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Neighbor intervention: A game-theoretic model

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ABSTRACT

It has long been argued that a resident may benefit from helping its neighbor defend a territory against a challenger to avoid renegotiating its boundaries with a new and potentially stronger individual. We quantify this theory by exploring games involving challengers, residents and potential allies. In a simplified discrete game with zero variation of fighting strength, helping neighbors is part of an evolutionarily stable strategy (ESS) only if fighting costs are low relative to those of renegotiation. However, if relative fighting costs are high then an interventional ESS remains possible with finite variation of strength. Under these conditions, neighbors may help residents fight off intruders, but only when the resident does not stand a reliable chance of winning alone. We show that neighbor intervention is more likely with low home advantage to occupying a territory, strengths combining synergistically or low probability that an ally will be usurped, amongst other factors. Our parameterized model readily explains occasional intervention in the Australian fiddler crab, including why the ally tended to be larger than both the assisted neighbor and the intruder. Reciprocity is not necessary for this type of cooperation to persist, but also it is by no means inevitable in territorial species.

1. Introduction

Following Fisher (1954), the term "dear–enemy effect" has been used to describe a less aggressive response to intrusions by territorial neighbors than to intrusions by strangers (Temeles, 1994). In some cases, this deference towards familiar neighbors may extend to active assistance to help ward off a heterospecific intruder. For example, male red-winged blackbirds (*Agelaius phoeniceus*) often cooperate with their neighbors in defending nests against predators such as crows (Olendorf et al., 2004). Likewise, pied flycatchers (*Ficedula hypoleuca*) assist in the mobbing of potential predators, particularly when the neighbor has helped in the recent past (Krams et al., 2008). However, in other species, individuals have been observed to intervene to help a neighbor defend its territory against a floating conspecific. For example, despite being competitors for mates, male rock pipits (*Anthus petrosus*) have been observed to engage in coordinated evictions of conspecific intruders from both within the border zones between territories, and from within established territories (e.g., Elfström, 1997). One of the most recent and compelling examples of neighbor intervention comes from work on the fiddler crab *Uca mjoebergi* on the northern coastlines of Australia, where burrow-holding males aggressively defend their burrows from wandering males (intruders). Backwell and Jennions (2004) found that male fiddler crabs may sometimes leave their own territories to help neighbors defend their territories against these floating intruders. In these cases, the ally was always larger than the assisted neighbor and typically larger than the intruder: we return to these intriguing observations later in our paper.

Why would a resident ever pay a cost to help its neighbor deter an intruder (a "floater")? In a seminal paper on the subject, Getty (1987) proposed two explanations for the phenomenon. First, the behavior may be maintained by a form of reciprocation in which established territory holders pay short-term costs to help one another to retain their territories. Second, inspired by arguments of Krebs (1982), Getty (1987) proposed that it may benefit a resident to help its neighbor to defend a territory, so that it can avoid having to renegotiate the boundaries with a new and potentially stronger individual. This second theory is particularly attractive, in part because as yet there is no evidence that competitive collusion among conspecifics is maintained by reciprocation (e.g., Elfström, 1997) and direct evidence to the contrary (e.g., Backwell and Jennions, 2004). Indeed there has been remarkably little evidence of any kind of reciprocity in nature (Hammerstein, 2003).

To date, there has been almost no formal treatment of the hypothesis that residents help neighbors to avoid future costs of renegotiation. Getty (1981) presented a crowding model in which territory holders can collude to deter or preempt the establishment of further competitors, but the model focused more on the

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phenomenon of sequential territorial establishment. To support the specific hypothesis he had raised, Getty (1987) discussed the relative benefits of helping compared to not helping from a phenomenological perspective, but did not delve into the underlying mechanics of interactions between residents, neighbors and intruders. Here we continue the work of Getty (1987) by developing just such a model. We attempt to predict when it is less costly to assist a familiar neighbor than to renegotiate boundaries with a new and potentially stronger one and the conditions under which such behavior would evolve. In particular, we aim to confirm that there need be no reciprocity.

In our analysis we consider a large population of individuals who interact in triads. Two members of each triad are territorial residents, and the third is a floating intruder. Thus each individual has two possible strategic roles, that of potentially intervening resident (role A, for ally) and potentially attacking non-resident (role C, for challenger). The role, B (for Buddy), of the resident who has been intruded upon is non-strategic: if offered help by his neighbor in the event of an attack, an individual in role B accepts the help, but otherwise he fights alone to defend his territory.

2. Discrete mathematical model

We will ultimately allow strength to vary, assuming that an intruder has no information about a resident's strength and vice versa, but that neighbors are sufficiently familiar to know one another's strengths, essentially because they have already settled upon a territorial boundary at the point where their strength-dependent territorial pressures balance (Adams, 2001, p. 283). To set the scene, however, we begin by assuming that variance of strength is zero and consider a simple bimatrix game. Suppose that in role A an individual either Helps (H) or Ignores (I), whereas in role C an individual either Fights (F) or Desists (D) from fighting. Then we have four conditional pure strategies as follows:

HAFC: Help neighbor in role A, Fight resident B in role C
IAFC: Ignore neighbor in role A, Fight resident B in role C
HADC: Help neighbor in role A, Do not challenge in role C
IADC: Ignore neighbor in role A, Do not challenge in role C

We assume for simplicity that a coalition of two will defeat a lone individual with probability ρ whereas a lone resident will defeat an intruder with probability $\frac{1}{2}(1+\mu)$, where $0 \leqslant \mu < 1$ and

$$\tfrac{1}{2}(1+\mu) \leqslant \rho \leqslant 1. \qquad (1)$$

Parameter μ can be interpreted as the advantage of ownership, i.e., the degree to which a resident's probability of winning is increased beyond $\frac{1}{2}$ (where $\mu = 0$) toward 1 (where $\mu = 1$) in a contest between evenly matched opponents. Parameter ρ can be interpreted as a measure of the reliability of numerical advantage or strength difference as a predictor of contest outcome. Reliability is perfect when $\rho = 1$; and, at the other extreme, if $\rho = \frac{1}{2}(1+\mu)$ then a challenger has the same probability $\frac{1}{2}(1-\mu)$ of winning, regardless of whether his opponent is an unaided individual or a coalition. Let V be the benefit of a territory, K_0 the cost of renegotiating a boundary and K_1 the cost of an ownership contest, of which an unaided individual pays all, whereas each half of a coalition pays only $\frac{1}{2}K_1$; V, K_0 and K_1 are all assumed to be constant. Then, assuming—temporarily, and only for ease of presentation—that roles A and C are equally likely, the payoff matrix is as shown in Table 1. For example, suppose HAFC meets IAFC. In role A the cost $-\frac{1}{2}K_1$ of fighting in a coalition is always paid, and with probability $1-\rho$ there is an additional boundary re-negotiation cost K_0 because the intruder wins (and either way there is zero change in territorial benefit). In role C the benefit is $-K_1$ (lose and incur whole cost) with probability $\frac{1}{2}(1+\mu)$ or $V - K_1 - K_0$ (win, pay costs of fight and boundary negotiation) with probability $\frac{1}{2}(1-\mu)$. Hence the payoff is $\frac{1}{2}\cdot\{-\frac{1}{2}K_1 - (1-\rho)K_0\} + \frac{1}{2}\cdot\{\frac{1}{2}(1+\mu)(-K_1) + \frac{1}{2}(1-\mu)(V-K_1-K_0)\} = \frac{1}{4}\{(1-\mu)(V-K_0) - 3K_1\} - \frac{1}{2}(1-\rho)K_0$. Similarly for the other 15 cases. Because this game is asymmetric, it cannot have an evolutionarily stable strategy (ESS) in mixed strategies (Selten, 1980): the only candidates for ESS are the four pure strategies. Let a_{ij} denote the element in row i and column j of the payoff matrix. Then neither HADC nor IADC is an ESS because $a_{43} < a_{33}$ and $a_{34} < a_{44}$ are both false. But HAFC (Help as Ally, Fight as Challenger) is an ESS when $a_{11} > \max\{a_{21}, a_{31}, a_{41}\}$ or

$$K_1 < \min\{(1-\rho)(V-K_0), (2\rho-\mu-1)K_0\} \qquad (2)$$

and IAFC (Ignore as Ally, Fight as Challenger) is an ESS when $a_{22} > \max\{a_{12}, a_{32}, a_{42}\}$ or

$$(2\rho-\mu-1)K_0 < K_1 < \tfrac{1}{2}(1-\mu)(V-K_0). \qquad (3)$$

These are mutually exclusive possibilities: $(2\rho-\mu-1)K_0$ cannot be both greater and less than K_1. Note that (2) can hold only if (1) is satisfied with strict inequality, i.e., if $\frac{1}{2}(1+\mu) < \rho < 1$: helping cannot be evolutionarily stable if the reliability parameter assumes an extreme value, i.e., if a coalition is either guaranteed to win or has no more chance of winning than an unaided resident. Furthermore, because $2\rho-\mu-1 \leqslant 1$, (2) can hold only if $K_1 < K_0$, i.e., if the costs of renegotiating a boundary exceed those of fighting. Correspondingly, if $K_1 > K_0$ so that the costs of fighting exceed those of renegotiation, then only (3) can hold.

We pause to emphasize that our assumption of equal probabilities for roles A and C is purely for presentational convenience. The above results do not depend on it in any way: because of Selten's theorem (Selten, 1980), the only essential requirement is that roles A and C are mutually exclusive. The statement that, for example, HAFC is an ESS is then the dual statement that (i) H is the best response in role A to an individual who selects F (in role C) and (ii) F is the best response in role C to an individual who selects H (in role A). To establish (i), we note that the payoff to H against F is $-\frac{1}{2}K_1 - (1-\rho)K_0$, because a helper always pays half the cost of the fight but pays the additional renegotiation cost only in the event of a loss; whereas the payoff to I against F is $-\frac{1}{2}(1-\mu)K_0$, because a potential helper who ignores its buddy pays a (renegotiation) cost only if the unaided buddy loses. So H is the best response when $-\frac{1}{2}K_1 - (1-\rho)K_0 > -\frac{1}{2}(1-\mu)K_0$ or $K_1 < (2\rho-\mu-1)K_0$. To establish (ii), we note that the payoff to F against H is $\rho(-K_1) + (1-\rho)(V-K_0-K_1) = (1-\rho)(V-K_0) - K_1$, because a challenger always pays the full cost of the fight but gains a territory only if the coalition loses;

Table 1
Payoff matrix $[a_{ij}]$ for the discrete game with zero variance

	HAFC	IAFC	HADC	IADC
HAFC	$-\frac{3}{4}K_1 + \frac{1}{2}(1-\rho)(V-2K_0)$	$\frac{1}{4}\{(1-\mu)(V-K_0) - 3K_1\} - \frac{1}{2}(1-\rho)K_0$	$-\frac{1}{2}K_1 + \frac{1}{2}(1-\rho)(V-K_0)$	$\frac{1}{4}\{(1-\mu)(V-K_0) - 2K_1\}$
IAFC	$-\frac{1}{4}\{(1-\mu)K_0 + 2K_1\} + \frac{1}{2}(1-\rho)(V-K_0)$	$\frac{1}{4}\{(1-\mu)(V-2K_0) - 2K_1\}$	$-\frac{1}{2}K_1 + \frac{1}{2}(1-\rho)(V-K_0)$	$\frac{1}{4}\{(1-\mu)(V-K_0) - 2K_1\}$
HADC	$-\frac{1}{4}K_1 - \frac{1}{2}(1-\rho)K_0$	$-\frac{1}{4}K_1 - \frac{1}{2}(1-\rho)K_0$	0	0
IADC	$-\frac{1}{4}(1-\mu)K_0$	$-\frac{1}{4}(1-\mu)K_0$	0	0

whereas the payoff to D against H is zero. So F is the best response when $(1-\rho)(V-K_0)-K_1$ is positive or $K_1<(1-\rho)(V-K_0)$. Thus (i) and (ii) are equivalent to (2). Similarly for IAFC.

