



Defection on the bounty? Kinship and cooperative exploitation of a rich, essential but dangerous resource

Mike Mesterton-Gibbons^{a,*} , Ian C. W. Hardy^{b,1} 

^a Department of Mathematics, Florida State University, Tallahassee, FL, U.S.A.

^b School of Biosciences, University of Nottingham, Sutton Bonington Campus, Loughborough, Leics, U.K.

ARTICLE INFO

Article history:

Received 22 May 2020

Initial acceptance 28 December 2020

Final acceptance 1 February 2021

MS. number: A20-00384R

Keywords:

animal contest
evolutionarily stable strategy
game-theoretic model
host attack
parasitoid
predator
Sclerodermus

We develop a game-theoretic model to explore the question of whether two animals should cooperate in the dangerous activity of obtaining a rich and essential resource. We consider variation in the risks incurred to individuals and in how the activities of the two animals interact to influence the probability of success. We also consider that the animals may be relatives and thus share evolutionary interests. The model is general and can, for instance, be applied to mammalian predators attempting to capture and subdue large and dangerous prey or to female parasitoid wasps that attack and, if successful, paralyse aggressive hosts that then provide the only feeding resource for their offspring. This minimal model of cooperation contains three dimensionless parameters: vulnerability (the ratio between the average time for a lone attacker to subdue the defending resource and the average time for the defender to fatally strike the attacker), the dilution ratio (the extent to which attack by animals acting in tandem reduces a defender's ability to kill its attackers) and the relatedness between the potential attackers. The model predicts that higher values of all three parameters favour cooperation and that for small values cooperation is not evolutionarily stable. Cooperation can arise from an ancestral state of non-cooperation if values of all parameters are sufficiently high but cannot arise among non-relatives, irrespective of other parameter values. Once cooperation has emerged in a population, it can be maintained among non-relatives at modest values of dilution ratio and vulnerability. We discuss these general predictions in particular relation to the parasitoid genus *Sclerodermus*, in which multiple females may attack unusually large and aggressive hosts and in which host attack behaviour is mediated by kinship.

© 2021 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Essential resources for reproduction are sometimes rich, that is, they are of such a size that they can be exploited by multiple individuals with no significant reduction in reproductive benefit for any of the exploiters. A well-known example is a rare ephemeral food bonanza, such as a carcass on which juvenile ravens feed (Heinrich, 1989). Access to a carcass may be both essential to a juvenile's survival and uncertain, since the resource is often defended by resident adults, even though the resource is so great that use of it by one juvenile does not impinge on another's ability to feed, once access is gained. Nevertheless, attempting to exploit the resource is not especially dangerous: residents may defend their bonanza aggressively, but there is no significant risk to a juvenile raven of death or even serious injury.

By contrast, if a rich and essential prey or host resource is still alive, then attempting to exploit it may prove fatal. Henceforward,

we refer to a potentially fatal resource as a 'dangerous' one. It is convenient also to have a single term for a rich, essential and dangerous resource, and so we will refer to such a resource henceforward as a 'bounty' (which in other usage has two meanings, one of which captures the do-or-die aspect of essential and dangerous while the other captures abundance). Ungulates pursued by starving carnivores could exemplify such a bounty if sufficiently capable of inflicting fatal injury on their attackers; in this regard, Mukherjee and Heithaus (2013, p. 554) note the potential for physical injury or even death when wolves pursue elk and Packer (1986, p. 440) reports that predatory lions can be killed by buffalo, one of their largest species of prey. Hosts of some species of parasitoid wasps could likewise exemplify a bounty; in particular, for parasitoids in the genus *Sclerodermus* (Hymenoptera: Bethyliidae), beetle larvae hosts essential to reproduction are, when large, both dangerous and rich (Abdi, Hardy, Jucker, & Lupi, 2020; Abdi, Lupi, Jucker, & Hardy, 2020). Note that, in theory, an essential resource is one for which there is no alternative source of fitness, which in practice means that the resource is very rare.

Even if it is common for a resource to satisfy one or two of the three criteria for a bounty (that the resource is essential, that it is

* Corresponding author.

E-mail address: mesterto@math.fsu.edu (M. Mesterton-Gibbons).

¹ Present address: Department of Agricultural Sciences, PO Box 27, Viikki Campus, 00014 University of Helsinki, Finland.

rich, and that it is dangerous), how often a bounty occurs in nature is largely unknown. It is precisely in such circumstances that theoretical exploration can prove most useful, by answering basic questions about the ecological circumstances in which a phenomenon is most likely to be observed.

One such question, which we address here, is the following. Faced with an essential and rich but also dangerous resource (a bounty), should each of a pair of potential exploiters attack in tandem immediately, or hold back, remaining in the vicinity in the hope that the other will take the risk of attacking first? We expect the answer to depend on the attack capability of an attacker versus the aggressive defence or counterattack ability of the defender, and on the relative extents to which operating in tandem reinforces the strike capability of two attackers and/or weakens the defence capability of the resource. We also expect the answer to depend on the extent to which potential attackers share common evolutionary interests via relatedness, because in the field of behavioural evolution, inclusive fitness is often invoked to understand a range behaviours, including conflict resolution and cooperation (Davies, Krebs, & West, 2012; Hamilton, 1964). We explore the importance of all three factors in our analysis.

A standard game-theoretic framework for the study of cooperation is a 'cooperator's dilemma' whose payoffs incorporate relevant temporal aspects of the phenomenon at issue (Mesterton-Gibbons & Dugatkin, 1992). This framework has been used, for example, by Packer and Ruttan (1988) to predict the evolution of cooperative hunting in pairs, by Mesterton-Gibbons (1991) to analyse cooperative exploitation of oviposition sites by insects and by Mesterton-Gibbons and Dugatkin (1999) to study the evolution of delayed recruitment to food bonanzas via mutualistic information sharing at communal roosts in ravens. These models do not apply to a bounty, because they do not allow for the possibility that a resource may be dangerous to exploit (and in the second case the resource is not even rich). Nevertheless, the underlying framework is flexible, and here we utilize it to construct a new model for exploring factors that favour cooperative exploitation of a bounty. We begin by considering a single individual attempting to exploit a bounty, then consider the problem as a game between two unrelated individuals. Later we consider the influence of kinship between potential attackers. Details of the analyses including consideration of kinship are presented in two appendices. The model we develop is potentially applicable to many animal taxa.

In the case of *Sclerodermus* attacking beetle larvae, which we consider in the Discussion, the standard terms for the potential exploiters and resource in question would be parasitoid and host; whereas in the case of carnivores attacking ungulates, the standard terms would be predators and prey. We use the terms predator and prey in developing our model, not to suggest that potential mammalian examples of a bounty are either more common or more important than invertebrate examples, but because predators can be understood to include parasitoids and prey can be understood to include hosts, and we wish to emphasize the breadth of applicability of our model. Likewise, an act of aggression would typically be called a sting, bite or kick, according to whether the actor is an invertebrate attacker, an invertebrate defender or a mammalian attacker, or a mammalian defender; however, we will instead use the word strike to cover all such cases using just one term.

