are more common in vertebrates than once realized (Riehl, 2013). Previous models have mostly focused on mechanisms of how nonkin members cooperate and increase group productivity (i.e. cases where $f(n + 1) > f(n)$); Aviles et al., 2004; Kokko et al., 2001). For example, Kokko et al. (2001) proposed group augmentation as a mechanism for the formation of nonkin groups where individuals survive or reproduce better in large groups and where it, therefore, pays to
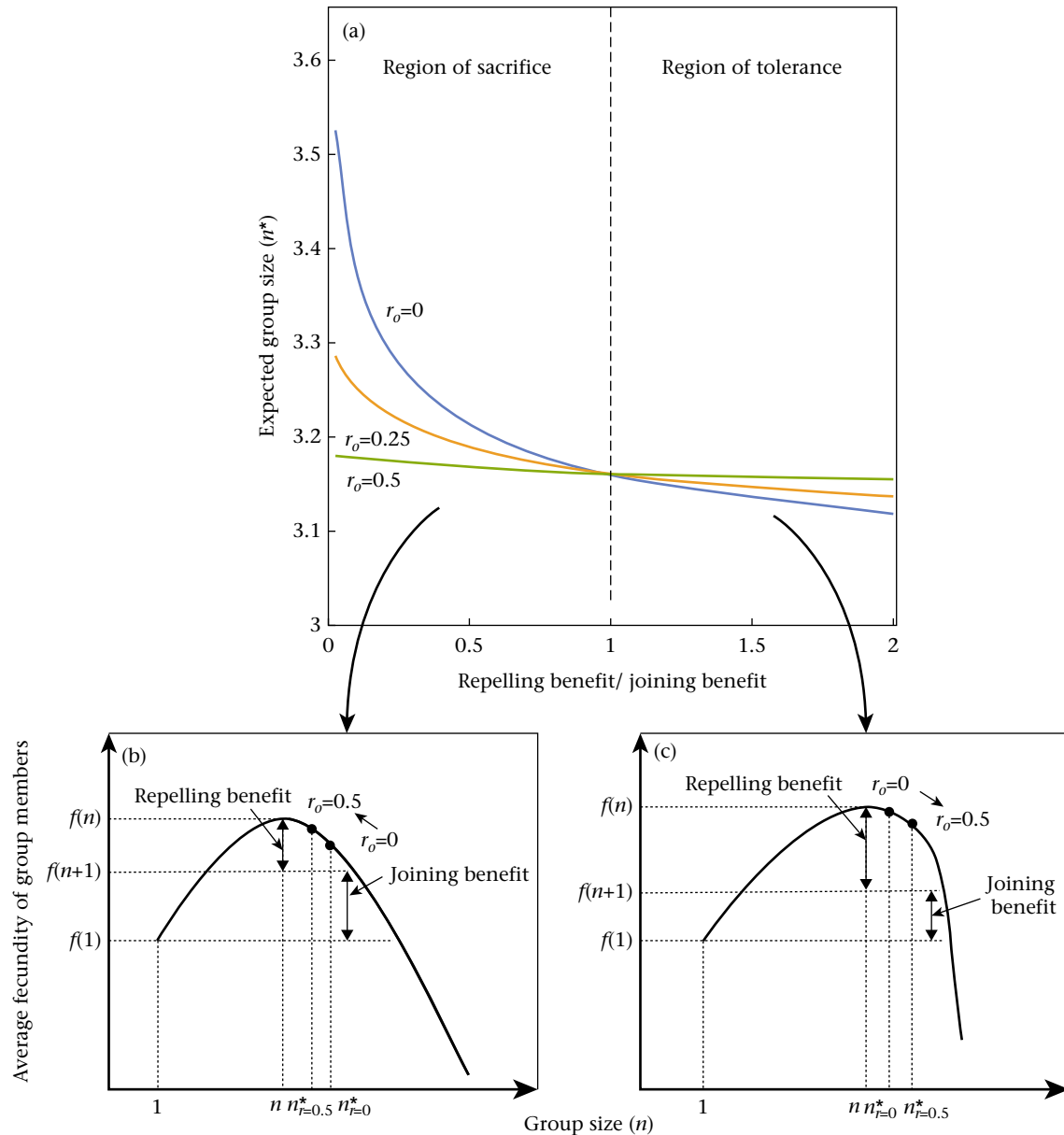
Figure 4. (a) The expected group size, n^*, in relation to the ratio of the benefit for insiders of repelling a joining outsider, $f(n) - f(n + 1)$, and the benefit for an outsider of joining a group, $f(n + 1) - f(1)$, at different genetic relatednesses r_o between a potential joining outsider and insiders and $n = 3$. (b, c) Illustrations of theoretical predictions of the relationships between expected group size, n^*, and r_o when the per capita repelling benefit is (b) smaller than the joining benefit (i.e. region of sacrifice) and (c) larger than the joining benefit (i.e. region of tolerance). The dashed vertical lines emphasize the average fecundity of group members when the group sizes are 1, n, expected group size n^* while $r_o = 0.5$, and n^* while $r_o = 0$.