We have now shown that helping can be evolutionarily stable if K_1 (the cost of an ownership contest) is sufficiently low, although it should be noted from (2) that sufficiently low would mean very close to zero if reliability were very high ($\rho \approx 1$). However, the original qualitative arguments for neighbor intervention rested in part on recognizing that any challenger that ousted its neighbor was likely to be stronger than the neighbor. So, any strategic decision to intervene is likely to involve "judicious decision making" rather than automatic intervention, as the results of Backwell and Jennions (2004) confirm. To explore this issue further—and thus show that helping can be evolutionarily stable even if the costs of fighting exceed those of renegotiation—we require a more sophisticated model allowing for variation in fighting ability, which we now proceed to develop and explore.

3. Continuous mathematical model

Here we describe our continuous model. Beyond allowing for variance of strength, our assumptions remain as before. That is, we still consider a large population of individuals who interact in triads; two members of each triad are residents, and the third is an intruder; a focal u-strategist in a population of v-strategists still has two possible roles, that of potentially intervening resident (role A, for ally) and potentially attacking non-resident (role C, for challenger); and the role, B (for Buddy), of the resident who has been intruded upon remains non-strategic—if offered help by his neighbor in the event of an attack, an individual in role B accepts the help, but otherwise he fights alone to defend his territory.

Let X be the strength of the focal u-strategist, let Y be the strength of the individual in role B and let Z be the strength of the v-strategist in the role complementary to that of the focal u-strategist. The strengths X, Y and Z are drawn from a common distribution on [0, 1] with probability density function g and cumulative distribution function G. In nature, distributions of fighting ability are typically fairly symmetric (see, e.g., McDonald, 1981, p. 135 and seq.), so an appropriate choice of distribution for theoretical purposes is one that is perfectly symmetric on [0,1] with mean $\frac{1}{2}$. We choose the symmetric Beta distribution defined by

$$g(\xi) = \frac{\Gamma(2a)}{\{\Gamma(a)\}^2}\xi^{a-1}(1-\xi)^{a-1}, \tag{4}$$

where Γ denotes Euler's gamma function, i.e., $\Gamma(\eta) = \int_0^\infty e^{-\xi}\xi^{\eta-1}\,d\xi$ (see, e.g., Kempthorne and Folks, 1971, p. 107). For $a=1$ this distribution is uniform; for $a>1$ it is unimodal, and its variance decreases with a according to

$$\sigma^2 = \frac{1}{4(1+2a)}. \tag{5}$$

Throughout, we assume that $a \geqslant 1$, or $\sigma^2 \leqslant \frac{1}{12}$.

We assume that the neighbors in roles A and B have established a mutual territorial boundary and are therefore sufficiently familiar with one another that an individual in role A will know the strength of an individual in role B; however, he does not know the strength of the individual in role C, and the individual in role C does not know the strength of either resident. Thus the information structure allows each member of the population to condition his behavior on the strengths of himself and his neighbor when occupying role A, but only on his own strength when occupying role C. Accordingly, we define strategy $u=(u_0,u_1,u_2)$ to mean that a focal individual in role A will help his neighbor in role B in the event of an attack if $X>u_0$ and $Y<u_1$ but desist from helping if $X \leqslant u_0$ or $Y \geqslant u_1$; and that a focal individual in role C, having intruded upon a resident (who is therefore in role B), will attack if $X>u_2$ but desist from attacking if $X \leqslant u_2$. Thus the vector (u_0,u_1,u_2) contains the thresholds that define the behavior a focal individual of strength X with respect to one of strength Y, regardless of whether its role is that of neighbor and potential ally (first two components) or intruder and potential challenger (third component); and the strategy space is the unit cube where $0 \leqslant u_0,u_1,u_2 \leqslant 1$. Note that both the front and right-hand faces of this cube, where $u_1=0$ or $u_0=1$, respectively, consist entirely of non-interventional strategies.

Two kinds of contest are involved in this system, a contest for ownership and a contest for territorial division. A contest between animals in roles B and C is for ownership of a site centered at some indivisible resource, such as a burrow. We assume that costs are dependent on differences in fighting strength and that contests take longer between more evenly matched opponents, because they take longer to discover who is stronger. Let $K(\Delta s)$ denote the cost of such a contest between opposing parties whose effective strengths differ by Δs; K must be an even function (i.e., a function of $|\Delta s|$), and we assume that $K(\Delta s)=0$ for $|\Delta s| \geqslant 2$. For $|\Delta s| \leqslant 2$ we choose

$$K(\Delta s) = K_1\{1-\tfrac{1}{4}|\Delta s|^2\}^k \tag{6}$$

as in Mesterton-Gibbons and Sherratt (2007). Here k is a measure of the sensitivity of cost to strength difference, in the sense that a small difference in strength implies a large cost reduction when k is very high but virtually no cost reduction when k is very low. The graph of K is plotted in Fig. 1 for four different values of k.

We assume that fighting costs in an ownership contest are equally borne by all members of a coalition. So a lone individual bears the whole cost of fighting, whereas a pair of allies splits the cost equally. Hence an ownership contest between individuals of strength S_1 and S_2 costs each

$$c_1(S_1,S_2) = K(S_1-S_2), \tag{7}$$

where K is defined by (6). On the other hand, a contest between allies of strengths S_1, S_2 and a third individual of strength S_3 costs each ally

$$c_{21}(S_1,S_2,S_3) = \tfrac{1}{2}K(q\{S_1+S_2\}-S_3), \tag{8}$$

where q $(>\frac{1}{2})$ denotes synergicity and $q(S_1+S_2)$ is the effective strength of the coalition, as in Mesterton-Gibbons and Sherratt (2007); whereas an individual of strength S_1 pays

$$c_{12}(S_1,S_2,S_3) = K(S_1-q\{S_2+S_3\}) \tag{9}$$

to fight alone against a pair of allies of strengths S_2 and S_3.

Let $p_R(\Delta s)$ denote the probability of winning for a resident coalition or individual whose combined effective strength exceeds that of its opponent by Δs, and let $p_I(\Delta s)$ denote the corresponding probability of winning for an intruder. Then

$$p_R(\Delta s) + p_I(-\Delta s) = 1 \tag{10}$$

for all Δs, with

$$p_R(0) = \tfrac{1}{2}(1+\mu), \tag{11}$$

where μ denotes advantage of ownership, i.e., degree to which a resident's probability of winning is increased beyond $\frac{1}{2}$ toward 1 in a contest between evenly matched opponents. We set $p_R=0$ for $\Delta s<-2$ and $p_R=1$ for $\Delta s>2$ (both possible only if $q>1$); and for $\Delta s \in [-2, 2]$, for all $r>0$ we choose

$$p_R(\Delta s) = \left\{\frac{\Gamma(2r)}{\Gamma(r)^2}B\left(\tfrac{1}{2}+\tfrac{1}{4}\Delta s, r, r\right)\right\}^{1-\ln(1+\mu)/\ln(2)}, \tag{12}$$

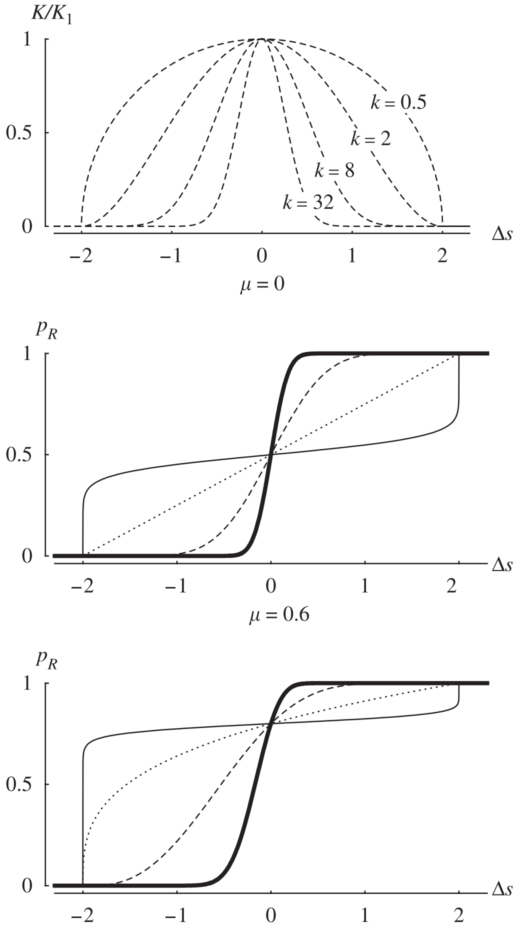

Fig. 1. Top: How K (the cost of fighting) defined by (6) varies with difference in fighting strength between parties for four different values of the sensitivity parameter k. Middle and bottom: How p_R (resident probability of winning an ownership fight) defined by (12) varies with difference in fighting strength for $r = 0.1$ (thin solid curve), $r = 1$ (dotted), $r = 10$ (dashed) and $r = 100$ (thick solid curve) for two different values of μ.

where B is the incomplete Beta function, i.e., $B(\eta, \xi_1, \xi_2) = \int_0^\eta \zeta^{\xi_1 - 1} (1-\zeta)^{\xi_2 - 1}\,d\zeta$. Note that (12) satisfies both $p_R(-2) = 0$ and $p_R(2) = 1$, in addition to (11). The graph of p is plotted in Fig. 1 for $\mu = 0$ and 0.6 for four different values of r, which is a measure of the reliability of strength difference as a predictor of fight outcome. Hence for consistency we set $p_R = \frac{1}{2}(1+\mu)$ for all Δs when $r = 0$ (which is also the limit of (12) as $r \to 0$). The middle figure corresponds to Figure 1a of Mesterton-Gibbons and Sherratt (2007).

By contrast, a contest between an animal in roles A and an animal who has been successful in role C is to settle a boundary between neighboring burrows. The resource is divisible: more evenly matched opponents will settle on a boundary nearer to the midpoint between burrows, but we would not expect the length of the contest to depend on the strength difference between individuals. On the other hand, the cost could depend on the strengths of the contestants for other reasons; e.g., it could be higher for a weaker animal, as assumed by Mesterton-Gibbons and Adams (2003). Accordingly, we allow for greater generality in the initial formulation of our model by using $c_0(S_1, S_2)$ to denote the cost of such a contest between individuals of strengths S_1 and S_2. But it is surely at least not unreasonable to assume that this type of contest is of fixed length; and so, for the sake of tractability, we will largely assume that

$$c_0(S_1, S_2) = K_0. \tag{13}$$

We follow Mesterton-Gibbons and Adams (2003) in determining the residents' mutual territorial boundary. We assume that their burrows (or the focal points of their territories in the case of birds) are at opposite ends of a line segment, whose length is defined (without loss of generality) to be the unit of distance, and that the boundary is established where their effective fighting abilities are equal. Thus the line segment divides into two smaller segments that represent the territories of the residents. We assume that these territories always fill the expanse between the burrows. The marginal value of territory expansion is the same constant b for all residents, and so the value of the territory thus obtained is simply b times the length of the relevant segment. Let S denote strength. For all residents, the effective fighting ability that can be brought to bear at a particular location increases with S but declines with distance from the burrow, denoted by d. For the sake of simplicity, we assume that both relationships are linear: specifically, we assume that the territorial pressure P that an animal exerts increases at rate r_1 with respect to strength and decreases at rate r_2 with respect to distance, according to

$$P = P_0 + r_1 S - r_2 d, \tag{14}$$

where all parameters are positive. To simplify our analysis, we also assume that $r_1 < r_2$, so that even the weakest owner exerts a greater pressure at its own burrow than even the strongest neighbor. A territorial boundary between animals in roles A and B occurs where the neighbors exert equal pressure. Let the boundary be at distance $\xi(X, Y)$ from the focal individual's burrow when it occupies role A. Then, from (14), $P_0 + r_1 X - r_2 \xi = P_0 + r_1 Y - r_2(1-\xi)$ or

$$\xi(X, Y) = \tfrac{1}{2}\{1 + \theta(X - Y)\}, \tag{15}$$

where

$$\theta = r_1 / r_2 \tag{16}$$

satisfies $\theta < 1$. The greater the value of r_1 relative to r_2, the more effective is greater strength in rolling back the boundary toward the neighbor's burrow, and so we will refer to θ as elasticity of territorial pressure. Note that θ is the length of the interval (centered around the midpoint of the line segment between burrows) in which the boundary can lie; or equivalently, the boundary falls at least $\frac{1}{2}(1-\theta)$ from an animal's burrow. Note also that $1 - \xi(X, Y) = \xi(Y, X)$.