THE GAME AMONG UNRELATED INDIVIDUALS

One Attacker, One Defender

We consider a predator attacking a potential prey that may defend itself and is thus dangerous. For example, a parasitoid may attempt to suppress a potential host by stinging it with paralyzing venom and the host may attempt to kill the parasitoid by biting it

into pieces; Abdi, Hardy et al. (2020) and Abdi, Lupi et al. (2020) document empirical examples. Similarly, both zebras and buffalo may be dangerous to hunting lions (Scheel & Packer, 1991), and snakes may be dangerous to predatory birds (Bowman, 2003; Frye & Gerhardt, 2001).

Let random variable S denote the time that elapses until the attacker is able to deliver a strike that is fatal or at least inactivating; for example, a parasitoid may deliver a paralyzing sting, or a predator may wound its prey nonfatally, but such that its defence capabilities are greatly diminished (Mukherjee & Heithaus, 2013, p. 555). We assume that S is exponentially distributed with mean τ , so that the attacker is delivering disabling strikes at a rate of $1/\tau$ per unit time. Note that the predator may be attacking the prey at a much higher rate than $1/\tau$ because the prey may frequently shake its attacker off, and only disabling strikes concern us here. Thus, $\text{Prob}(S > t) = e^{-t/\tau}$, and the density function for the distribution is g , where

$$g(t) = \frac{1}{\tau} e^{-t/\tau} \quad (1)$$

for all $t > 0$. Correspondingly, let random variable B denote the time that elapses until the defender is able to deliver a fatal blow. We again assume that B is exponentially distributed, but with mean T , so that the defender is delivering fatal strikes at a rate of $1/T$ per unit time. Thus $\text{Prob}(B > t) = e^{-t/T}$ and the density function for the distribution is h , where

$$h(t) = \frac{1}{T} e^{-t/T}. \quad (2)$$

The attack has one of two outcomes: either the attacker disables the defender before it can deliver a fatal strike, or the defender kills the attacker before it is disabled. In the first case the attacker has fitness 1, in the second case its fitness is zero. The probability of reproduction is thus

$$p_R = \text{Prob}(S < B) = \iint_{0 < \xi < \eta < \infty} g(\xi) h(\eta) d\xi d\eta = \frac{T}{\tau + T} = \frac{1}{\theta + 1} \quad (3)$$

where

$$\theta = \frac{\tau}{T} \quad (4)$$

is the ratio between means of the two distributions. We note that the property of yielding fitness 1 with access to the resource and fitness 0 without access to the resource is the de facto definition of a rich and essential resource (when fitness is scaled with respect to its maximum value).

The larger the value of θ , the longer on average it takes a predator to disable a prey, compared to how long it takes on average for the prey to deliver a lethal strike. Thus, the higher the value of θ , the more vulnerable is a predator to being killed before it can subdue the prey and gain resources for ultimate reproduction: we refer to θ as the vulnerability. Our analysis will be valid for any $\theta > 0$.

For *Sclerodermus*, it has been shown that vulnerability is greater when hosts are larger (Abdi, Hardy et al., 2020; Abdi, Lupi et al., 2020), and so for this species we can use host size as a proxy for vulnerability. Nevertheless, we should not assume that vulnerability increases with prey size for other taxa, because at least among mammals there is evidence that small prey can be dangerous (Kerley, 2018).

Two Attackers (and One Defender)

We now suppose that two predators are present and either or both may attack the prey. If the attackers neither reinforce nor interfere with one another in the attack process, then the rate at which disabling strikes are delivered doubles from $1/\tau$ to $2/\tau$, reducing the mean time elapsing before a first disabling strike to $\tau/2$. There is likely, however, to be at least some reinforcement, the magnitude of which depends upon the strength of the confusion or dilution effect caused by the prey now having more than one active attacker (as observed in Florida scrub-jays, *Aphelocoma coerulescens*, attacking a snake; Bowman, 2003), so that the new rate of delivery exceeds $2/\tau$; although this effect is more commonly invoked in the context of additional prey confusing a predator (Lehtonen & Jaatinen, 2016) than in that of additional predators confusing a prey, the logic is the same. However, our analysis also allows for the possibility that the attackers interfere with one another (Packer & Ruttan, 1988), so that the new rate of delivery is intermediate between $1/\tau$ and $2/\tau$. Suppose that the new rate is $2q/\tau$, where $q > 1$ for reinforcement and $1/2 < q < 1$ for interference; $q = 1$ implies neither reinforcement nor interference, so that the effect of a second attacker is purely additive. We refer to the parameter q as the synergicity. This terminology is consistent with the use of the term by Mesterton-Gibbons and Sherratt (2007), with synergy for $q > 1$ and antergy for $q < 1$.

Now $\text{Prob}(S > t) = e^{-2qt/\tau}$, the mean of the distribution for S becomes $\tau/2q$ and the density function becomes g_D , where

$$g_D(t) = \frac{2q}{\tau} e^{-2qt/\tau} \tag{5}$$

for all $t > 0$ and D denotes that the predators attack as a duo. The greater the value of the synergicity q , the greater is the extent to which two predators reinforce one another in attacking the prey.

Correspondingly, the rate at which prey deliver fatal strikes changes from $1/T$ to α/T per unit time, so that the mean time until a fatal strike is delivered changes from T to T/α . It seems likely that $\alpha < 1$: it may be more difficult to deliver a fatal strike to one of a pair than to a lone individual because the effect of having multiple attackers reduces the defender's ability to manoeuvre effectively, with the effect being stronger when α is smaller. Nevertheless, our analysis allows for the possibility that a second attacker has no effect on the average time to a fatal strike ($\alpha = 1$) or even reduces it ($\alpha > 1$), if, for instance, the prey now has twice as many targets and doesn't get confused by multiple attackers. We refer to α as the manoeuvrability.

Because a stronger effect of dilution can manifest itself either as a higher value of q or as a lower value of α , or both, we use

$$\delta = \frac{q}{\alpha} \tag{6}$$

to measure the overall strength of the dilution effect; we refer to the ratio δ as the dilution ratio. From the discussion above, our expectation is that $\alpha < 1 < q$ and hence $\delta > 1$; however, our analysis allows for $\delta \leq 1$ as well. Because now $\text{Prob}(B > t) = e^{-\alpha t/T}$, the density function for the distribution of B becomes h_D where

$$h_D(t) = \frac{\alpha}{T} e^{-\alpha t/T} \tag{7}$$

so that the probability that one of the attackers delivers a disabling strike to the prey before it can deliver a fatal strike to either attacker is

$$p_D = \text{Prob}(S < B) = \iint_{0 < \xi < \eta < \infty} g_D(\xi) h_D(\eta) d\xi d\eta = \frac{2qT}{2qT + \alpha\tau} = \frac{2\delta}{2\delta + \theta} \tag{8}$$

by equations (4) and (6).

Attacker Strategies

Suppose that the predators are in a game consisting of each deciding whether and when to attack the prey. Each predator has two possible strategies. To cooperate means to start attacking the prey immediately, thus sharing the risk of being killed when the other individual also cooperates, but also to take all of the risk if the other individual does not attack. To defect means to wait for the other individual to be the first attacker. Defectors thus engage with the prey only if necessary, that is, when the other animal has been killed by the prey (if the focal individual is defecting against a cooperator) or when losing the war of attrition that ensues after defecting against a defector (see below). We term defection strategy 1 and cooperation strategy 2.

