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Note

Kin Blackmail as a Coercive Route to Altruism

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ABSTRACT: The evolution of altruism (helping a recipient at personal cost) often involves conflicts of interest. Recipients frequently prefer greater altruism than actors are prepared to provide. Coercion by recipients normally involves limiting an actor's options. Here, we consider the possibility of a coercive recipient limiting its own options. Forty years ago, Amotz Zahavi suggested that nesting birds may be "blackmailed" into increased parental care if offspring threaten to harm themselves (and therefore jeopardize the direct fitness of their parents). In a simple kin selection model, we expand blackmail to indirect fitness and highlight that blackmail can occur between any kin to drive reproductive division of labor. In principle, a recipient may place its own fitness at risk (brinkmanship), imposing sanctions on a relative's indirect fitness if the relative fails to cooperate. To use its own survival or reproduction as leverage in a sequential game, a recipient must increase the extent to which its existing fitness depends on the actor's behavior and therefore credibly commit to a cost if the actor does not comply. As it requires opportunities for commitment, kin blackmail can arise only under stringent conditions, but existing kin blackmailers may pass unnoticed because of their strategic success.

Keywords: blackmail, inclusive fitness, altruism, coercion, cooperation, kin selection.

Introduction

Altruism (increasing the Darwinian fitness of another individual at personal cost) can evolve only when Hamilton's rule, $rb > c$, is satisfied (Hamilton 1964; Gardner et al. 2011), where r is the relatedness between altruist and recipient, b is the fitness benefit for the recipient, and c is the fitness cost for the actor. The indirect fitness effect rb must exceed the direct fitness cost c, leading to a net gain in inclusive fitness (the sum of direct and indirect fitness). In cooperatively breeding families, inclusive-fitness disagreements about the optimum level of altruism are widespread. A wasp foundress, for instance, may have much to gain from higher levels of help by other females. Her daughters may prefer to depart as foundresses themselves. Such tensions can drive the evolution of coercion. In the small carpenter bee *Ceratina calcarata*, mothers starve their first daughters to curtail their abilities to breed (Lawson et al. 2016); in *Diacamma* ants, gamergate females mutilate emerging daughters to produce a compliant eunuch caste of helpers (Baratte et al. 2006); and across many social insects, worker-laid eggs are destroyed by policing (Wenseleers et al. 2004; Wenseleers and Ratnieks 2006). These acts of coercion attempt to eliminate a kin-selected helper's outside options (Ratnieks and Wenseleers 2008). Here, we consider whether a recipient can also coerce higher levels of altruism by eliminating its own options.

We ask whether a recipient can extort a reluctant alloparental actor into becoming a helper by irreversibly making part of its own reproductive success dependent on the actor's behavior, extending the theory of "blackmail" to indirect fitness. Blackmail was originally proposed as a potential resolution of parent-offspring conflict (Zahavi 1977), where offspring often prefer to receive more parental investment than parents prefer to provide (Trivers 1974). Zahavi was concerned with parental provisioning in Arabian babblers (*Argya squamiceps*): why do fledglings scream for food? He argued that parents—faced with a potential loss of direct fitness as a result of their offspring advertising themselves to predators—are extorted into higher levels of provisioning to quiet their blackmailing offspring. Recently, using field experiments, Thompson et al. (2013) have argued that young pied babblers (*Turdoides bicolor*) may place themselves in locations with high predation risk as a form of blackmail. Zahavian blackmail does not require predators: in principle, offspring may adopt any action that actively reduces their fitness (Eshel and Feldman 1991; Godfray 1995), including wasting energy reserves. However, the scope for blackmail-style traits in biology has remained unclear. First, Zahavi argued that indirect fitness is irrelevant to social behavior (Zahavi 1977; Clutton-Brock and Ridley 2017), and blackmail models have been restricted to extortion by offspring

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through the direct fitness interests of parents: only parents are victims, held hostage by their own reproductive success. Second, Zahavian blackmail faces the problem that the threat can lack credibility (Dawkins 1989). All else being equal, if parents were to call the bluff of the chick (by not increasing their provisioning rate), the chick would have no incentive to continue advertising itself to predators (unless such costly behavior remains rational because it serves some other purpose [e.g., honest signaling; Johnstone 1996]). If superior outside options remain available to the blackmailer (allowing it rationally to stop putting itself at risk), blackmail is an empty threat.