4. Analysis of reward

Consider first a u-strategist in role A whose neighbor has been attacked. Then $Z > v_2$, because the intruder is a v-strategist. If $X \leqslant u_0$ or $Y \geqslant u_1$ then the potential ally does not help. With probability $p_R(Y - Z)$, the neighbor evicts the intruder unaided and there is zero change in the protagonist's fitness because the boundary remains where it was. With probability $p_I(Z - Y)$, however, the invader wins and the protagonist must re-negotiate the boundary through a contest that costs $c_0(X, Z)$. The new boundary will fall at distance $\xi_n = \xi(X, Z)$ from his burrow; and because the old boundary was at distance $\xi_o = \xi(X, Y)$, the payoff to the u-strategist in these circumstances—the change in his fitness—is $b(\xi_n - \xi_0) - c_0(X, Z) = \frac{1}{2} b\theta(Y - Z) - c_0(X, Z)$, on using (15).

If, on the other hand, $X > u_0$ and $Y < u_1$ then the potential ally intervenes on behalf of his neighbor at cost $c_{21}(X, Y, Z)$. With probability $p_R(q\{X + Y\} - Z)$ the coalition wins, and the territorial boundary between the allies remains unchanged. The payoff to the u-strategist in these circumstances—the change in his fitness—is simply $-c_{21}(X, Y, Z)$. With probability $p_I(Z - q\{X + Y\})$, however, the intruder evicts the individual in role B and the focal individual must renegotiate his boundary as above, the payoff in these circumstances being $b(\xi_n - \xi_0) - c_0(X,Z) - c_{21}(X,Y,Z) = \frac{1}{2}b\theta(Y-Z) - c_0(X,Z) - c_{21}(X,Y,Z)$. Hence, conditional upon $X > u_0$ and $Y < u_1$, the u-strategist's payoff is $p_R(q\{X+Y\} - Z)\{-c_{21}(X,Y,Z)\} + p_I(Z - q\{X+Y\})\{\frac{1}{2}b\theta(Y-Z) - c_0(X,Z) - c_{21}(X,Y,Z)\} = p_I(Z - q\{X+Y\})\{^12b\theta(Y-Z) - c_0(X,Z)\} - c_{21}(X,Y,Z)$, on using (10).

There is, however, a further complication. It is possible that in leaving his territory to help his neighbor, the focal individual risks being usurped by another floater. Let ε be the probability of being so usurped when helping a neighbor. Then the above conditional payoff arises only with probability $1-\varepsilon$; with probability ε the focal individual finds that he has lost his territory, so that his conditional payoff from interacting with the v-strategist is no longer $p_I(Z - q\{X+Y\})\{\frac{1}{2}b\theta(Y-Z) - c_0(X,Z)\} - c_{21}(X,Y,Z)$ but rather $-b\xi(X,Y) - c_{21}(X,Y,Z)$, regardless of whether his neighbor won or lost. Thus the payoff in role A to the focal individual is $F_A(X,Y,Z,u,v) = H_i(X,Y,Z)$ for $(X,Y,Z) \in \Omega_i(u,v)$, where the events Ω_i and the payoffs H_i are defined in Table 2 for $i = 1,\ldots,3$.

Consider now a u-strategist in role C who has made the decision to attack the resident in role B: then $X > u_2$, because the intruder is now a u-strategist. If $Z \leqslant v_0$ or $Y \geqslant v_1$ then the potential ally, now a v-strategist, does not help. With probability $p_R(Y-X)$ the u-strategist is evicted with fitness gain $-c_1(X,Y)$. With probability $p_I(X-Y)$, however, the protagonist wins and must negotiate a boundary through a contest that costs $c_0(X,Z)$. The boundary will fall at distance $\xi(X,Z)$ from his burrow, the payoff—the change in his fitness—being $b\xi(X,Z) - c_0(X,Z) - c_1(X,Y)$. Hence, conditional upon $Z \leqslant v_0$ or $Y \geqslant v_1$, the u-strategist's payoff is $p_R(Y-X)\{-c_1(X,Y)\} + p_I(X-Y)\{b\xi(X,Z) - c_0(X,Z) - c_1(X,Y)\} = p_I(X-Y)\{b\xi(X,Z) - c\ 0(X,Z)\} - c_1(X,Y)$, on using (10).

If, on the other hand, $Z > v_0$ and $Y < v_1$ then the potential ally intervenes on behalf of his neighbor. With probability $p_R(q\{Y+Z\} - X)$ the coalition wins, and the territorial boundary between the allies remains unchanged. The payoff to the u-strategist in these circumstances—the change in his fitness—is simply $-c_{12}(X,Y,Z)$. With probability $p_I(X - q\{Y+Z\})$, however, the focal individual evicts the individual in role B and must negotiate his boundary as above, the payoff being $b\xi(X,Z) - c_0(X,Z) - c_{12}(X,Y,Z)$. Hence, conditional upon $Z > v_0$ and $Y < v_1$, the u-strategist's payoff is $p_R(q\{Y+Z\} - X)\{-c_{12}(X,Y,Z)\} + p_I(X - q\{Y+Z\})\{b\xi(X,Z) - c_0(X,Z) - c_{12}(X,Y,Z)\} = p_I(X - q\{Y+Z\})\{b\xi(X,Z) - c_0(X,Z)\} - c_{12}(X,Y,Z)$, on using (10). Thus the payoff in role C to the focal individual is $F_C(X,Y,Z,u,v) = h_i(X,Y,Z)$ for $(X,Y,Z) \in \omega_i(u,v)$, where the events ω_i and payoffs h_i are defined in Table 3 for $i = 1,\ldots,3$. If roles A and C are occupied with probabilities q_A and q_C, respectively, then the reward to a u-strategist in a population of v-strategists is the expected value of $q_A F_A(X,Y,Z,u,v) + F_C(X,Y,Z,u,v)q_C$over the joint distribution of X, Y and Z, that is,

$$f(u,v) = q_A f_A(u_0,u_1,v_2) + q_C f_C(v_0,v_1,u_2), \tag{17}$$

where

$$f_A(u_0,u_1,v_2) = \sum_{i=1}^{3} \int\int\int_{(x,y,z)\in\Omega_i(u,v)} H_i(x,y,z) g(x) g(y) g(z)\,\mathrm{d}x\,\mathrm{d}y\,\mathrm{d}z \tag{18}$$

and

$$f_C(v_0,v_1,u_2) = \sum_{i=1}^{3} \int\int\int_{(x,y,z)\in\omega_i(u,v)} h_i(x,y,z) g(x) g(y) g(z)\,\mathrm{d}x\,\mathrm{d}y\,\mathrm{d}z \tag{19}$$

(the first contribution to the sum being zero in either case, from Tables 2 to 3).

Table 2
Payoff to a focal u-strategist of strength X, conditional on being in role A, where Y and Z are the strengths of the individuals in roles B and C

Case i	Event $\Omega_i(u,v)$	Payoff $H_i(X,Y,Z)$
1	$Z \leqslant v_2$	0
2	$X \leqslant u_0$ or $Y \geqslant u_1$, $Z > v_2$	$\{\frac{1}{2}b\theta(Y-Z) - c_0(X,Z)\}p_I(Z-Y)$
3	$X > u_0$, $Y < u_1$, $Z > v_2$	$(1-\varepsilon)\{\frac{1}{2}b\theta(Y-Z) - c_0(X,Z)\}p_I(Z - q\{X+Y\})$ $-\varepsilon\{b\xi(X,Y) + c_{21}(X,Y,Z)\}$

Table 3
Payoff to a focal u-strategist of strength X, conditional on being in role C, where Y and Z are the respective strengths of the individuals in roles B and A

Case i	Event $\omega_i(u,v)$	Payoff $h_i(X,Y,Z)$
1	$X \leqslant u_2$	0
2	$X > u_2$, $Y \geqslant v_1$ or $Z \leqslant v_0$	$p_I(X-Y)\{b\xi(X,Z) - c_0(X,Z)\} - c_1(X,Y)$
3	$X > u_2$, $Y < v_1$, $Z > v_0$	$p_I(X - q\{Y+Z\})\{b\xi(X,Z) - c_0(X,Z)\} - c_{12}(X,Y,Z)$

5. Evolutionarily stable strategy

Strategy $v = (v_0, v_1, v_2)$ is a strong ESS in the sense of Maynard Smith (1982) if it is uniquely the best reply to itself, i.e., if $f(v,v) > f(u,v)$ for all $u \neq v$. For v to be such an ESS in the interior of the strategy space we require the gradient of f with respect to u to vanish where $u = v$ in such a way that v yields a maximum (as opposed to a minimum or a saddle point) of $f(u,v)$. Hence, from (17), we require

$$\left.\frac{\partial f_A}{\partial u_0}\right|_{u_0=v_0,u_1=v_1} = \left.\frac{\partial f_A}{\partial u_1}\right|_{u_0=v_0,u_1=v_1} = \left.\frac{\partial f_C}{\partial u_2}\right|_{u_2=v_2} = 0 \tag{20}$$

with $\chi_0(v)$, $\chi_1(v)$, $\chi_2(v)$ and $\chi_3(v)$ all negative, where

$$\chi_0(v) = \left.\frac{\partial^2 f_A}{\partial u_0^2}\right|_{u_0=v_0,u_1=v_1}, \quad \chi_1(v) = \left.\frac{\partial^2 f_A}{\partial u_1^2}\right|_{u_0=v_0,u_1=v_1}, \quad \chi_2(v) = \left.\frac{\partial^2 f_C}{\partial u_2^2}\right|_{u_2=v_2} \tag{21}$$

and χ_3 is defined in Appendix A; the negativity of all four quantities ensures that the Hessian matrix of f with respect to u is negative-definite at $u = v$. Appendix A describes the required modifications of these conditions for a boundary ESS. Note that the conditions do not depend in any way on q_A or q_C in (17): as in the discrete model of Section 2, the probabilities of roles A and C have no effect on the ESS.

From Appendix A, (20) requires v_0, v_1 and v_2 to satisfy the following simultaneous nonlinear equations:

$$\begin{aligned}&\int_{v_2}^{1} g(z) \int_{0}^{v_1} \{\tfrac{1}{2}b\theta(y-z) - c_0(v_0,z)\}\{(1-\varepsilon)p_I(z - q\{v_0+y\})\\ &\quad - p_I(z-y)\}g(y)\,\mathrm{d}y\,\mathrm{d}z\\ &\qquad = \int_{v_2}^{1} g(z) \int_{0}^{v_1} \{\varepsilon b\xi(v_0,y) + c_{21}(v_0,y,z)\}g(y)\,\mathrm{d}y\,\mathrm{d}z,\end{aligned} \tag{22a}$$

$$\begin{aligned}&\int_{v_2}^{1} g(z) \int_{v_0}^{1} \{\tfrac{1}{2}b\theta(v_1-z) - c_0(y,z)\}\{(1-\varepsilon)p_I(z - q\{v_1+y\})\\ &\quad - p_I(z-v_1)\}g(y)\,\mathrm{d}y\,\mathrm{d}z\\ &\qquad = \int_{v_2}^{1} g(z) \int_{v_0}^{1} \{\varepsilon b\xi(y,v_1) + c_{21}(y,v_1,z)\}g(y)\,\mathrm{d}y\,\mathrm{d}z,\end{aligned} \tag{22b}$$

and

$$\begin{aligned}&\int_0^1 g(y)\int_0^1 p_I(v_2-y)\{b\xi(v_2,z)-c_0(v_2,z)\}g(z)\,\mathrm{d}z\,\mathrm{d}y\\&\quad+\int_0^{v_1} g(y)\int_{v_0}^1\{p_I(v_2-q\{y+z\})-p_I(v_2-y)\}\{b\xi(v_2,z)\\&\quad-c_0(v_2,z)\}g(z)\,\mathrm{d}z\,\mathrm{d}y\\&\qquad=\int_0^1 g(y)\int_0^1 c_1(v_2,y)g(z)\,\mathrm{d}z\,\mathrm{d}y+\int_0^{v_1} g(y)\\&\qquad\times\int_{v_0}^1\{c_{12}(v_2,y,z)-c_1(v_2,y)\}g(z)\,\mathrm{d}z\,\mathrm{d}y.\end{aligned}\tag{22c}$$

We can reduce the number of parameters from 10 to 9 by using b to scale the maximum-cost parameters K_0 and K_1 in (6)–(13):

$$\gamma_0=\frac{K_0}{b},\quad \gamma_1=\frac{K_1}{b}.\tag{23}$$

Then any solution $v=(v_0,v_1,v_2)$ of (22) is a function of a, γ_0, γ_1, k, q, r, ε, θ and μ.