The payoff to a cooperator against a defector is 1 if it succeeds in disabling the prey before it gets killed, and otherwise 0. That is, the payoff to a cooperator against a defector is $a_{21} = p_R \times 1 + (1 - p_R) \times 0 = p_R$, where p_R is defined by equation (3). The payoff to a defector against a cooperator is 1 if the cooperator disables the prey before it gets killed, or if the cooperator is killed but the defector subsequently disables the prey, and otherwise 0. That is, the payoff to a defector against a cooperator is

$$a_{12} = p_R \times 1 + (1 - p_R) \times \{p_R \times 1 + (1 - p_R) \times 0\} = p_R(2 - p_R) = \frac{1 + 2\theta}{(1 + \theta)^2} \tag{9}$$

by equation (3).

If neither individual is willing ever to attack, then neither gains any resources for survival or reproduction. So, if neither animal is willing to be the first attacker in the first instance, then there will follow a war of attrition, with each defector hoping that the other individual will commence an attack. We assume that the two individuals are equally likely to attack first. It follows that the average of the two payoffs we have calculated, namely,

$$a_{11} = \frac{1}{2} \times p_R + \frac{1}{2} \times \frac{1 + 2\theta}{(1 + \theta)^2} = \frac{2 + 3\theta}{2(1 + \theta)^2} \tag{10}$$

is the payoff to a defector against a defector.

We note that our defector is more of a reluctant attacker: a 'true' defector would simply not attack – even after the death of its cooperator. The payoff to such a defector against a cooperator would clearly be p_R , which is always lower than the payoff in equation (9); and the payoff to such a defector against another defector would be zero, which is lower than the payoff in equation (10). So the strategy of defection in our chosen sense would always dominate a strategy of true defection.

If the individuals cooperate, then the three pertinent events that must happen at different times during the interval $(0, \infty)$ are the death of the focal individual, the death of the nonfocal individual and the suppression of the prey (and the eventual cause of death at some later time during $(0, \infty)$ for a predator that outlives the prey need not be specified, since it has no effect on our analysis). Let us denote these events by F , N and H , respectively. The six possible underlying temporal sequences of relevant events are as shown in

Table 1, where q_F is the probability that the prey kills the focal predator while the nonfocal predator survives at least until a later time, and q_N is the probability that the prey kills the nonfocal predator while the focal predator survives at least until a later time, so that $1 - q_F - q_N$ is the probability that both predators survive at least until a later time and therefore reproduce. By symmetry, $q_N = q_F$; moreover, $1 - q_F - q_N$ is the probability that the death of the prey precedes the death of either predator, that is, $1 - q_F - q_N = p_D$, where p_D is defined by equation (8). Thus $q_N = q_F = 1/2 (1 - p_D)$, and adding the terms in the final column of **Table 1** shows that the fitness to a cooperator against a cooperator is

$$a_{22} = q_N \times p_R + 1 - q_F - q_N = p_D + \frac{1}{2}(1 - p_D)p_R = \frac{1}{2\delta + \theta} \left\{ 2\delta + \frac{\theta}{2(1 + \theta)} \right\} \tag{11}$$

by equations (3), (4), (6) and (8). It follows that the payoff matrix A for the game is

$$\begin{array}{cc|cc}
 & D & C & \\
 \hline
 D & \begin{bmatrix} a_{11} & a_{12} \end{bmatrix} & & \\
 C & \begin{bmatrix} a_{21} & a_{22} \end{bmatrix} & & \\
 \hline
 & D & C & \\
 \hline
 D & \begin{bmatrix} \frac{2 + 3\theta}{2(1 + \theta)^2} & \frac{1 + 2\theta}{(1 + \theta)^2} \end{bmatrix} & & \\
 C & \begin{bmatrix} \frac{1}{\theta + 1} & a_{22} \end{bmatrix} & & \\
 \hline
 \end{array} \tag{12}$$

where C denotes cooperate, D denotes defect and a_{22} is defined by equation (11). Note that

$$a_{12} > a_{11} > a_{21} \tag{13}$$

for all θ . Also $\delta > 1/2$ implies $a_{22} > a_{11} = a_{12} + a_{21}$, and so $a_{22} > \max(2a_{11}, a_{21} + a_{12})/2$, confirming that the game is a cooperator’s dilemma (Mesterton-Gibbons, 2019, p. 175).

Because $a_{21} < a_{11}$, it is always better to defect against a defector than to cooperate. So D is a best reply to itself and therefore also an evolutionarily stable strategy (ESS). But whether it is better to cooperate or defect against a cooperator depends on the sign of

$$a_{22} - a_{12} = \frac{\theta(\{4\delta - 3\}\theta - 1)}{2(1 + \theta)^2(2\delta + \theta)} \tag{14}$$

This expression must be negative if $\delta \leq 3/4$, that is, if the predators interfere with one another sufficiently strongly and/or the presence of a pair of attackers makes it easier for the prey to deliver a fatal strike to one of them. Nevertheless, as noted above, our expectation is that

$$\delta > 1, \tag{15}$$

Table 1
Possible event sequences

First event	Probability	Second event	Conditional probability	Third event	Fitness to protagonist	Fitness × Probability
F	q_F	N	$1 - p_R$	H	0	0
		H	p_R	N	0	0
N	q_N	F	$1 - p_R$	H	0	0
		H	p_R	F	1	$q_N \times p_R$
H	$1 - q_F - q_N$	F	$1/2$	N	1	$1 - q_F - q_N$
		N	$1/2$	F	1	

The relevant events are F, N and H , where F denotes the death of the focal individual, N denotes the death of the nonfocal individual and H denotes the suppression of the prey. So the six possible event sequences are FNH, FHN, NFH, NHF, HFN and HNF .

implying $4\delta - 3 > 0$. Then equation (14) is negative and D is therefore a dominant strategy whenever the point (θ, δ) lies below the curve

$$\delta = \frac{1 + 3\theta}{4\theta} \tag{16}$$

in the $\theta - \delta$ plane, that is, in the shaded region of **Fig. 1**: D is the sole ESS, and there is no cooperation. Needless to say, D is also the sole ESS in the unlikely scenario of strong predator interference ($\delta \leq 3/4$), but we assume henceforward that equation (15) holds.

If (θ, δ) lies above the curve defined by equation (16), however, then equation (14) is positive, and so it is better to cooperate with a cooperator than to defect against it. That is, C is a best reply to itself and therefore also an ESS. A unique ESS no longer exists. Because $a_{22} > a_{12} > a_{11} > a_{21}$ by equation (13), the game becomes a special case of the discrete population game for which the population evolves to C whenever the initial proportion of cooperators exceeds

$$\gamma = \frac{a_{11} - a_{21}}{a_{22} - a_{12} + a_{11} - a_{21}} = \frac{2\delta + \theta}{(2\delta - 1)(1 + \theta)} \tag{17}$$

and otherwise evolves to D (Mesterton-Gibbons, 2019, p. 91). Straightforward differentiation shows that γ is a decreasing function of both θ and δ . Therefore, the higher the vulnerability or the stronger the dilution effect, the smaller the initial proportion of cooperators needed for the population to evolve to C , as illustrated by the contour map in **Fig. 1** and the dashed curves in **Fig. 2**. Nevertheless, it is clear from **Fig. 1** that this proportion becomes