We argue that blackmail by reproductive adults through a victim's indirect fitness (kin blackmail) is a theoretical possibility in the evolution of sociality, promoting reproductive division of labor. By deliberately increasing risks to its own survival or reproductive success, a recipient (such as a social insect foundress) can extort alloparental kin into becoming altruistic helpers. Crucially, to ensure that the threat is credible, the blackmailer must change the payoff

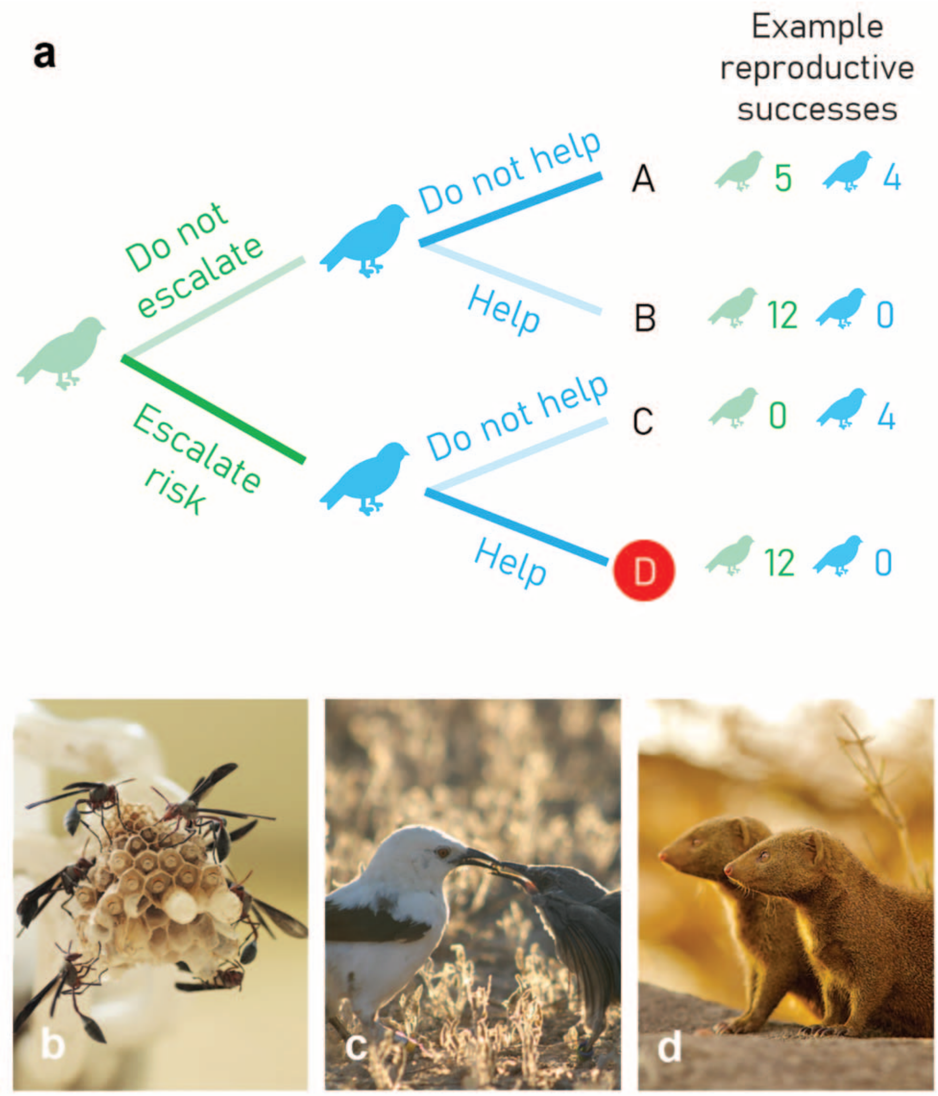


Figure 1: Kin blackmail in social evolution. *a*, Optimal choices for each node are in bold. Player 1 is shown in green, and player 2 is shown in blue. We assume relatedness $r = 0.5$ for illustration, with example reproductive success outcomes. The subgame-perfect equilibrium is *D*. *b*–*d*, In principle, kin blackmail might arise in sequential games, such as the joining decisions of wasp foundresses (*b*). Hand-tying devices in vertebrate societies, such as pied babblers (*c*) and dwarf mongooses (*d*), may involve strategic reduction of energy reserves. Photographs: *Belonogaster juncea*, P. Kennedy. *Turdoides bicolor*, A. N. Radford. *Helogale parvula*, © Shannon Wild.

function for the actor (Eshel and Feldman 1991; Godfray 1995; Cant 2006). Here, we use a kin selection model to explore how a blackmailer can irreversibly alter the payoff function by committing its future self to losing control of its own fitness if its partner makes an undesirable move (Schelling 1960). The blackmailer makes credible a threat that would be against its own interests if it could still make a choice, changing the rational behavior of a related partner. Kin blackmail in the evolution of sociality has not yet received explicit attention, theoretically or empirically. This may reflect rarity among social organisms but may also reflect its being easily overlooked; an effective deterrent is rarely seen to be used. By outlining conditions under which kin blackmail can and cannot evolve, we hope to stimulate empirical tests for kin blackmail in the real world.