Here we have a huge parameter space and we need to restrict it sensibly. With $V=\frac{1}{2}b$, four of our continuous model's original 10 parameters, namely, b, K_0, K_1 and μ, correspond to parameters of our discrete model in Table 1. By restricting them so that IAFC—never intervening, always challenging—would be the ESS of our discrete model if reliability were perfect, i.e., on using (3) with $\rho=1$ and (23), by requiring $\gamma_0<\gamma_1/(1-\mu)<\frac{1}{4}-\frac{1}{2}\gamma_0$, we can focus on how finite variance of strength with imperfect reliability enables neighbor intervention to be evolutionarily stable. However, we would also like to be able to vary μ independently of the cost parameters, which the above inequalities preclude. Therefore, as a practical compromise, we restrict the parameter space only so that IAFC must be the ESS of the discrete model with perfect reliability in the absence of ownership advantage, thus requiring

$$\gamma_0<\gamma_1<\tfrac{1}{4}-\tfrac{1}{2}\gamma_0\tag{24}$$

and hence, in particular, $\gamma_0<\frac{1}{6}$. Note that (23) and (24) ensure that fighting costs exceed those of renegotiation.

Numerical calculations indicate the following. Eqs. (22) have at most one solution within the strategy space such that $\chi_j(v)<0$ for $j=0,1,2,3$. If ε is sufficiently small, which we assume, and if other parameters are likewise not extreme (in ways to be illustrated below), then there is always such a solution when r is sufficiently large; i.e., r_i exists such that there is a unique interior ESS for all $r>r_i$. Furthermore, there is a second critical value r_c such that no ESS exists for $r\leqslant r_c$. It is possible to have $r_c=r_i$; otherwise, there is a range of values $r_c<r\leqslant r_i$ in which the ESS, although unique, need not lie in the interior of the strategy space because either v_1 or v_2 can assume extreme values. More precisely, there are values of r satisfying $r_c<r\leqslant r_i$ such that either $v_1=1$ at the ESS with $0<v_0,v_2<1$, or $v_2=0$ at the ESS with $0<v_0,v_1<1$; and in either case, conditions (22) require modification, as described in Appendix A. Regardless, for $r>r_c$ there exists a unique ESS, which is interventional in the sense that at least the strongest potential allies should intervene on behalf of at least their weakest neighbors because $v_0<1$ and $v_1>0$. Indeed with finite variance there cannot exist a non-interventional ESS because any non-interventional strategy can spread by random drift among any other non-interventional strategy, as established in Appendix A.

These points are illustrated by Fig. 2, which shows the ESS as a function of r for fixed values of the other eight parameters. These values are chosen so that variance is maximal, there is zero risk of usurpation, there is no advantage of ownership, synergy is absent and the cost sensitivity is at least moderately high, in the sense that a strength difference over one's opponent of the equivalent of an individual of maximum strength reduces the cost of a territorial contest to 10% of its maximum value. In the following discussion we use an asterisk to distinguish between an arbitrary population strategy $v=(v_0,v_1,v_2)$ and an ESS population strategy $v^*=(v_0^*,v_1^*,v_2^*)$, which is necessarily a solution of (22) if $r>r_i$ (but otherwise satisfies the modified conditions described in Appendix A); and we use $v^*=v^*(r)=(v_0^*(r),v_1^*(r),v_2^*(r))$ to denote the ESS as a function of r. Furthermore, we use $r_1^-\leqslant r\leqslant r_1^+$ to denote a range of values of r for which v^* is a boundary ESS with $v_1^*=1$; and we use r_2^+ to denote a critical value such that $v_2^*=0$ for $r_c<r\leqslant r_2^+$.

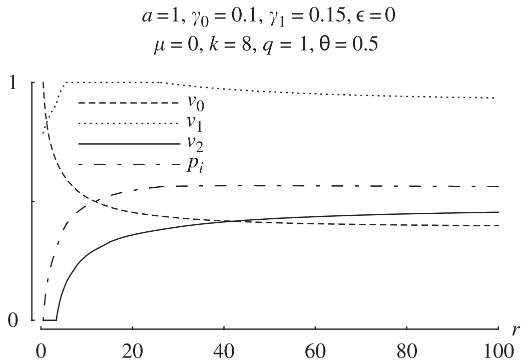

Fig. 2. An example of the ESS as a function of r, a measure of the reliability of strength difference as a predictor of contest outcome, for $r>r_c\approx 0.487$. As $r\to\infty$ the ESS asymptotes to $v^*(\infty)\approx(0.390, 0.916, 0.482)$ while p_i, the probability of intervention conditional upon a challenge, asymptotes to $p_i^\infty\approx 0.559$.

In the limit as $r\to 0$, the probability of winning approaches $\frac{1}{2}$ (because here we have set $\mu=0$), so that an ally should not help, because his buddy is no more likely to win with his support than without it. Correspondingly, v_0^* rises toward 1 and v_1^* falls toward 0 as r decreases toward r_c. As reliability increases, however, the probability of victory by a coalition increases. So allies should be more inclined to help, and intruders should be less inclined to challenge; correspondingly, v_2^* should increase with r and either v_0^* should decrease with r or v_1^* should increase with r, or both. The upshot is an increase with r at the ESS of the probability of intervention conditional upon a challenge, i.e.,

$$p_i=\mathrm{Prob}(X>v_0^*,Y<v_1^*)=\{1-G(v_0^*)\}G(v_1^*),\tag{25}$$

where G is the distribution function defined by $G(\eta)=\int_0^\eta g(\xi)\,\mathrm{d}\xi$. This probability is also plotted as a function of r in Fig. 2.

We now consider the effects of varying parameters other than r, using obvious modifications of our above notation for critical values (e.g., ε_1^+ to denote a value below which $v_1^*=1$). If there is any risk of being usurped, then an ally should be less inclined to help. Fig. 3 shows $v^*=v^*(\varepsilon)$, i.e., the ESS as a function of ε, for three different values of r and the same fixed values of the other seven parameters as in Fig. 2. Note that raising ε only slightly (from zero to $\varepsilon_1^+\approx 0.33\times 10^{-2}$ if $r=10$) suffices for the boundary ESS apparent in Fig. 2 to disappear. As ε increases further, $v_0^*(\varepsilon)$ increases and $v_1^*(\varepsilon)$ decreases until ε reaches the critical value ε_c above which there is no longer an ESS because v_0^* has risen to 1: intuitively, if the risk of usurpation is too high, then not even the strongest neighbors should intervene.

The effect of varying elasticity of territorial pressure is illustrated by Fig. 4, which shows $v^*=v^*(\theta)$ for $\varepsilon=0.04$, three different values of r and the same fixed values of the other six parameters as in Fig. 2. Note in particular how increasing θ increases the probability that an ally will help a larger buddy at the ESS (because the dotted curve lies over the dashed one, and the difference between them increases). Our ally does not want a bigger neighbor who will enforce a smaller territory—far better to see him off with the help of a neighbor before it even gets that

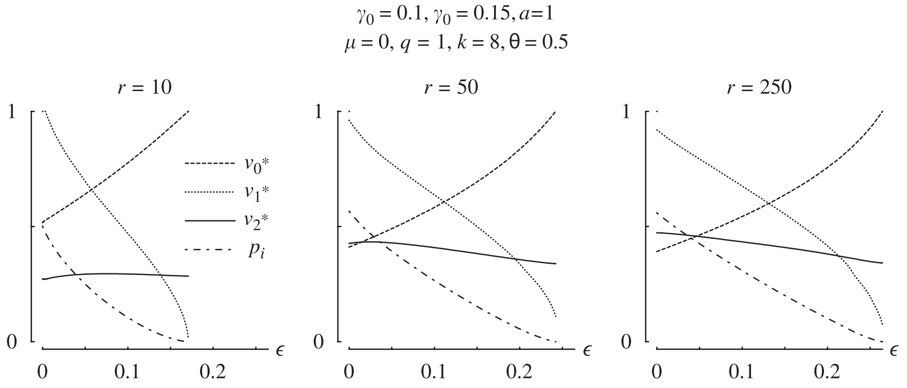

Fig. 3. An example of the ESS as a function of ε, the ally's probability of usurpation, for $\varepsilon<\varepsilon_c$, where $\varepsilon_c \approx 0.171$ for $r = 10$, $\varepsilon_c \approx 0.242$ for $r = 50$ and $\varepsilon_c \approx 0.264$ for $r = 250$.

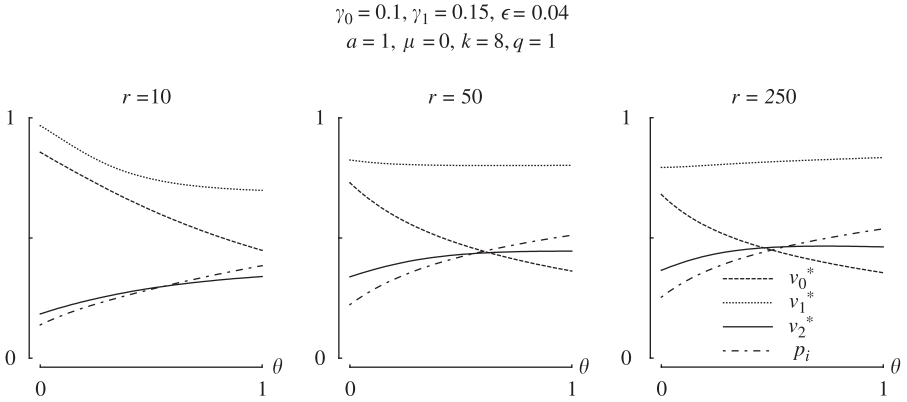

Fig. 4. An example of the ESS as a function of θ, a measure of the elasticity of territorial pressure. In this case the ESS exists for all values of θ (although it may not exist at low θ if $\mu>0$, as illustrated by Fig. 10).

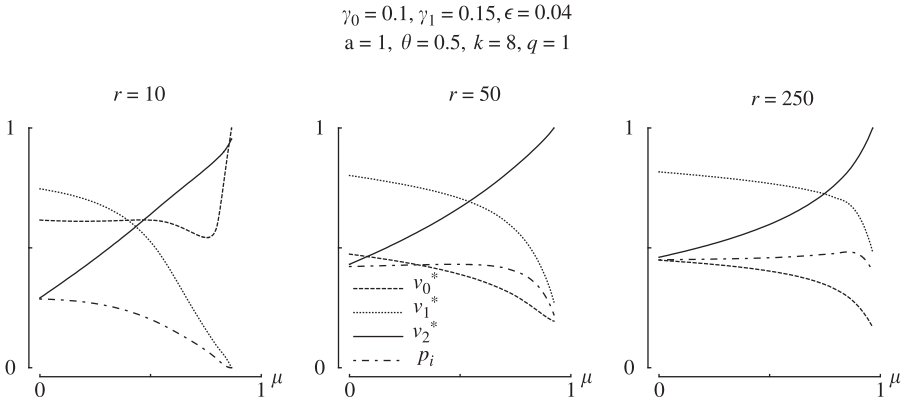

Fig. 5. An example of the ESS as a function of ownership advantage μ for $\mu<\mu_c$, where $\mu_c \approx 0.866$ for $r = 10$, $\mu_c \approx 0.924$ for $r = 50$ and $\mu_c \approx 0.966$ for $r = 250$.

far—and the consequent reduction of territory would be larger for larger values of θ.