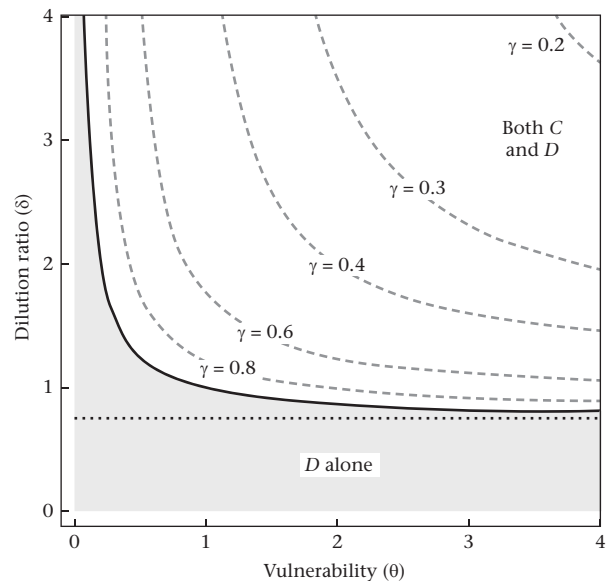


Figure 1. Dependence of the ESS among unrelated individuals on the model’s two dimensionless parameters: vulnerability θ (the ratio between the average time for a lone predator to deliver a disabling strike to a prey and the average time for the prey to deliver a fatal strike to the predator) and dilution ratio δ (in essence, the overall extent to which a prey’s confusion by multiple attackers both reinforces predators’ ability to deliver a disabling strike when acting in tandem and reduces the prey’s ability to deliver fatal strikes). The shaded region of the $\theta - \delta$ plane is where only defect, D , is an ESS; the unshaded region is where C and D are both ESSes. As $\theta \rightarrow \infty$, the boundary between regions asymptotes towards $\delta = 3/4$, as indicated by the dotted line. The boundary curve is the contour $\gamma = 1$ of the proportion defined by equation (17), namely, the critical value that the initial proportion of cooperators must exceed for cooperation to go to fixation. Other contours are shown dashed. Each contour value indicates the initial proportion at which (θ, δ) values above the contour would correspond to fixation of C . Thus, for example, an initial C frequency of 20% would suffice for fixation only if θ and δ were both almost 4, whereas an initial frequency of over 40% would be required if θ and δ were both 2.

small only at very high values of both θ and δ . It is therefore effectively impossible for cooperation between unrelated individuals to emerge; however, having emerged, it could sustain itself at much lower values of θ and δ , specifically, anywhere in the unshaded region of Fig. 1.

THE GAME AMONG KIN

We now explore the effect of kinship between potential attackers. For this purpose, it is convenient to recast the discrete

population game developed in the previous section as a continuous game among kin. Accordingly, let r be the relatedness, that is, the probability that a strategy encounters itself by virtue of kinship; then $1 - r$ is the probability that the strategy encounters an opponent at random. We assume that $0 < r < 1$. Note that the opponent may still have the same strategy.

We now apply the formalism developed in Mesterton-Gibbons (2019, p. 224). Let the focal individual's strategy u be defined as the probability of defection, so that $1 - u$ is that of cooperation, with C corresponding to $u = 0$ and D to $u = 1$. Let v and $1 - v$ be the corresponding probabilities for the nonfocal individual representing the population. Then, in the absence of kinship, the reward to a u -strategist in a population of v -strategists is

$$f(u, v) = (u, 1 - u)A(v, 1 - v)^T \quad (18)$$

where A is defined by equation (12). An ESS of the game among kin with relatedness r is equivalent to an ordinary ESS of the game with reward function ϕ , where the kin-modified reward of the original game with matrix A is defined by

$$\phi(u, v) = (1 - r)f(u, v) + rf(u, u) \quad (19)$$

(Mesterton-Gibbons, 2019, p. 225). It is shown in Appendix 1 that there cannot be an ESS in the interior of $[0, 1]$: any ESS of the game among kin must be a boundary ESS. It is further shown in Appendix 1 that defection fails to remain an ESS of the game among kin above the curve with equation

$$r = \frac{2\delta + \theta}{(4\delta - 1)(1 + \theta)} \quad (20)$$

in the θ - r plane. In Fig. 3, this curve descends from the point $(0, r_2)$ and asymptotes towards the line $r = r_1$ as $\theta \rightarrow \infty$, where

$$r_1 = \frac{1}{4\delta - 1}, \quad r_2 = \frac{2\delta}{4\delta - 1} \quad (21)$$

Thus D fails to remain an ESS in the darker shaded regions of Fig. 3 (but is still an ESS below the bounding curve).

Correspondingly, it is shown in Appendix 1 that cooperation is an ESS of the game among kin above the curve with equation $\theta = \theta_c$ where we define

$$\theta_c = \frac{1 - 2\delta r}{4\delta - 3 + r} \quad (22)$$

(but C fails to be an ESS below the curve). It is convenient to define three critical values as follows:

$$r_c = \frac{1}{2\delta}, \quad \theta_c^1 = \frac{1}{4\delta - 3}, \quad \theta_c^2 = 2\delta - 1. \quad (23)$$

Then in Fig. 3 the curve with equation $\theta = \theta_c$ joins $(0, r_c)$ to $(\theta_c^1, 0)$.

Thus, in Fig. 3, C fails to be an ESS in a lighter shaded region. In an unshaded region, both C and D are ESSes. Note that equation (A4) must be positive, and hence C must be an ESS, whenever $r > r_c$ (for any value of θ) or $\theta > \theta_c^1$ (for any value of r). Moreover, the line $r = r_c$ intersects the lower boundary of a darker shaded region at (θ_c^2, r_c) . So C is guaranteed to be the sole ESS among kin if both $r > r_c$ and $\theta > \theta_c^2$, as illustrated by the dotted lines in the middle panel of Fig. 3. Nevertheless, for $r > r_c$, C will become the sole ESS at a lower value of θ than θ_c^2 , specifically, the value of θ at which a horizontal line of height r intersects the boundary, as illustrated with $\theta \approx 3.167$ by the dotted lines in the final panel of Fig. 3 for $r = 0.2$ and $\delta = 3$. This value of θ is the one for which the lowermost solid curve in Fig. 2b becomes horizontal.