Brinkmanship

We consider a simple sequential game between relatives. Player 2 (blue in fig. 1*a*) must choose whether to help player 1 (green in fig. 1*a*). The players might be, for example, social insects tending nests (fig. 1*b*) or an offspring choosing whether to help its parent in a cooperatively breeding bird (fig. 1*c*) or mammal (fig. 1*d*). We assume that, all else being equal and before the evolution of blackmail by player 1, player 2 prefers not to help (i.e., in fig. 1*a*, its preferences involve outcomes $A > B$). However, player 1 has the option (before player 2 makes its decision) to place itself or its reproductive success at risk. If player 1 escalates the risk, its (expected) reproductive success will be lowered in the event that player 2 chooses not to help (outcome C), but

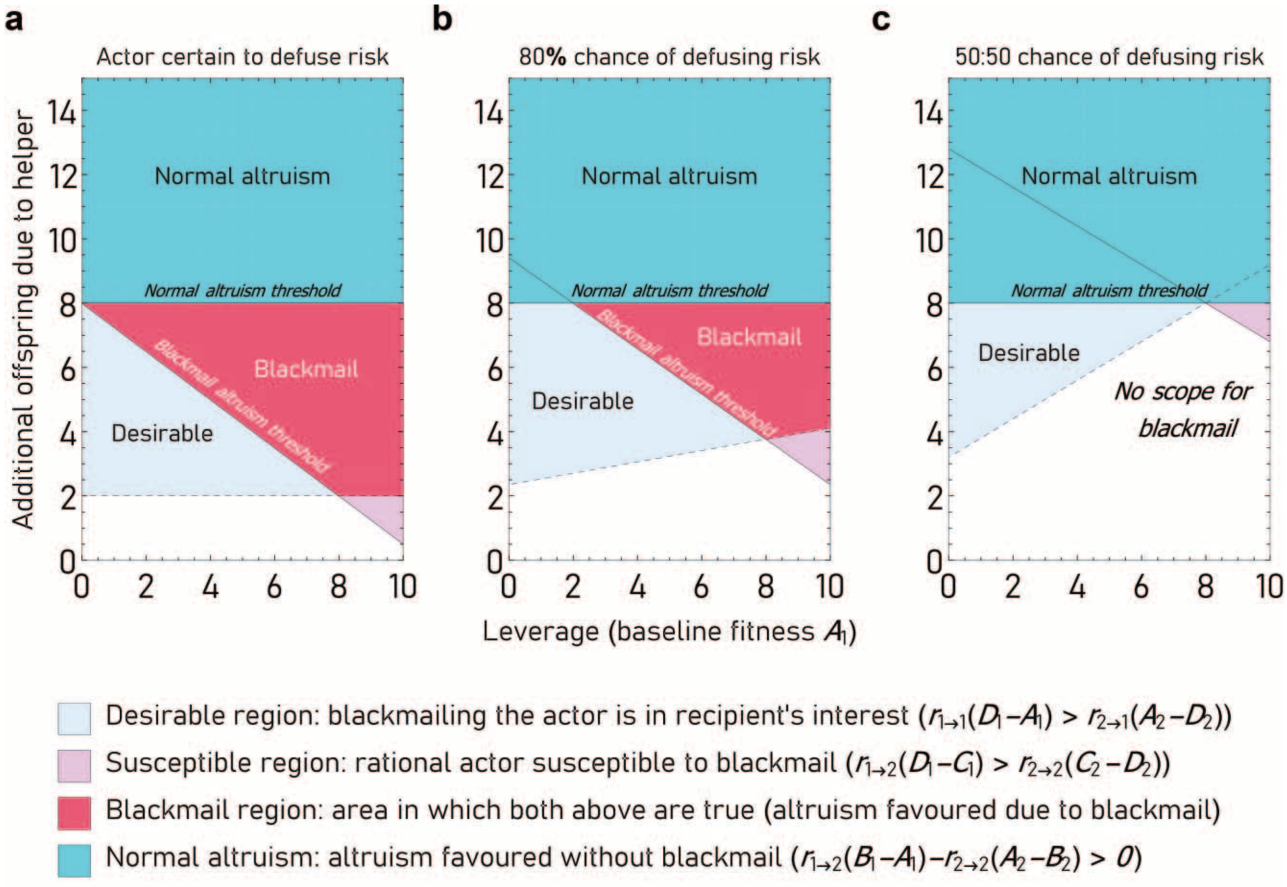


Figure 2: Conditions under which rational inclusive-fitness-maximizing players should play kin blackmail (red zone). We consider an illustrative actor, with symmetrical relatedness $r = 0.5$ to the recipient, choosing whether to sacrifice four offspring from its baseline $A_2 = 5$ offspring (i.e., $B_2 = D_2 = 1$) to help the recipient. Normally, this would require providing a benefit of more than eight offspring for the recipient (normal altruism threshold). Blackmail by the recipient reduces the required benefit (blackmail altruism threshold). We plot an illustrative blackmail in which, by escalating risks, the recipient commits its baseline expected fitness A_1 to be reduced to a quarter of its total if the actor does not help ($\lambda = 0.25$). Blackmail is most effective when an actor would be highly likely to defuse the risk if it were to choose to become a helper. *a*, Certain defusing ($z = 1$). *b*, With an 80% chance of a helping actor defusing the risk ($z = 0.8$), the blackmail region is reduced. *c*, With a low (50%) chance of the actor being able to defuse the risk, blackmail is too risky to be worthwhile for the recipient.

its (expected) reproductive success if player 2 helps (outcome *D*) will be no greater than it would be if player 2 helped normally (outcome *B*). Failing to become a helper will now cause player 1 to suffer a loss in expected reproductive success, altering player 2's inclusive fitness interests.

To identify the outcome that will maximize each player's inclusive fitness, we consider which option would be taken by an allele at each decision point to result in the largest number of copies of itself at the end of the game, given what the other player will rationally do (Pen and Taylor 2005). For a rational player 1 to extort reluctant altruism (outcome *D*) by a rational player 2 with an $A > B$ preference, player 2's preferences must be $D > C$, while the first mover (player 1) must prefer $D > A$. Outcome *D* is then subgame perfect. Player 2's $D > C$ preference occurs (via Hamilton's rule) when the indirect fitness costs of failing to acquiesce to blackmail (left-hand side) are greater than the direct fitness costs of acquiescing (right-hand side):