The effect of varying ownership advantage is illustrated by Fig. 5, which shows $v^* = v^*(\mu)$ for $\theta = 0.5$ and the same fixed values of the other seven parameters as in Fig. 4. Perhaps the most noticeable consequences of increasing μ are the increase in v_2^* and the sudden increase of v_0^* as $\mu \to 1$ when r is low. If μ is large, and if an ally does not help a larger buddy, and if the intruder wins then, because of the influence of the resident's advantage on the outcome of the ownership contest, if reliability is high then it is highly likely that the new neighbor is much stronger than the old one and therefore likely to inflict a reduction of territory as well as a re-negotiation cost, which together far outweigh the cost of the intervention that would very likely have prevented it; however, at low reliability and high owner advantage it pays only the strongest allies to help.

The effect of varying sensitivity of cost to strength difference is illustrated in Fig. 6, which shows $v^* = v^*(k)$ for $\mu = 0$ and the same fixed values of the other seven parameters as in Fig. 5. Perhaps the most surprising consequence of increasing k is that v_2^* falls to zero for sufficiently large k, denoted by k_2^-: thereafter the ESS is a boundary ESS. If k is very large, then the costs of an ownership contest are negligible except for almost identically matched opponents (see Fig. 1). Hence an intruder has very little to lose by challenging and losing because two almost identical strengths are very unlikely at maximum variance: we would therefore expect the threshold to go to zero at sufficiently high k. The lower the value of r, the sooner the threshold goes to zero, because the challenger's chances of winning are higher when r is lower.

The effect of varying synergicity is illustrated in Fig. 7, where it is assumed that $\frac{1}{2} \leqslant q \leqslant \frac{3}{2}$. The justification for $q \geqslant \frac{1}{2}$ is that effective fighting strength should at least equal or exceed average fighting strength. The justification for $q \leqslant \frac{3}{2}$ is that the strength difference between a pair of average individuals and an individual of maximum possible strength is $q(\frac{1}{2}+\frac{1}{2})-1 = q-1$, which should not yield an advantage of more than the equivalent of one individual of average strength. We see that v_0^* decreases and v_1^* increases with q: the higher the synergicity, the greater the range of sizes of stronger allies who help and weaker neighbors who receive help.

The effect of reducing variance is illustrated in Fig. 8. Intuition suggests that, for a given mean (and with a symmetric Beta distribution of strength on [0, 1], we assume the mean to be fixed at $\frac{1}{2}$), aggression thresholds should decrease with variance because at higher variance an opponent is more likely to be stronger. This intuition is confirmed in Fig. 8, in which v_2^* increases with a, an inverse measure of variance.

6. Relative sizes of individuals in triad

Here we use the terms "strength" and "size" interchangeably, because they both reflect an ability to win fights, although size is often an easier character to measure empirically. Let p_{lh} denote the probability that a resident in role B is larger (stronger) than any challenger in role C at the ESS, conditional on being helped by his neighbor in role A; and let p_{li} denote the probability that a resident in role B is larger than any challenger in role C at the ESS, conditional on not being helped—or being ignored—by his neighbor in role A. Then

$$p_{lh} = \frac{\mathrm{Prob}(X > v_0^*, Y < v_1^*, Y > Z > v_2^*)}{\mathrm{Prob}(X > v_0^*, Y < v_1^*, Z > v_2^*)} \tag{26}$$

if $v_1^* > v_2^*$ (as in Fig. 2), although $p_{lh} = 0$ if $v_2^* > v_1^*$ (as in Fig. 5 for large μ); and

$$p_{li} = \frac{\mathrm{Prob}(X \leqslant v_0^* \text{ or } Y \geqslant v_1^*, Y > Z > v_2^*)}{\mathrm{Prob}(X \leqslant v_0^* \text{ or } Y \geqslant v_1^*, Z > v_2^*)}. \tag{27}$$

These two probabilities are readily calculated, as described in Appendix B.

If $v_0^* > v_1^*$ at the ESS then an ally is inevitably stronger than his buddy. If $v_1^* > v_0^*$, however, then it is possible for the buddy to be the stronger. Thus another probability of interest is the probability that a buddy is larger at the ESS than an ally who helps him, i.e.,

$$p_{ba} = \frac{\mathrm{Prob}(v_1^* > Y > X > v_0^*, Z > v_2^*)}{\mathrm{Prob}(X > v_0^*, Y < v_1^*, Z > v_2^*)} \tag{28}$$

(which is zero if $v_0^* \geqslant v_1^*$). A related probability of interest is the probability that an intruder is bigger at the ESS than an ally who intervenes, namely,

$$p_{ca} = \frac{\mathrm{Prob}(Z > X > v_0^*, Y < v_1^*, Z > v_2^*)}{\mathrm{Prob}(X > v_0^*, Y < v_1^*, Z > v_2^*)}. \tag{29}$$

These two probabilities are also readily calculated, again as described in Appendix B. For an illustration, see Fig. 9. Note in particular that allies are predicted to be larger than their buddies unless the elasticity of territorial pressure is very high—in that case it may even pay to help a stronger neighbor because a lot of territory is up for renegotiation should the neighbor be usurped.

7. A case study: the Australian fiddler crab

One of the best-documented examples of territory holders coming to the assistance of neighboring territory holders is seen in the behavior of the fiddler crab *Uca mjoebergi*, which breeds in mixed-sex colonies on inter-tidal mudflats in Australia (Backwell and Jennions, 2004). Backwell and Jennions (2004) tracked 268 floaters until they saw them fight a resident. Only 17 of 268 cases (6.3%) ended with an intervention, suggesting that it is a relatively rare occurrence in these crabs ($p_i \approx 0.063$). Here we examine the wealth of behavioral data that has accumulated on this species (and, as necessary, related species) with the aim of understanding why the helping behavior occasionally arises.

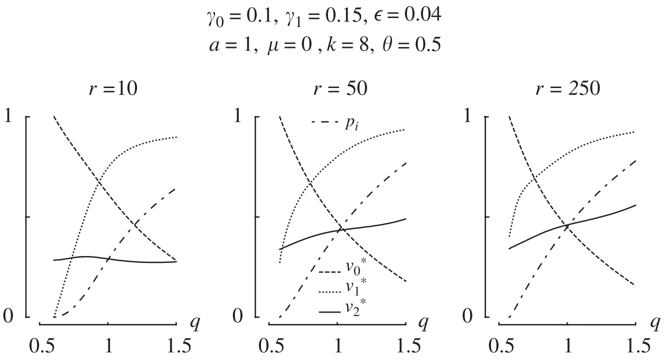

Fig. 7. An example of the ESS as a function of synergicity q for $q > q_c$, where $q_c \approx 0.606$ for $r = 10$, $q_c \approx 0.579$ for $r = 50$ and $q_c \approx 0.576$ for $r = 250$.

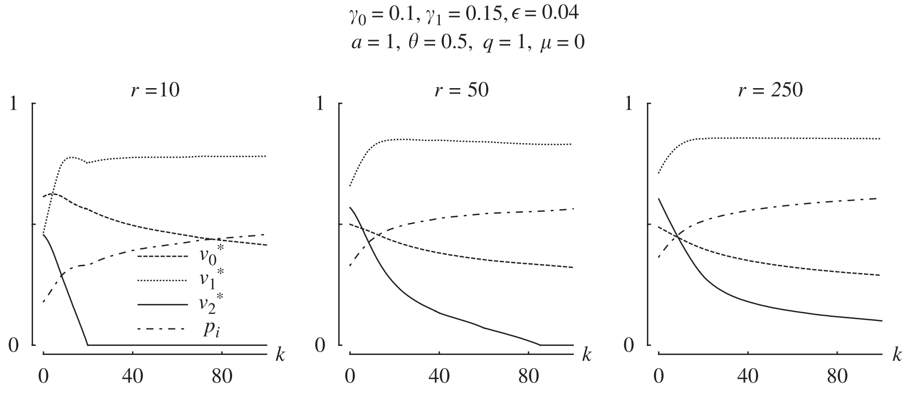

Fig. 6. An example of the ESS as a function of k, a measure of the sensitivity of fighting costs to strength difference. Note that this is a boundary ESS for $k \geqslant k_2^-$ where $k_2^- \approx 19.8$ for $r = 10$, $k_2^- \approx 85.4$ for $r = 50$ and $k_2^- \approx 400$ for $r = 250$.

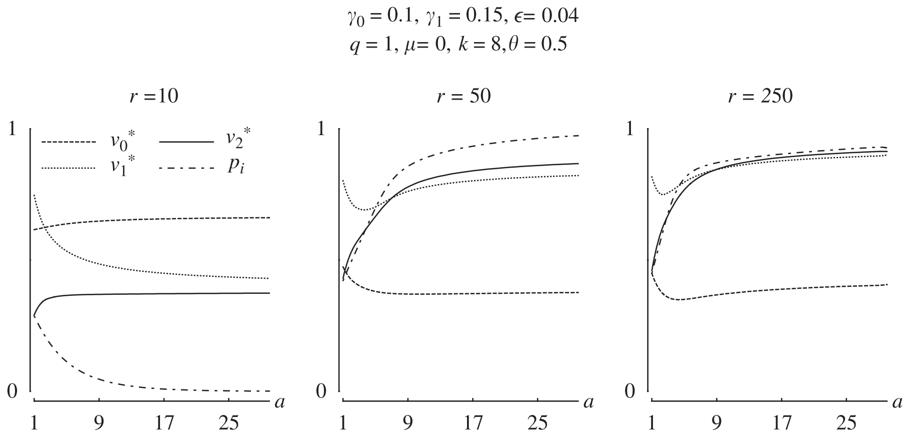

Fig. 8. An example of the ESS as a function of a, an inverse measure of variance in fighting strength, for values of a between 1 (corresponding to maximum variance) and 30 (5% of maximum).

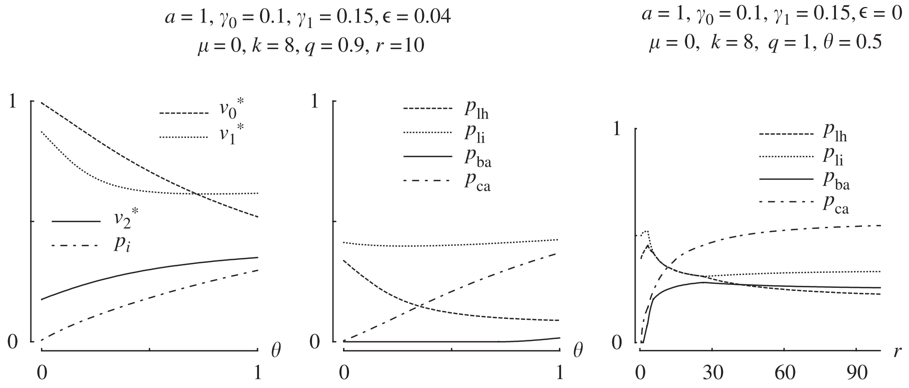

Fig. 9. Examples of relative-size probabilities for the ESS as a function of θ (which measures elasticity of territorial pressure) and as a function of r (which measures reliability of strength difference as a predictor of fight outcome). In the last panel, which corresponds to Fig. 2, the asymptotic probabilities that a helped buddy is larger than a challenger, an ignored buddy is larger than a challenger, a helped buddy is larger than an ally and a challenger is larger than a helping ally asymptote to $p_{lh}^{\infty} \approx 0.198$, $p_{li}^{\infty} \approx 0.336$, $p_{ba}^{\infty} \approx 0.248$ and $p_{ca}^{\infty} \approx 0.576$, respectively, as $r \to \infty$.