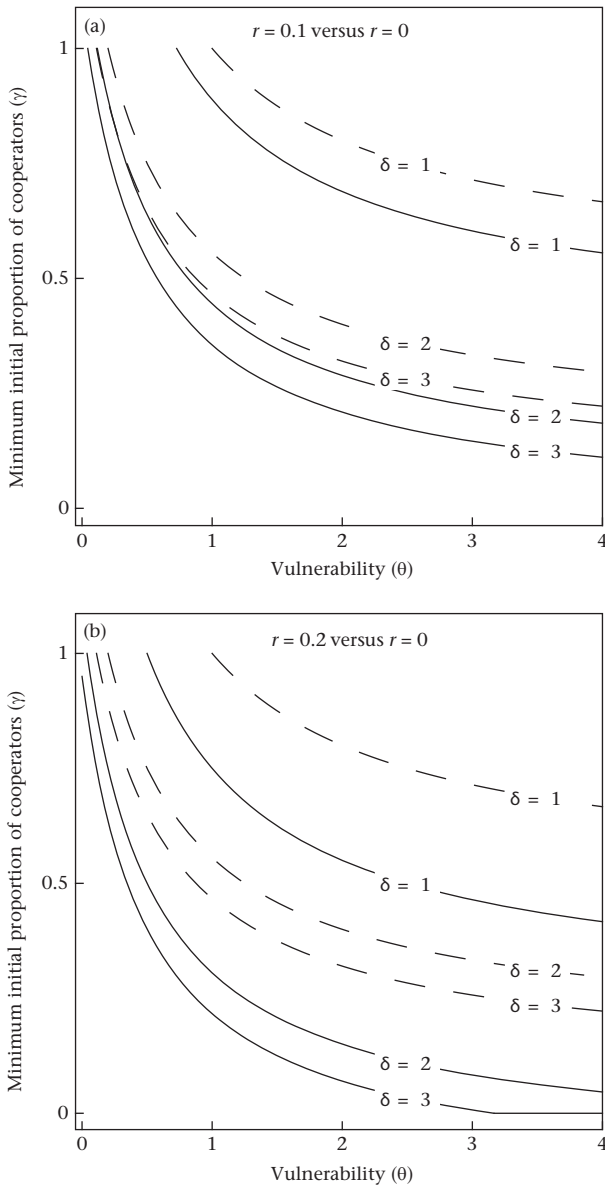


Figure 2. Minimum proportion of initial cooperators at relatedness $r = 0$ (dashed) versus relatedness (a) $r = 0.1$ and (b) $r = 0.2$ (both solid) for three different dilution ratios. Note that, with the exception of the lowermost curve in (b), curves are plotted for values of θ between θ_c and 4, and $\gamma \rightarrow 1$ as $\theta \rightarrow \theta_c$ from above, because θ_c defined by equation (22) is the value of θ at which a line at height r crosses the boundary between the unshaded and lighter shaded regions of Fig. 3, and so D becomes the sole ESS; for $r = 0$ (dashed curves), $\theta_c = \theta_c^1$, where θ_c^1 is defined by equation (23). The lowermost solid curve in (b) is plotted for values of θ between 0 and 4, because in this case $r > r_c \approx 0.167$; also in this case, $\gamma \rightarrow 0$ as $\theta \rightarrow 19/6 \approx 3.167$ from below, because that is the value of θ for which the dashed line at height 0.2 in the final panel of Fig. 3 intersects the boundary of the darker shaded region, so that C becomes the sole ESS.

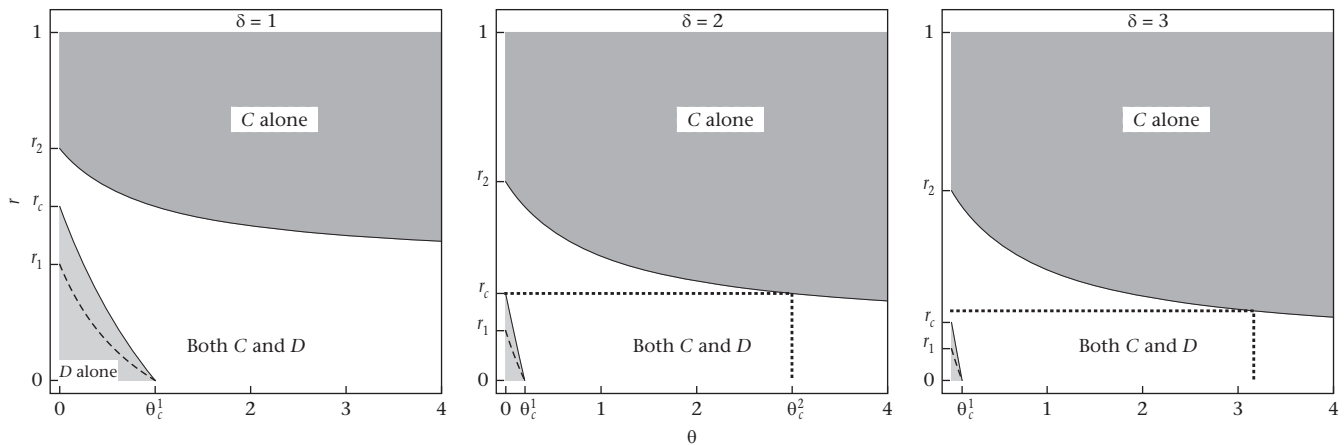


Figure 3. Dependence of the ESS among kin on the model's three dimensionless parameters: relatedness r , vulnerability θ (the ratio between the average time for a lone predator to deliver a disabling strike to a prey and the average time for the prey to deliver a fatal strike to the predator) and dilution ratio δ (the extent to which multiple attack disfavors prey). For three different values of δ , the lighter shaded region of the θ – r plane is where only D is an ESS; the darker shaded region is where only C is an ESS; and the unshaded region is where C and D are both ESSes. The significance of the dashed curve through the lighter shaded region is explained in [Appendix 2](#). The significance of the dotted lines is explained in the first new paragraph after equation (23).

When both C and D are ESSes, the critical initial proportion of cooperators above which the population will evolve to C can be found by using the payoff matrix B for the associated discrete population name among kin, namely,

$$D \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix} = C \begin{bmatrix} \phi(1,1) & \phi(1,0) \\ \phi(0,1) & \phi(0,0) \end{bmatrix} \quad (24)$$

and replacing A by B in equation (17), yielding

$$\gamma = \frac{b_{11} - b_{21}}{b_{22} - b_{12} + b_{11} - b_{21}} = \frac{2\delta + \theta - (4\delta - 1)(1 + \theta)r}{(1 - r)(2\delta - 1)(1 + 2\theta)} \quad (25)$$

Note that γ is a decreasing function of all three parameters (θ , δ and r) and agrees with equation (17) in the limit as $r \rightarrow 0$ (Fig. 2).

DISCUSSION

We have developed a game-theoretic model to explore the question of whether two individuals are favoured to cooperate in exploiting a bounty – a rich but dangerous resource that is essential for reproduction. Our model is a minimal model of cooperation in the sense of [Mesterton-Gibbons and Sherratt \(2011\)](#). It reduces issues to their fundamentals by reducing description of the relevant interaction to a dependence on only three dimensionless parameters: relatedness r ; vulnerability θ (the ratio between the average time for a lone predator to deliver a disabling strike to a prey and the average time for the prey to deliver a fatal strike to the predator); and dilution ratio δ (the extent to which attack by more than one predator disfavors the prey).

The model shows that higher values of all three parameters favour cooperation by reducing the critical initial proportion of cooperators above which cooperation will sustain itself and go to fixation; whereas, for sufficiently small values of these three parameters, cooperation is not even evolutionarily stable. Our main result is that no matter how high the dilution ratio and vulnerability, cooperation cannot emerge among nonrelatives from an ancestral state of noncooperation; however, it can emerge if the dilution ratio, vulnerability and relatedness are all sufficiently high. Furthermore, once cooperation has emerged, it can be maintained

among nonrelatives at modest values of dilution ratio and vulnerability that do not seem unlikely to be found in nature (specifically, any values of θ and δ corresponding to the unshaded region of Fig. 1). In particular, once established, cooperation sustains itself among unrelated individuals whenever both θ and δ exceed 1. This requires only that on average a predator can deliver a disabling strike sooner than a prey can deliver a fatal strike, and that a prey is at least marginally more confused by a pair of predators than it would be by a sole attacker.