$$r_{1\rightarrow2}(D_1 - C_1) > r_{2\rightarrow2}(C_2 - D_2), \tag{1}$$

where $r_{1\rightarrow2}$ and $r_{2\rightarrow2}$ are player 2's (life-for-life) relatedness to player 1's offspring and its own offspring, respectively. The term D_1 denotes the reproductive success belonging to player 1 in outcome *D* at the end of the game and so on. Player 1's $D > A$ preference occurs when the direct fitness benefits of extorting help (left-hand side) exceed the indirect fitness costs of the relative surrendering its own reproduction (right-hand side):

$$r_{1\rightarrow1}(D_1 - A_1) > r_{2\rightarrow1}(A_2 - D_2), \tag{2}$$

where $r_{1\rightarrow1}$ and $r_{2\rightarrow1}$ are player 1's relatedness to its own and player 2's offspring, respectively. (Relatednesses are not necessarily symmetrical between the players: for instance, in diploids if player 1 is player 2's mother, $r_{2\rightarrow1} = 0.25$, while $r_{1\rightarrow2} = 0.5$ and $r_{2\rightarrow2} = r_{1\rightarrow1} = 0.5$).

In figure 2, we plot required benefit thresholds for rational players with perfect information maximizing their inclusive fitnesses, assuming that (i) the actor's fitness cost for altruism is the same whatever strategy the recipient plays ($A_2 = C_2$ and $B_2 = D_2$), (ii) the risk introduced by the altruism recipient (who enacts the blackmail) reduces its fitness to a proportion $0 \leq \lambda < 1$ if the altruism actor (who is the victim of blackmail) does not provide altruism ($C_1 = \lambda A_1$), and (iii) the probability with which, by providing help, the actor will successfully "defuse" a risk introduced by the recipient is $0 \leq z \leq 1$ (i.e., $D_1 = ((1 - z)\lambda + z)B_1$). A recipient with a higher baseline fitness to use as leverage (horizontal axis in fig. 2) can extort altruism for smaller payoffs (declining blackmail altruism threshold in fig. 2*a*, 2*b*). For instance, in figure 2*a*, a recipient can threaten to reduce its $A_1 = 10$ offspring to 25% of its total ($\lambda = 0.25$), blackmailing an actor into helping, despite the actor ultimately providing only a quarter of the threshold benefit (two offspring instead of eight) that would normally be required to satisfy Hamilton's rule. However, the scope for blackmail is reduced when actors' abilities to defuse the risk are weaker: at 50% probability of successful defusing (fig. 2*c*), blackmail becomes too risky to be worthwhile for a recipient, regardless of its leverage.