Owner's advantage (μ): Our model allows for the possibility of an owner's home advantage in that, all else being equal, the probability of winning a territorial contest exceeds $\frac{1}{2}$ simply by virtue of prior ownership. The ownership advantage in fiddler crabs is often considerable, and seems to come about by having both a foothold and a retreat (Jennions and Backwell, 1996; Pratt et al., 2003; Fayed et al., 2008). Backwell and Jennions (2004) note that unassisted residents had the same median size as the challengers (51% were bigger), yet unassisted residents won 71% of fights, suggesting $\frac{1}{2}(1+\mu) \approx 0.71$ or $\mu \approx 0.42$. This value is somewhat lower than the ownership advantage that can be calculated from other behavioral studies on the same species (Morrell et al., 2005; Fayed et al., 2008), but it was derived from observations made in the same place and time as the interventions were observed and therefore considered particularly appropriate.

Reliability of contest outcome (r): Over and above a residency advantage, we have assumed that larger (or stronger) individuals tend to win fights over smaller (or weaker) ones, although we have also allowed for an element of chance through our reliability parameter r. There is considerable evidence that, all else being equal, larger crabs are more likely to win fights over smaller crabs, for example in *Ilyoplax pusilla* (Wada, 1993), *Uca annulipes* (Jennions and Backwell, 1996) and *U. mjoebergi* (Morrell et al., 2005). Nevertheless, small individuals occasionally beat larger individuals, particularly if the size difference is small, so the outcome of these fights is not entirely predictable on the basis of size. Figure 3 of Pratt et al. (2003, p. 949) provides a graphical representation of the fitted relationship in *Uca pugilator*, in which the probability of winning varies sigmoidally with the size difference of the contestants; an analogous graph is Figure 2 of Takahashi et al. (2001, p. 95). Visually comparing Pratt et al's graph with theoretical distributions (cf. Fig. 1b of this paper) suggests an r value in the region of 10—certainly no less than 1, and unlikely more than 100.

Cost of fighting as a function of size difference (k): Evidence that more evenly size-matched opponents have longer (and presumably more costly) fights is widespread in the fiddler crab literature, e.g., in *U. annulipes* (Jennions and Backwell, 1996), *U. pugilator* (Pratt et al., 2003) and *U. mjoebergi* (Morrell et al., 2005). In all cases the duration of the contest is negatively correlated with the absolute difference in size between contestants, with the longest fights between closely matched individuals. The size of k, a measure of the sensitivity of the fighting cost with respect to strength difference, is challenging to estimate, but we note that when individuals were one and two size-classes different in size, then the mean durations of fights were about 25% and 15% of the duration when there was no size difference (Pratt et al., 2003, Table 2) suggesting a value of k in the order $k = 8$ (Fig. 1). By contrast, the fitted model for contest duration (Y) vs size difference ($X, 0 \leqslant X \leqslant 14$) for *U. mjoebergi* was $Y = -0.57X + 19.56$, suggesting a decline of only about 40% in fight duration with maximum size difference, and therefore a value of k considerably less than 2.

Extent of synergy in coalitions (q): Backwell and Jennions (2004) found that assisted residents were evicted during contests significantly less often than unassisted residents (12% compared to 29%), yet somewhat surprisingly the coalition did occasionally fail to win. Taking into account the fact that the ally was generally larger than the floater, then this suggests a value of q considerably less than 1, otherwise two individuals (one with residency advantage) would much more frequently beat off the intruder.

Elasticity of territorial pressure (θ): Our model assumes a decline in territorial pressure as the distance to the burrow increases. In support, several studies have reported that male fiddler crabs more vigorously defend their territories the closer they are to them, e.g., in *Uca terpsichores* (Zucker, 1974) and *Uca vomeris* (Hemmi and Zeil, 2003). We have also proposed that larger individuals end up with larger territories. We can find few observational data to confirm or refute this assertion, but the fiddler crab *Ilyoplax pusilla* in Japan does show a positive correlation between body size and territory size (Wada, 1993). In short, we can say very little about the likely size of θ. While we suspect that θ is non-zero (such that it is not completely egalitarian), we also expect that it is considerably less than 1 (otherwise this asymmetry would likely have been reported).

Comparison of predictions with observations: The detailed summary provided by Backwell and Jennions (2004) allows us to estimate p_{lh}, p_{li}, p_{ba} and p_{ca} as 0.06, 0.49, 0 and 0.18, respectively, such that helped residents tended to be smaller than the challenger (unassisted residents were sometimes larger and sometimes smaller), and allies were always larger than the challenger. Although our model was not intended as a specific model of any particular system, it is reassuring that we can fit a model with a plausible range of parameter values that simultaneously helps us understand both the relatively low incidence of neighbor intervention and the various size relationships among allies, buddies and challengers. Thus, assuming the above parameter values and setting θ such that $p_i = \frac{17}{268}$ produces predicted probabilities p_{lh}, p_{li}, p_{ba} and p_{ca} of 0, 0.46, 0, and 0.18, respectively, which are not far from the actual estimates based on observations. That many of the relevant parameters can be directly estimated indicates that our model is reasonably well grounded biologically. Note that there is nothing absolute about $p_{lh} = 0$ or $p_{ba} = 0$: as Fig. 9 demonstrates, both probabilities can be non-zero under the appropriate conditions.

8. Discussion

We have used a game-theoretic model to establish that intervention by stronger neighbors on behalf of weaker neighbors—and sometimes stronger ones—can be evolutionarily stable in the absence of any reciprocity. A general explanation for this phenomenon was identified by Getty (1987) over 20 years ago, and subsequently categorized by Mesterton-Gibbons and Dugatkin (1992, p. 274) as an instance of by-product mutualism, in which the resident incidentally benefits from the ally's self-interested intervention. Although our approach invokes the same fundamental arguments as Getty (1987) in explaining neighbor intervention, we have constructed a more elaborate and directly parameterizable model, and we have incorporated effects that Getty did not consider. Most importantly, we have explicitly incorporated non-zero variance of strength; and we have explicitly identified two separate components of the costs of renegotiation, i.e., fighting costs with a new neighbor and potential loss of territory, the latter being strength-dependent.

Although the general argument that neighbor intervention evolves to reduce renegotiation costs is appealing, formal comparison of our discrete and continuous models shows that neighbor intervention cannot be evolutionarily stable when strength difference is a perfectly reliable predictor of fight outcome ($\rho \to 1$ in the discrete model, $r \to \infty$ in the continuous model) without variance in strength: for neighbor intervention to be evolutionarily stable at perfect reliability, some individuals must be better fighters than others. At perfect reliability in the discrete model, the strategy "help as ally, challenge as intruder" is invadable by "help as ally, don't challenge as intruder" because all challengers are destined to lose when facing a coalition; in turn, "help as ally, don't challenge as intruder" is weakly invadable by "ignore as ally, don't challenge as intruder" because there are no longer any challengers. By contrast, the interventional ESS of the continuous model with finite variance persists in the limit $r \to \infty$ of perfect reliability, as illustrated by Fig. 2. We note in passing that, at the other extreme, where strength difference is a completely unreliable reliable predictor of fight outcome ($\rho \to \frac{1}{2}\{1+\mu\}$ in the discrete model, $r \to 0$ in the continuous model), both models predict that helping is not evolutionarily stable.

Here two remarks are in order. First, although in practice reliability will never be perfect, we would expect the outcome at perfect reliability to be an excellent approximation of the outcome when reliability is merely high. Second, even if $r = 10$ for *Uca mjoebergi* is considered to be a relatively low value of reliability, there are likely many other systems—even among crabs—in which reliability is very much higher. Thus we expect that variance of strength is in practice a far more important driver of neighbor intervention than very low fighting cost—which, in the absence of variance, is essentially what is required for (2) to hold with imperfect reliability. In any event, because helping is evolutionarily stable in the discrete model only if $\gamma_1 < \gamma_0$ by (2) and (23) while in our continuous model we assumed $\gamma_1 > \gamma_0$, we have clearly established that finite variance allows neighbor intervention to be evolutionarily stable when the costs of fighting are too high—relative to those of negotiation—to support an interventional ESS in the absence of variance.

Nevertheless, helping neighbors is by no means a consistently profitable strategy even when individuals vary in their fighting strengths, and our model helps to identify these limits. For example, if strength difference is a highly unreliable predictor of the outcome of fights (r low, see Fig. 2), if the ally stands to lose its own territory in the act of helping its neighbor (ε high, see Fig. 3), if coalition formation is highly antergic (q low, see Fig. 7), if there is a very high probability that the resident wins simply because of ownership (μ high, see Fig. 5) or if there is a moderately high probability that the resident wins because of ownership and territorial pressure is highly inelastic (θ very low, see Fig. 10), then

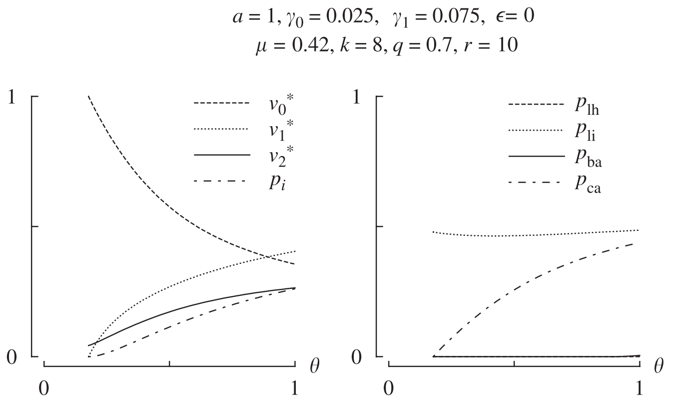

Fig. 10. Another example of the ESS as a function of elasticity θ of territorial pressure for $\theta > \theta_c \approx 0.177$ with associated relative-size probabilities. Here $p_i = \frac{17}{268}$ where $\theta \approx 0.377$, $p_{lh} = 0$, $p_{li} \approx 0.464$, $p_{ba} = 0$ and $p_{ca} \approx 0.176$.

neighbor intervention would not be expected to evolve. Conversely, as territorial pressure becomes more elastic (θ increases) and the effect of strength difference on territory size increases or the cost of fighting between mismatched opponents decreases (k increases), individuals should be more liable to help one another. The very fact that elasticity of territorial pressure θ so influences the outcome (see Fig. 4) demonstrates that the decision to help a neighbor can be a consequence not only of negotiation costs, but also of strength-dependent territorial benefits.

Typically all three ESS thresholds in our model respond in a consistent and predictable way to changes in any given parameter, but at different rates, at least under the range of conditions considered. For example, the principal effect of increasing ε (Fig. 3) is to increase the strength threshold v_0^* beyond which a potential ally should help its neighbor, and to reduce the strength threshold v_1^* below which a neighbor should be helped—as one might expect, the threshold v_2^* for the challenger is relatively insensitive to ε. By contrast, challengers have to be particularly strong (v_2^* high) to warrant a territory intrusion as the advantage to ownership, μ, increases (Fig. 5).

Our model also predicts a suite of conditional probabilities based on the ESS thresholds identified, including the probabilities that a helped or ignored resident is larger than a challenger (p_{lh} or p_{li}, respectively), and the probabilities that a resident or challenger is larger than a helping ally (p_{ba} or p_{ca}, respectively). Just as Backwell and Jennions (2004) have found, our model generally predicts that p_{lh} is smaller than p_{li}, so that helped individuals are generally relatively small when compared to unassisted individuals, although these two probabilities are equal if $v_1^* = 1$ (as when $r_1^- \leqslant r \leqslant r_1^+$ in Fig. 2, see Appendix B). This outcome can be understood on two levels—there is more to gain from helping a weak neighbor (since the ally can continue to enjoy a sizeable territory), and stronger neighbors can fend for themselves, so there is less need to get involved. While Backwell and Jennions (2004) observed that the ally was always larger than the helped resident, and our predictions are broadly consistent with this view under a range of plausible conditions, we have also identified circumstances when strong allies should come to the assistance of even stronger neighbors. Consider the consequences of not helping a buddy when there is high reliability r and high home advantage μ. Clearly under these conditions any successful challenger is likely to be much stronger than the former neighbor and therefore likely to inflict both a significant reduction of territory as well as a re-negotiation cost. Collectively these costs may be sufficient to far outweigh the cost of the intervention that would very likely have prevented it.