recruit new members to the group, even if they are unrelated (Shah & Rubenstein, 2023). A recent theoretical model also suggests that direct benefits may be the primary force driving offspring philopatry (García-Ruiz et al., 2022). However, another possibility is that an unrelated potential joiner can force its way into joining a group, especially when the group size is small and the fecundity of being solitary is low. This alternative explanation has not yet been explicitly tested, and more empirical studies of insider−outsider conflict during the process of group formation are clearly needed.

Levels of Insider−Outsider Conflict

Finally, our model also generates predictions for studying levels of insider−outsider conflict during the process of group formation.

Previous insider−outsider conflict models predicted that, even if potential conflict exists, (1) a related potential joiner will voluntarily leave or (2) insiders will accept a related potential joiner without engaging in any actual conflict in the 'region of sacrifice' or the 'region of tolerance' parameter spaces, respectively (Higashi & Yamamura, 1993). In contrast, our model predicts that actual conflict occurs whenever potential conflict exists (i.e. $f(n) > f(n + 1) > f(1)$). However, the actual level of conflict and the probability of outsiders joining are still influenced by kinship. Therefore, we can consider the reduction in joining or repelling effort by the relatives as a kind of altruistic behaviour which reduces one's own direct benefit to increase the direct benefit of the interactor. That is, the concepts of 'region of sacrifice' and 'region of tolerance' can still be applied to explain our results. Although many empirical studies

have demonstrated the existence of actual insider–outsider conflict (e.g. Griesser et al., 2008; Jordan et al., 2010; Thompson et al., 2017; Zöttl et al., 2013), the nature of insider–outsider conflict and its resolution have largely been unexplored in natural systems. We envision that testing the predictions of our model (e.g. effects of $f(n + 1)$ on expected group sizes with varying outsider relatedness) will help us to better understand the evolution of sociality and the nature of conflict resolution in animal societies. Ultimately, our model highlights the importance of studying insider–outsider conflict, a largely neglected but crucial form of social conflict, for understanding the evolution of membership control, group size dynamics and the genetic composition and structure of animal social groups.

Author Contributions

Sheng-Feng Shen: Conceptualization, Writing- Original draft, Software, Visualization. **H. Kern Reeve:** Conceptualization, Writing–Review & editing. **Stephen T. Emlen**: Conceptualization, Writing–Review & editing. **Ming Liu:** Visualization, Writing–Review & editing. **Dustin Rubenstein:** Conceptualization, Writing–Review & editing.

Data Availability

No data were used for the research described in the article.

Declaration of Interest

The authors declare they have no conflicts of interest.