Although our model constitutes the first instance of using a cooperator's dilemma to investigate cooperative exploitation of a bounty, this framework has been used by [Packer and Ruttan \(1988, p. 165\)](#) to investigate the evolution of cooperative hunting in pairs. In their model, [Packer and Ruttan \(1988\)](#) do not consider the possibility that the prey can fatally wound a predator, and are concerned with aspects of encounter and pursuit, whereas in our model engagement is assumed. Although there are points of contact between our model and theirs, they are essentially different. To make the most direct comparison between the models, we need to set $E_1 = E_2 = 0$ (no pursuit cost, whether solitary or in tandem) in the model of [Packer and Ruttan \(1988\)](#), so that their prey encounter parameter L_2 scales out (equivalent to setting $L_2 = 1$). It is assumed that hunting success depends on predator-related factors, and in particular that $H_2 = H_1(2 - H_1)$, where H_i is the probability of capturing prey in a group of i individuals, assumed to be independent for each individual ([Packer & Ruttan, 1988, p. 162](#)). Then 'cheater' (equivalent to 'defect') is always an ESS, and 'cooperate' is also an ESS if $(1 - H_1)V > 2(2 - H_1)C_2$, requiring in particular that $V > 4C_2$, where V is the value of the prey and C_2 the cost of cooperation to each animal. However, although species-specific estimates of H_1 can be obtained from field studies, fitness costs and benefits like C_2 and V are not directly measurable; and [Packer and Ruttan \(1988\)](#) do not address how V and C_2 might depend on measurable ecological parameters, whereas our model does. Furthermore, although [Packer and Ruttan \(1988, p. 185\)](#) noted that kinship can promote cooperation, their treatment was much less explicit than that provided by our model.

As noted in the Introduction, how often a bounty occurs in nature is largely unknown, but there are potential examples of bounties scattered across the literature. We regard a resource as a potential bounty if it satisfies one or more of the three criteria for a bounty (that the resource is essential, that it is rich, and that it is

dangerous) and the other criteria are not clearly contradicted. Among vertebrates, facultatively cooperative mammalian predators versus large (rich) and dangerous prey scenarios include wolves hunting elk and lions hunting buffalo or zebra (Mukherjee & Heithaus, 2013; Packer, 1986; Scheel & Packer, 1991), but such predators also have alternative, smaller, prey species, diminishing the fit to the criterion of 'essential'. Similarly, in avian species, individuals may cooperate in their attacks on relatively large prey, some of which may be dangerous but perhaps not essential (Bowman, 2003; Frye & Gerhardt, 2001) while others may be essential but perhaps not especially dangerous (Bednarz, 1988). One example of an avian species that can hunt in cooperative pairs and has prey that fit all three criteria of a bounty may be African crowned eagles, *Stephanoaetus coronatus* (Swatridge, Monadjem, & Hardy, 2009): these have geographically varying diet ranges (Swatridge, Monadjem, Steyn, Batchelor, & Hardy, 2014) and in some areas may depend on feeding on prey species that are both large and dangerous to attack (Ellis, Bednarz, Smith, & Flemming, 1993).

Among invertebrates there are similar examples of prey being rich and dangerous to predators, such as spiders attacking large ants, which sometimes kill the spider, and in which the spiders may exhibit behaviours related to cooperation (Pekár, Hrušková, & Lubin, 2005); given that some spider species hunt only ants (Líznavá & Pekár, 2013), it is likely that their prey can also be regarded as essential. For parasitoids, hosts are, by definition, an essential resource for offspring production and there are numerous examples of hosts being dangerous to attack due to their behavioural aggression or chemical defences, and also evidence that both danger and richness typically increase with host size (Godfray, 1994; Greeney, Dyer, & Smilanich, 2012; Gross, 1993). Although parasitoids do not typically exhibit simultaneous, potentially cooperative, host attack, a notable exception occurs in the genus *Sclerodermus*, as we discuss below.

As implied above, all three of our model's ecological parameters (θ , δ and r) are measurable. Measuring relatedness, r , may be regarded as a fairly standard procedure (e.g. Charmentier, Garant, & Kruuk, 2014; Davies et al., 2012). Estimates of the dilution ratio, δ , can be obtained from separate estimates of the manoeuvrability, α , and the synergicity, q . The vulnerability, θ , can be estimated as described below and by Abdi, Hardy et al. (2020) for interactions between females of the parasitoid species *Sclerodermus brevicornis* (Kieffer) (Hymenoptera: Bethyridae) and its host, the yellow long-horned beetle *Psacotha hilaris hilaris* (Pascos) (Coleoptera: Cerambycidae). The relevant values appear in their Table 3. Among 34 interactions in which either the parasitoid died before the host was paralysed or the host was paralysed before the parasitoid was killed (but not both), there were 12 instances of the first outcome and 20 of the second. It thus seems reasonable to estimate the overall probability (ignoring effects of host size variation) that the parasitoid fatally stings the host before the host can deliver a fatal bite as $12/20 = 0.625$. Of the 12 interactions in which the host was not paralysed, there were four cases in which the parasitoid died intact and eight in which it was bisected. Of the 20 interactions in which the host was paralysed before it could kill its attacker, there were only 13 cases in which the host was oviposited on. It could be argued that the eight cases involving bisection of the parasitoid and the 13 cases involving oviposition are more representative of the attack interactions described by our model. If only these 21 instances are included, then we instead estimate the probability of the parasitoid fatally stinging the host before the host can kill its attacker as $13/21 \approx 0.619$.

By substituting either of these two estimates into equation (3), we infer that 0.6 is a reasonable estimate of θ for aggressive interactions between these two particular species. Although $\theta < 1$, the

point (θ , δ) will lie inside the unshaded region of Fig. 1 as long as $\delta > 1.17$, by equation (16). While it remains unnecessary for δ to greatly exceed 1, synergy between *Sclerodermus* attackers will likely play a positive role in selecting for multifemale 'quasisocial' reproduction on individual hosts, especially if females are not kin (Tang et al., 2014).

While it may be possible for quasisociality to evolve in *Sclerodermus* due to direct fitness benefits of multifemale host attack accruing to individuals within groups exploiting a host (Tang et al., 2014), relatedness between females is likely to play a role. Abdi, Hardy et al. (2020); Abdi, Lupi et al. (2020) used empirical estimates of the risks involved in host attack and the reproductive benefits of success to explore, using the pre-existing framework of Hamilton's rule (which considers the interplay between costs, benefits and relatedness, Hamilton, 1964), circumstances in which *Sclerodermus* females should be selected to attack and then, if successful, share a host with others as a public good. In all parasitoid–host associations considered, the risk of the parasitoids dying increased monotonically with host size while benefits increased monotonically in some but had a domed relationship with host size in others. It was predicted in all cases that public goods attack will be favoured by high relatedness (in most cases > 0.5) but also that when hosts are large and very dangerous, females would only be expected to attack and share hosts when benefits were also large (the epitome of a bounty).

There are some key differences between the formulation of our model and the parameters considered by Abdi, Hardy et al. (2020); Abdi, Lupi et al. (2020). First, Abdi et al.'s heuristic treatment focused on whether individual females in a group of potential attackers should be prepared to attack a host alone: possible synergistic effects of multiple-female attack (the dilution ratio) were thus not considered, and these are clearly likely to reduce risk and thus favour the decision to attack, as predicted by our game-theoretic analysis. This potentially reduces, but is unlikely to entirely eclipse, the importance of kinship suggested by Abdi, Hardy et al.'s (2020); Abdi, Lupi et al.'s (2020) use of Hamilton's rule. While it has been found that larger groups of *Sclerodermus* females suppress hosts more rapidly (Abdi, Lupi et al., 2020; Tang et al., 2014), compatible with a dilution effect disfavouring the host or with the net result of functionally independent attacks, this effect can operate alongside an effect of female relatedness (Abdi, Lupi et al., 2020).