Our model was not based on reciprocal altruism, and indeed the strength-dependent nature of the emergent helping rules preclude such an outcome, just as reciprocal altruism has been ruled out in the fiddler crab study (Backwell and Jennions, 2004). Our model clearly supports earlier qualitative arguments that individuals may experience selection to help neighbors under the appropriate circumstances. Moreover, our formalization indicates that such an outcome is particularly likely when the winner of fights can be reliably predicted, the combined strength of the coalition is greater than the sum of its parts, a high proportion of the established territory is subject to renegotiation if the current neighbor loses, the ally's own probability of usurpation is low, and there is low fighting advantage to territory ownership. Clearly, not all systems will have these features. For example, damselflies and dragonflies (Odonata) are highly territorial, frequently defending adjoining territories from floating intruders. In these systems, however, there may be both a very high home ownership advantage, and a very high probability of losing one's territory if one is away fighting on behalf of a neighbor (e.g., see Corbet, 1999). Given the complex dependency of intervention on these ecological and behavioral parameters, we would therefore expect neighbor intervention to be a patchily distributed taxonomic phenomenon.

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Appendix A. Calculation of the reward function and ESS

From (18) and Table 2 we obtain

$$\begin{aligned} f_A = & \int_{v_2}^{1} g(z) \int_0^1 g(x) \int_0^1 \left\{\frac{1}{2}b\theta(y-z) - c_0(x,z)\right\} \\ & \times p_I(z-y) g(y)\,\mathrm{d}y\,\mathrm{d}x\,\mathrm{d}z \\ & + \int_{v_2}^{1} g(z) \int_{u_0}^{1} g(x) \int_0^{u_1} \left\{(1-\varepsilon)\left\{\frac{1}{2}b\theta(y-z)\right.\right. \\ & \left. -c_0(x,z)\right\} p_I(z-q\{x+y\}) \\ & - \{\varepsilon b\xi(x,y) + c_{21}(x,y,z)\} - \left\{\frac{1}{2}b\theta(y-z)\right. \\ & \left.\left. -c_0(x,z)\right\} p_I(z-y)\right\} g(y)\,\mathrm{d}y\,\mathrm{d}x\,\mathrm{d}z \end{aligned} \tag{A.1}$$

implying

$$\begin{aligned} \frac{\partial f_A}{\partial u_0} = & -g(u_0) \int_{v_2}^{1} g(z) \int_0^{u_1} \left\{(1-\varepsilon)\left\{\frac{1}{2}b\theta(y-z) - c_0(u_0,z)\right\}\right. \\ & \times p_I(z-q\{u_0+y\}) \\ & - \{\varepsilon b\xi(u_0,y) + c_{21}(u_0,y,z)\} - \left\{\frac{1}{2}b\theta(y-z)\right. \\ & \left.\left. -c_0(u_0,z)\right\} p_I(z-y)\right\} g(y)\,\mathrm{d}y\,\mathrm{d}z \end{aligned} \tag{A.2}$$

and

$$\begin{aligned} \frac{\partial f_A}{\partial u_1} = & g(u_1) \int_{v_2}^{1} g(z) \int_{u_0}^{1} \left\{(1-\varepsilon)\left\{\frac{1}{2}b\theta(u_1-z)\right.\right. \\ & \left. -c_0(x,z)\right\} p_I(z-q\{x+u_1\}) \\ & - \varepsilon b\xi(x,u_1) - c_{21}(x,u_1,z) - \left\{\frac{1}{2}b\theta(u_1-z)\right. \\ & \left.\left. -c_0(x,z)\right\} p_I(z-u_1)\right\} g(x)\,\mathrm{d}x\,\mathrm{d}z \end{aligned} \tag{A.3}$$

after simplification. Also, from (19) and Table 3 we obtain

$$\begin{aligned} f_C = & \int_{u_2}^{1} g(x) \int_0^1 g(y) \int_0^1 \{p_I(x-y)\{b\xi(x,z) \\ & - c_0(x,z)\} - c_1(x,y)\} g(z)\,\mathrm{d}z\,\mathrm{d}y\,\mathrm{d}x \\ & + \int_{u_2}^{1} g(x) \int_0^{v_1} g(y) \int_{v_0}^{1} \{\{p_I(x-q\{y+z\}) - p_I(x-y)\} \\ & \times\{b\xi(x,z) - c_0(x,z)\} - c_{12}(x,y,z) + c_1(x,y)\} g(z)\,\mathrm{d}z\,\mathrm{d}y\,\mathrm{d}x \end{aligned} \tag{A.4}$$

implying

$$\begin{aligned} \frac{\partial f_C}{\partial u_2} = & -g(u_2)\left\{\int_0^1 g(y) \int_0^1 \{p_I(u_2-y)\{b\xi(u_2,z) - c_0(u_2,z)\}\right. \\ & - c_1(u_2,y)\} g(z)\,\mathrm{d}z\,\mathrm{d}y \\ & + \int_0^{v_1} g(y) \int_{v_0}^{1} \{\{p_I(u_2-q\{y+z\}) - p_I(u_2-y)\}\{b\xi(u_2,z) \\ & \left. - c_0(u_2,z)\} - c_{12}(u_2,y,z) + c_1(u_2,y)\} g(z)\,\mathrm{d}z\,\mathrm{d}y\right\}. \end{aligned} \tag{A.5}$$

Strategy v is a strong ESS in the sense of Maynard Smith (1982) if v uniquely maximizes $f(u,v)$ defined by (17) as a function of u (see, e.g., Mesterton-Gibbons, 2001). Accordingly, for an interior ESS we require the gradient of f to vanish and the Hessian of f to be negative-definite at $u=v$ (see, e.g., Luenberger, 1984), where the Hessian $H(u)$ of f is the symmetric matrix defined by $H_{ij}=\partial^2 f/\partial u_i \partial u_j$ for $i,j=0,1,2$. On setting $u_0=v_0$, $u_1=v_1$ and $u_2=v_2$ in (A2), (A3) and (A5) and changing the integration variable x in (A.3) to y, it follows that (20) implies (22) because $g(s)\neq 0$ for $s\in(0,1)$. Moreover, using $\chi_{01}(v)$ to denote $\partial^2 f_A/\partial u_0 \partial u_1|_{u_0=v_0,u_1=v_1}$, from (A2) and (A3) and (A5) with (15), (13), (8), (10) and (21) we obtain

$$
\begin{aligned}
\chi_0(v) = {} & -g'(v_0)\int_{v_2}^{1} g(z)\int_0^{v_1}\Big\{(1-\varepsilon)\Big\{\frac{1}{2}b\theta(y-z)-K_0\Big\} \\
& \times p_I(z-q\{v_0+y\})-\{\varepsilon b\xi(v_0,y)+c_{21}(v_0,y,z)\} \\
& -\Big\{\frac{1}{2}b\theta(y-z)-K_0\Big\}p_I(z-y)\Big\}g(y)\,\mathrm{d}y\,\mathrm{d}z \\
& -g(v_0)\int_{v_2}^{1} g(z)\int_0^{v_1}\Big\{-q(1-\varepsilon)\Big\{\frac{1}{2}b\theta(y-z)-K_0\Big\} \\
& \times p_R'(q\{v_0+y\}-z) \\
& -\frac{1}{2}\varepsilon b\theta-\frac{1}{2}qK'(q\{v_0+y\}-z)\Big\}g(y)\,\mathrm{d}y\,\mathrm{d}z,
\end{aligned}
\tag{A.6}
$$

$$
\begin{aligned}
\chi_1(v) = {} & g'(v_1)\int_{v_2}^{1} g(z)\int_{v_0}^{1}\Big\{(1-\varepsilon)\Big\{\frac{1}{2}b\theta(v_1-z)-K_0\Big\} \\
& \times p_I(z-q\{x+v_1\}) \\
& -\varepsilon b\xi(x,v_1)-c_{21}(x,v_1,z)-\Big\{\frac{1}{2}b\theta(v_1-z)-K_0\Big\} \\
& \times p_I(z-v_1)\Big\}g(x)\,\mathrm{d}x\,\mathrm{d}z \\
& +g(v_1)\int_{v_2}^{1} g(z)\int_{v_0}^{1}\Big\{-q(1-\varepsilon)\Big\{\frac{1}{2}b\theta(v_1-z)-K_0\Big\} \\
& \times p_R'(q\{x+v_1\}-z) \\
& +\frac{1}{2}(1-\varepsilon)b\theta p_I(z-q\{x+v_1\})-\frac{1}{2}b\theta p_I(z-v_1) \\
& +\frac{1}{2}\varepsilon b\theta-\frac{1}{2}qK'(q\{x+v_1\}-z)+\Big\{\frac{1}{2}b\theta(v_1-z)-K_0\Big\} \\
& \times p_R'(v_1-z)\Big\}g(x)\,\mathrm{d}x\,\mathrm{d}z,
\end{aligned}
\tag{A.7}
$$

$$
\begin{aligned}
\chi_{01}(v) = {} & -g(v_0)g(v_1)\int_{v_2}^{1} g(z)\Big\{(1-\varepsilon)\Big\{\frac{1}{2}b\theta(v_1-z)-K_0\Big\} \\
& \times p_I(z-q\{v_0+v_1\}) \\
& -\{\varepsilon b\xi(v_0,v_1)+c_{21}(v_0,v_1,z)\}-\Big\{\frac{1}{2}b\theta(v_1-z)-K_0\Big\} \\
& \times p_I(z-v_1)\Big\}\,\mathrm{d}z
\end{aligned}
\tag{A.8}
$$

and

$$
\begin{aligned}
\chi_2(v) = {} & -g'(u_2)\Big\{\int_0^1 g(y)\int_0^1\{p_I(u_2-y)\{b\xi(u_2,z)-K_0\} \\
& -c_1(u_2,y)\}g(z)\,\mathrm{d}z\,\mathrm{d}y \\
& +\int_0^{v_1} g(y)\int_{v_0}^{1}\{p_I(u_2-q\{y+z\})-p_I(u_2-y)\} \\
& \times\{b\xi(u_2,z)-K_0\} \\
& -c_{12}(u_2,y,z)+c_1(u_2,y)\}g(z)\,\mathrm{d}z\,\mathrm{d}y\Big\} \\
& -g(u_2)\Big\{\int_0^1 g(y)\int_0^1\{p_R'(y-u_2)\{b\xi(u_2,z)-K_0\} \\
& -K'(u_2-y)\}g(z)\,\mathrm{d}z\,\mathrm{d}y+\frac{1}{2}b\theta p_I(u_2-y)\}g(z)\,\mathrm{d}z\,\mathrm{d}y \\
& +\int_0^{v_1} g(y)\int_{v_0}^{1}\{\{p_R'(q\{y+z\}-u_2)-p_R'(y-u_2)\}\{b\xi(u_2,z) \\
& -K_0\}+K'(u_2-y) \\
& +\frac{1}{2}b\theta\{p_I(u_2-q\{y+z\})-p_I(u_2-y)\}-K'(u_2-q\{y+z\})\} \\
& \times g(z)\,\mathrm{d}z\,\mathrm{d}y\Big\},
\end{aligned}
\tag{A.9}
$$

where primes denote differentiation with respect to argument, i.e., from (6), (10) and (12), $p_R'(\Delta s)=-4^{1-2r}\{4-|\Delta s|^2\}^{r-1}\ln(\frac{1}{2}\{1+\mu\})\,p_R(\Delta s)/\{B(\frac{1}{2}+\frac{1}{4}\Delta s,r,r)\ln(2)\}$ and $K'(\Delta s)=-\frac{1}{2}kK_1\Delta s\{1-\frac{1}{4}\,|\Delta s|^2\}^{k-1}$. From (17) and (21) the Hessian at $u=v$ is

$$
H(v)=\begin{bmatrix} q_A\chi_0(v) & q_A\chi_{01}(v) & 0 \\ q_A\chi_{01}(v) & q_A\chi_1(v) & 0 \\ 0 & 0 & q_C\chi_2(v) \end{bmatrix}
\tag{A.10}
$$

with eigenvalues λ_0, λ_1, λ_2 where λ_0 and λ_1 are the roots of the quadratic equation $\lambda^2-q_A\{\chi_0(v)+\chi_1(v)\}\lambda-q_A^2\chi_3(v)=0$, $\lambda_2=q_C\chi_2(v)$ and

$$
\chi_3(v)=\chi_{01}(v)^2-\chi_0(v)\chi_1(v).
\tag{A.11}
$$

Because $\lambda_0+\lambda_1=q_A\{\chi_0(v)+\chi_1(v)\}$ and $\lambda_0\lambda_1=-q_A^2\chi_3(v)$, $H(v)$ has negative eigenvalues when all components of the vector $\chi(v)=(\chi_0(v),\chi_1(v),\chi_2(v),\chi_3(v))$ are negative; then v defined by (22) uniquely maximizes $f(u,v)$ and is therefore a strong ESS. To illustrate: in Fig. 2 for $r=50$ the ESS is $v=(0.4110,0.9613,0.4268)$ with $\chi_0(v)/b=-0.1134$, $\chi_1(v)/b=-0.2067\times 10^{-1}$, $\chi_2(v)/b=-0.1786$ and $\chi_3(v)/b=-0.2238\times 10^{-2}$, where b denotes the marginal value of territory expansion. (Strictly speaking, the negativity of $\chi(v)$ guarantees only a local maximum; however, it is readily verified by numerical means that the maximum is unique and hence the ESS is global.)