Acknowledgments

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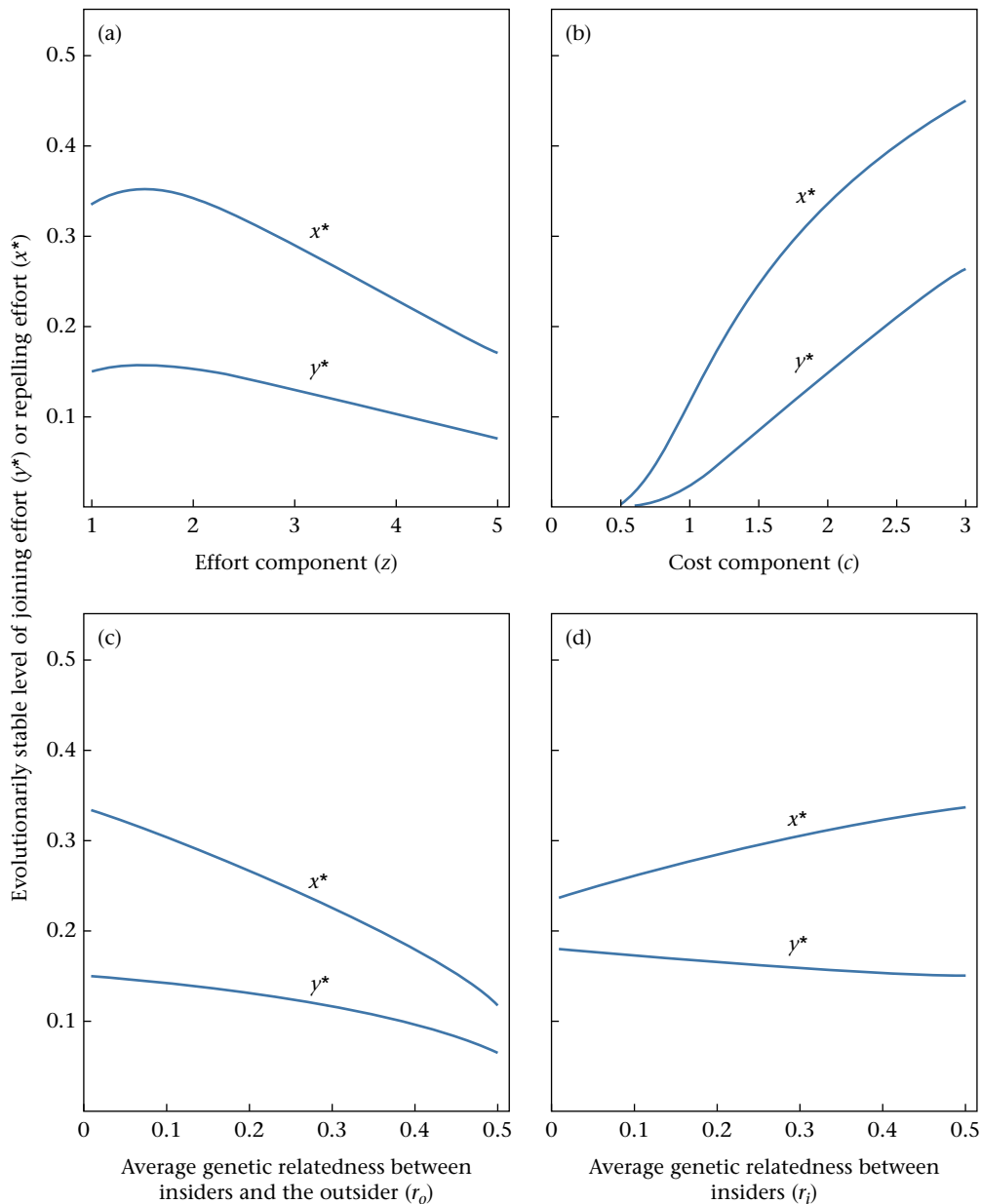
Appendix

Figure A1. The evolutionarily stable repelling effort x^* and joining effort y^* in relation to the (a) effort component z, (b) cost component c, (c) average genetic relatedness between insiders and an outsider r_o, at $r_i = 0.5$ and (d) average genetic relatedness between insiders r_i at $r_o = 0$, where $f(1) = 0.8$, $f(n+1) = 1$, $f(n) = 2$ and $a = 0.5$.