Second, we assume that the host resource is invariantly rich and its richness is uncorrelated with parasitoid vulnerability, while Abdi, Hardy et al. (2020); Abdi, Lupi et al. (2020) included host size dependency of both the benefit of success (\approx richness) and the cost of attack (\approx vulnerability).

The assumptions of the two approaches best coincide when, in our model, vulnerability is high with no dilution effect and, in Abdi et al.'s approach, benefits increase monotonically with host size and hosts are large and at their most dangerous (Liu, Xu, Li, & Sun, 2011). Both approaches conclude that unrelated females should generally not attack the host and also that higher relatedness can favour attack. Abdi, Hardy et al. (2020) additionally found empirically that small and medium-sized hosts were attacked earlier when pairs of *Sclerodermus* females were more closely related, again indicating a role of kinship in promoting the cooperative exploitation of bounties, as predicted by our model.

Conclusion

In a review of how foragers manage risks, Mukherjee and Heithaus (2013, p. 550) concluded that 'understanding the prevalence and consequences of hunting dangerous prey should be a priority for behavioural ecologists'. We have taken a step towards

addressing this priority. Our game-theoretic model predicts that, when faced with a dangerous but potentially high-payoff challenge, pairs of individuals will be more likely to cooperate when the risk they each would take when acting alone is higher and when acting in tandem most reduces that risk. Kinship among individuals also increases the likelihood of cooperation and, given the parameters explored, is essential for it to be selectively favoured within populations of noncooperators.

Author Contributions

The key question was identified during mutual discussion. M.M.-G. contributed the game-theoretic model and analysis and both authors wrote the manuscript.

Declaration of Interest

We declare that we have no competing interests.

Acknowledgments

We thank Mohamed K. Abdi for discussions about *Sclerodermus* that led towards this work and two anonymous referees for constructive comments on an earlier version of the manuscript.

References

- Abdi, M. K., Hardy, I. C. W., Jucker, C., & Lupi, D. (2020). Kinship effects in quasi-social parasitoids II: Co-foundress relatedness and host dangerousness interactively affect host exploitation. *Biological Journal of the Linnean Society*, *130*, 642–660.
- Abdi, M. K., Lupi, D., Jucker, C., & Hardy, I. C. W. (2020). Kinship effects in quasi-social parasitoids I: Co-foundress number and relatedness affect suppression of dangerous hosts. *Biological Journal of the Linnean Society*, *130*, 627–641.
- Bednarz, J. C. (1988). Cooperative hunting in Harris' hawks. *Science*, *239*, 1525–1527.
- Bowman, R. (2003). Apparent cooperative hunting in Florida scrub-jays. *Wilson Bulletin*, *115*, 197–199.
- Charmantier, A., Garant, D., & Kruuk, L. E. B. (2014). *Quantitative genetics in the wild*. Oxford, U.K.: Oxford University Press.
- Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology* (4th ed.). Oxford, U.K.: Wiley-Blackwell.
- Ellis, D. H., Bednarz, J. C., Smith, D. G., & Flemming, S. P. (1993). Social foraging classes in raptorial birds. *BioScience*, *43*, 14–20.
- Fagen, R. M. (1980). When doves conspire: Evolution of nondamaging fighting tactics in a nonrandom-encounter animal conflict model. *American Naturalist*, *115*, 858–869.
- Frye, G. F., & Gerhardt, R. P. (2001). Apparent cooperative hunting in loggerhead shrikes. *Wilson Bulletin*, *113*, 462–464.
- Godfray, H. C. J. (1994). *Parasitoids*. Princeton, NJ: Princeton University Press.
- Grafen, A. (1979). The hawk–dove game played between relatives. *Animal Behaviour*, *27*, 905–907.
- Greeney, H. F., Dyer, L. A., & Smilanich, A. M. (2012). Feeding by lepidopteran larvae is dangerous: A review of caterpillars' chemical, physiological, morphological, and behavioral defenses against natural enemies. *Insect Survival Journal*, *9*, 7–34.
- Gross, P. (1993). Insect behavioral and morphological defenses against parasitoids. *Annual Review of Entomology*, *38*, 251–273.
- Hamilton, W. D. (1964). The genetical theory of social behaviour, I & II. *Journal of Theoretical Biology*, *7*, 1–52.
- Heinrich, B. (1989). *Ravens in winter*. New York, NY: Simon & Schuster.
- Hines, W. G. S., & Maynard Smith, J. (1979). Games between relatives. *Journal of Theoretical Biology*, *79*, 19–30.
- Kerley, G. I. H. (2018). Dying for dinner: A cheetah killed by a common duiker illustrates the risk of small prey to predators. *African Journal of Wildlife Research*, *48*, Article 024001. <https://doi.org/10.3957/056.048.024001>
- Lehtonen, J., & Jaatinen, K. (2016). Safety in numbers: The dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, *70*, 449–458.
- Liu, Z., Xu, B., Li, L., & Sun, J. (2011). Host-size mediated trade-off in a parasitoid *Sclerodermus harmandi*. *PLoS One*, *6*, Article e23260. <https://doi.org/10.1371/journal.pone.0023260>
- Líznařová, E., & Pekár, S. (2013). Dangerous prey is associated with a type 4 functional response in spiders. *Animal Behaviour*, *85*, 1183–1190.
- Mesterton-Gibbons, M. (1991). An escape from the prisoner's dilemma. *Journal of Mathematical Biology*, *29*, 251–269.
- Mesterton-Gibbons, M. (1996). On the war of attrition and other games among kin. *Journal of Mathematical Biology*, *34*, 253–270.
- Mesterton-Gibbons, M. (2019). *An introduction to game-theoretic modelling* (3rd ed.). Providence, RI: American Mathematical Society.
- Mesterton-Gibbons, M., & Dugatkin, L. A. (1992). Cooperation among unrelated individuals: Evolutionary factors. *Quarterly Review of Biology*, *67*, 267–281.
- Mesterton-Gibbons, M., & Dugatkin, L. A. (1999). On the evolution of delayed recruitment to food bonanzas. *Behavioral Ecology*, *10*, 377–390.
- Mesterton-Gibbons, M., & Sherratt, T. N. (2007). Coalition formation: A game-theoretic analysis. *Behavioral Ecology*, *18*, 277–286. <https://doi.org/10.1093/beheco/arl084>
- Mesterton-Gibbons, M., & Sherratt, T. N. (2011). Information, variance and cooperation: Minimal models. *Dynamic Games and Applications*, *1*, 419–439.
- Mirmirani, M., & Oster, G. (1978). Competition, kin selection and evolutionary stable strategies. *Theoretical Population Biology*, *13*, 304–339.
- Mukherjee, S., & Heithaus, M. R. (2013). Dangerous prey and daring predators: A review. *Biological Reviews*, *88*, 550–563. <https://doi.org/10.1111/brv.12014>
- Packer, C. (1986). The ecology of sociality in felids. In D. I. Rubenstein, & R. Wrangham (Eds.), *Ecological aspects of social evolution: Birds and mammals* (pp. 429–451). Princeton, NJ: Princeton University Press.
- Packer, C., & Rutan, L. (1988). The evolution of cooperative hunting. *American Naturalist*, *132*, 159–198.
- Pekár, S., Hrušková, M., & Lubin, Y. (2005). Can solitary spiders (Araneae) cooperate in prey capture? *Journal of Animal Ecology*, *74*, 63–70.
- Scheel, D., & Packer, C. (1991). Group hunting behaviour of lions: A search for cooperation. *Animal Behaviour*, *41*, 679–709.
- Swatridge, C. J., Monadjem, A., & Hardy, I. C. W. (2009). Regal eagle: The African crowned eagle in Mpumalanga. *Africa Birds & Birding*, *14*, 55–58.
- Swatridge, C. J., Monadjem, A., Steyn, D. J., Batchelor, G. R., & Hardy, I. C. W. (2014). Factors affecting diet, habitat selection and breeding success of the African crowned eagle *Stephanoaetus coronatus* in a fragmented landscape. *Ostrich: Journal of African Ornithology*, *85*, 47–55.
- Tang, X., Meng, L., Kapranas, A., Xu, F., Hardy, I. C. W., & Li, B. (2014). Mutually beneficial host exploitation and ultra-biased sex ratios in quasisocial parasitoids. *Nature Communications*, *5*, 4942. <https://doi.org/10.1038/ncomms5942>
- Treisman, M. (1977). The evolutionary restriction of aggression within species: A game theory analysis. *Journal of Mathematical Psychology*, *16*, 167–203.