For a boundary ESS, necessary conditions (20) must be modified appropriately. If $v_i^*=0$ for some i, then $\partial f/\partial u_i|_{u=v^*}=0$ becomes $\partial f/\partial u_i|_{u=v^*}\leqslant 0$; and if $v_i^*=1$ for some i, then $\partial f/\partial u_i|_{u=v^*}=0$ becomes $\partial f/\partial u_i|_{u=v^*}\geqslant 0$. Suppose, for example, that $v=(v_0,v_1,0)$ with $0<v_0,v_1<1$ is a boundary ESS on the bottom face of the strategy cube where $u_2=0$. Then in place of (20) we require $\partial f_A/\partial u_0=0=\partial f_A/\partial u_1$ and $\partial f_C/\partial u_2\leqslant 0$ for $u_0=v_0$, $u_1=v_1$ and $u_2=0$. When v_0 and v_1 satisfying $\partial f_A/\partial u_0=0=\partial f_A/\partial u_1$ have been found numerically, we still require $\chi_0(v)<0$, $\chi_1(v)<0$ and $\chi_3(v)<0$ for $v=(v_0,v_1,0)$ to yield a maximum on the boundary; however, $\chi_2(v)<0$ is replaced by $\partial f_C/\partial u_2|_{u_2=0}<0$ unless $\partial f_C/\partial u_2|_{u_2=0}=0$ (which, by (4) and (A5), holds for all $a>1$, i.e., for any non-uniform distribution), in which case we still require $\chi_2(v)<0$. To illustrate: in Fig. 2 for $r=3$ the ESS is $v=(0.8263,0.5528,0)$ with $\chi_0(v)/b=-0.6475\times 10^{-1}$, $\chi_1(v)/b=-0.7996\times 10^{-2}$, $\chi_2(v)/b=-0.3874\times 10^{-1}$, $\chi_3(v)/b=-0.4852\times 10^{-3}$ and $\partial f_C/\partial u_2|_{u_2=0}/b=-0.4057\times 10^{-2}$. (We note in passing that the critical value r_2^+ is found by setting $v_2=0$ in (20) and solving for v_0, v_1 and r; likewise with $v_1=1$ for r_1^- and r_1^+.) Similarly, for $v=(v_0,1,v_2)$ with $0<v_0,v_2<1$ to be a boundary ESS on the back face of the strategy cube where $u_1=1$ we require $\partial f_A/\partial u_0=0=\partial f_C/\partial u_2$ and $\partial f_A/\partial u_1\geqslant 0$ for $u=v=(v_0,1,v_2)$ with $\chi_0(v)<0$, $\chi_2(v)<0$ and either $\partial f_A/\partial u_1|_{u_1=1}>0$ (for $a=1$) or $\partial f_A/\partial u_1|_{u_1=1}=0$ and $\chi_1(v)<0$ (for $a>1$). To illustrate in Fig. 2 for $r=10$ the ESS is $v=(0.5172,1,0.2732)$ with $\chi_0(v)/b=-0.1076$, $\chi_1(v)/b=-0.1275\times 10^{-1}$, $\chi_2(v)/b=-0.1251$, $\chi_3(v)/b=-0.1325\times 10^{-2}$ and $\partial f_C/\partial u_2|_{u_2=0}/b=0.4414\times 10^{-3}$.

As for the left-hand face of the strategy cube where $u_0=0$: although v_1 and v_2 satisfying $\partial f_A/\partial u_1=0=\partial f_C/\partial u_2$ with $u_0=0$,

$u_1 = v_1$ and $u_2 = v_2$ may be found numerically, we obtain $\partial f_A/\partial u_0|_{u_0=0} > 0$ for $a = 1$ and $\partial f_A/\partial u_0|_{u_0=0} = 0$, $\partial^2 f_A/\partial u_0^2|_{u_0=0} > 0$ for $a > 1$. Thus no boundary ESS of the form $v = (0, v_1, v_2)$ exists. A different argument establishes that there are no ESSs on either the front face of the cube where $u_1 = 0$ or the right-hand face where $u_0 = 1$. Let an overbar denote that strategy $\overline{u}$ lies on either of these two faces, i.e., either $\overline{u}_1 = 0$ or $\overline{u}_0 = 1$. Then $\overline{v}$ cannot be a strong ESS, because, from (17), (A1), and (A4), for any $\overline{u} = (\overline{u}_0, \overline{u}_1, \overline{v}_2)$ we have $f(\overline{u}, \overline{v}) = q_A f_A(\overline{u}_0, \overline{u}_1, \overline{v}_2) + q_C f_C(\overline{v}_0, \overline{v}_1, \overline{v}_2) = q_A f_A(\overline{u}_0, \overline{u}_1, \overline{v}_2) + q_C f_C(\overline{v}_0, \overline{v}_1, \overline{v}_2) = f(\overline{v}, \overline{v})$, so that $u \neq v$ exist for which $f(v, v)$ fails to exceed $f(u, v)$. It is still possible for $\overline{v}$ to be a weak ESS, which requires $f(\overline{v}, \overline{u}) > f(\overline{u}, \overline{u})$ for all such $\overline{u}$ (see, e.g., Mesterton-Gibbons, 2001). But here $f(\overline{u}, \overline{u}) = q_A f_A(\overline{u}_0, \overline{u}_1, \overline{v}_2) + q_C f_C(\overline{u}_0, \overline{u}_1, \overline{v}_2) = q_A f_A(\overline{v}_0, \overline{v}_1, \overline{v}_2) + q_C f_C(\overline{u}_0, \overline{u}_1, \overline{v}_2) = f(\overline{v}, \overline{u})$ from (A.1), so that $f(\overline{v}, \overline{u})$ fails to exceed $f(\overline{u}, \overline{u})$ and even a weak ESS is ruled out. A similar argument applies to the top face where $u_2 = 1$: there cannot be an ESS of the form $v = (v_0, v_1, 1)$ because for any $u = (u_0, u_1, 1)$ we have both $f(u, v) = f(v, v)$, which rules out a strong ESS, and $f(u, u) = f(v, u)$, which rules out a weak one. In sum, by a combination of numerical experiment and analytical argument, we conclude that the only boundary ESSs are of the form $v = (v_0, v_1, 0)$ or $v = (v_0, 1, v_2)$. We note in passing that, although it may well be true that the weak-ESS condition "rarely applies to continuous games" (McGill and Brown, 2007, p. 408), it sometimes plays a critical role.

Appendix B. Calculation of relative-size probabilities

From (26), the probability that a resident in role B is larger than a challenger in role C at the ESS, conditional on being helped by his neighbor in role A, is

$$p_{lh} == \frac{\int_{v_2^*}^{v_1^*} g(y) \int_{v_2^*}^{y} g(z)\,dz\,dy}{\int_0^{v_1^*} g(y) \int_{v_2^*}^{1} g(z)\,dz\,dy} \tag{B.1}$$

if $v_1^* > v_2^*$ (as in Fig. 2), although $p_{lh} = 0$ if $v_2^* > v_1^*$ (as in Fig. 8 for low variance and intermediate reliability); and from (27), the probability that a resident in role B is larger than a challenger in role C at the ESS, conditional on being ignored by his neighbor in role A, is

$$p_{li} = \frac{\int_0^{v_0^*} g(x) \int_{v_2^*}^{1} g(y) \int_{v_2^*}^{y} g(z)\,dz\,dy\,dx + \int_{v_0^*}^{1} g(x) \int_{\max(v_1^*, v_2^*)}^{1} g(y) \int_{v_2^*}^{y} g(z)\,dz\,dy\,dx}{\int_0^{v_0^*} g(x) \int_0^{1} g(y) \int_{v_2^*}^{1} g(z)\,dz\,dy\,dx + \int_{v_0^*}^{1} g(x) \int_{v_1^*}^{1} g(y) \int_{v_2^*}^{1} g(z)\,dz\,dy\,dx}. \tag{B.2}$$

For example, with a uniform distribution (as in Figs. 2–7 and 9–10) we obtain

$$p_{lh} = \frac{(v_1^* - v_2^*)^2}{2v_1^*(1 - v_2^*)}, \quad p_{li} = \frac{1 - (2 - v_0^* v_2^*) v_2^* + (2v_2^* - v_1^*)(1 - v_0^*) v_1^*}{2(1 - \{1 - v_0^*\} v_1^*)(1 - v_2^*)} \tag{B.3}$$

if $v_1^* > v_2^*$ but $p_{lh} = 0$ and $p_{li} = (1 - v_2^*)/\{2(1 - \{1 - v_0^*\} v_1^*)\}$ if $v_2^* > v_1^*$. Note that (B1) and (B2), and hence the two expressions in (B.3), are identical if $v_1^* = 1$ (as when $r_1^- \leqslant r \leqslant r_1^+$ in Fig. 2; see Fig. 9).

From (28), the probability that a buddy is larger at the ESS than an ally who helps him is

$$p_{ba} = \begin{cases} 0 & \text{if } v_1^* \leqslant v_0^*, \\ \dfrac{\int_{v_0^*}^{v_1^*} g(x) \int_x^{v_1^*} g(y)\,dy\,dx}{\int_{v_0^*}^{1} g(x)\,dx \int_0^{v_1^*} g(y)\,dy} & \text{if } v_1^* > v_0^*. \end{cases} \tag{B.4}$$

In particular, for a uniform distribution, if $v_1^* > v_0^*$ then $p_{ba} = (v_1^* - v_0^*)^2 / 2v_1^*(1 - v_0^*)$. Finally, from (29), the probability that an intruder is bigger at the ESS than an ally who intervenes is

$$p_{ca} = \begin{cases} \dfrac{\int_{v_0^*}^{1} g(x) \int_x^{1} g(z)\,dz\,dx}{\int_{v_0^*}^{1} g(x)\,dx \int_{v_2^*}^{1} g(z)\,dz} & \text{if } v_2^* \leqslant v_0^*, \\ \dfrac{\int_{v_2^*}^{1} g(z) \int_{v_0^*}^{z} g(x)\,dx\,dz}{\int_{v_0^*}^{1} g(x)\,dx \int_{v_2^*}^{1} g(z)\,dz} & \text{if } v_2^* > v_0^*. \end{cases} \tag{B.5}$$

In particular, for a uniform distribution,

$$p_{ca} = \begin{cases} \dfrac{1}{2} \dfrac{1 - v_0^*}{1 - v_2^*} & \text{if } v_2^* \leqslant v_0^*, \\ \dfrac{(1 - 2v_0^* + v_2^*)}{2(1 - v_0^*)} & \text{if} v_2^* > v_0^*. \end{cases} \tag{B.6}$$

Note that $p_{ca} = \frac{1}{2}$ when $v_0^* = v_2^*$ (for any distribution).

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