Appendix 1. EES Analysis

Because equation (15) implies that

$$\frac{\partial^2 \phi}{\partial u^2} = \frac{(2\delta - 1)(1 + 2\theta)\theta r}{(1 + \theta)^2(2\delta + \theta)} \quad (\text{A1})$$

is always positive for $r > 0$, there cannot be an ESS in the interior of $[0, 1]$: any ESS of the game among kin must be a boundary ESS. The condition for defection ($v = 1$) to be an ESS of this game becomes $\partial\phi/\partial u|_{u=v=1} > 0$ (so that somewhat smaller probabilities of defection cannot invade) with $\phi(1, 1) - \phi(0, 1) > 0$ (so that C cannot invade); and because

$$\frac{\partial\phi}{\partial u}\Big|_{u=v=1} = \frac{(1-r)\theta}{2(1+\theta)^2} \quad (\text{A2})$$

is always positive, defection remains an ESS for $r > 0$ whenever

$$\phi(1, 1) - \phi(0, 1) = \frac{\{2\delta + \theta - (4\delta - 1)(1 + \theta)r\}\theta}{2(1 + \theta)^2(2\delta + \theta)} \quad (\text{A3})$$

is positive, that is, below the curve in the θ – r plane with equation (20); above this curve, D fails to remain an ESS.

Correspondingly, the condition for cooperation ($v = 0$) to be an ESS of the game becomes $\partial\phi/\partial u|_{u=v=0} < 0$ (so that small positive probabilities of defection cannot invade) with $\phi(0, 0) - \phi(1, 0) > 0$ (so that D cannot invade); and because

$$\phi(0, 0) - \phi(1, 0) = \frac{(\{4\delta - 3 + r\}\theta + 2\delta r - 1)\theta}{2(1 + \theta)^2(2\delta + \theta)} \quad (\text{A4})$$

with

$$\left. \frac{\partial \phi}{\partial u} \right|_{u=v=0} = - \left\{ \phi(0, 0) - \phi(1, 0) + \frac{(2\delta - 1)\theta(1 + 2\theta)r}{2(1 + \theta)^2(2\delta + \theta)} \right\}, \quad (\text{A5})$$

(15) implies that cooperation is an ESS whenever equation (A4) is positive.

Appendix 2. Effect of Kinship: the Inclusive-fitness Approach

In the main body of this paper, the effect of kinship is incorporated using the ‘personal-fitness’ approach to games among kin that was first published by Grafen (1979), although discovered independently by Fagen (1980). In a contemporaneous review article, Hines and Maynard Smith (1979) observed that there are two approaches to extending the concept of ESS from ordinary games to games among kin. The personal-fitness method modifies an individual’s fitness to allow that if opponents are related, then a *u*-strategist is more likely than other members of its population to meet opponents adopting the strategy *u*. The ‘inclusive-fitness’ method, which ultimately derives from Hamilton (1964; see also Mirmirani & Oster, 1978; Treisman, 1977), adds to each contestant’s payoff *r* times its opponent’s payoff, where *r* is their coefficient of relatedness. Hines and Maynard Smith (1979) regarded the personal-fitness method as the correct one, but found the inclusive-fitness method useful in providing necessary conditions for a personal-fitness ESS. However, Mesterton-Gibbons (1996) showed that the inclusive-fitness method provides necessary conditions only for a special class of (matrix) games (hence we used the personal-fitness approach in our main analysis). Because the underlying game belongs to the special class considered by Hines and Maynard Smith (1979), we reanalyse it here using the inclusive-fitness approach.

In this alternative approach to games among kin, a *u*-strategist’s ordinary payoff against a *v*-strategist is augmented by *r* times the

payoff to the *v*-strategist, where *r* is their coefficient of relatedness. Thus *f*(*u*, *v*) is replaced by

$$\Psi(u, v) = f(u, v) + rf(v, u) \quad (\text{A6})$$

where *f* is defined by equation (18). Comparing equation (A6) with equation (19), we see that the personal-fitness approach and the inclusive-fitness approach yield different kin-modified reward functions, so it is unsurprising that in general their predictions differ (Mesterton-Gibbons, 1996). Despite that, their properties often overlap; in particular, if *f* is a bilinear function, as here, then *v** is a personal-fitness ESS among kin only if it is also an inclusive-fitness ESS (Hines & Maynard Smith, 1979).

An interior inclusive-fitness ESS *p* ∈ (0, 1) cannot exist, because the only possible candidate for *p* can be invaded by either *C* or *D*. So any ESS is again a boundary ESS.

In place of equation (A3) we obtain

$$\Psi(1, 1) - \Psi(0, 1) = \frac{(1 - r)\theta}{2(1 + \theta)^2} > 0, \quad (\text{A7})$$

so that *D* remains an ESS for any value of *r* (already a different prediction); and in place of equation (A4) we obtain

$$\Psi(0, 0) - \Psi(1, 0) = \frac{(\{4\delta - 3 + (4\delta - 1)r\}\theta + (4\delta - 1)r - 1)\theta}{2(1 + \theta)^2(2\delta + \theta)} \quad (\text{A8})$$

so that *C* is an inclusive-fitness ESS whenever (θ, *r*) lies above the dashed line from (0, *r*₁) to (θ_c¹, 0) in a lighter shaded region in Fig. 3, where *r*₁ and θ_c¹ are defined by equations (21) and (23), respectively. Thus, as expected, *C* or *D* is a personal-fitness ESS only if it is also an inclusive-fitness ESS. Nevertheless, there exists both a region in parameter space where *C* is an inclusive-fitness ESS but not a personal-fitness ESS (above the dashed line in a lighter shaded region of Fig. 3) and a sizeable region in parameter space where *D* is an inclusive-fitness ESS but not a personal-fitness ESS (the whole of a darker shaded region).