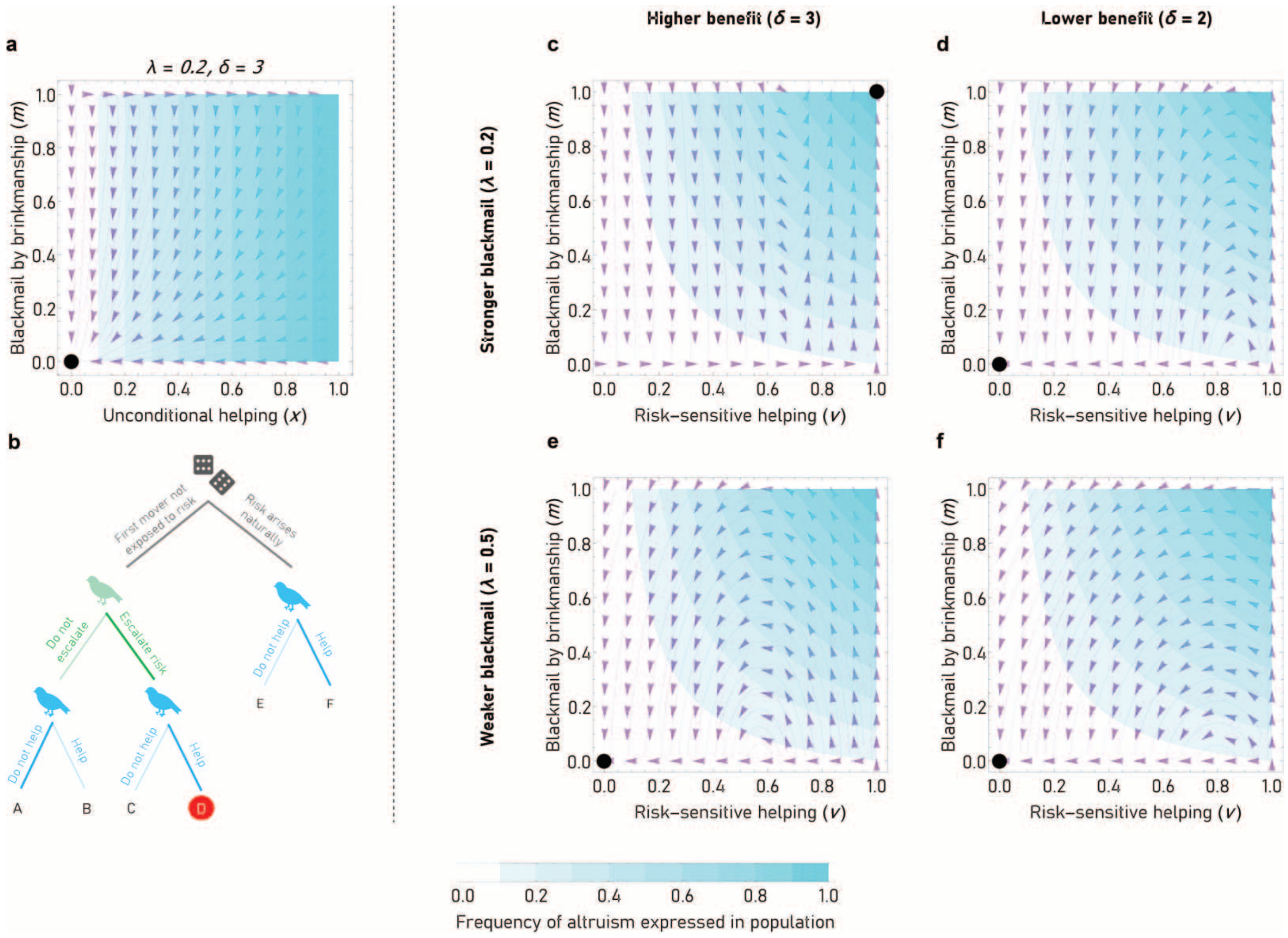
Reaching Stable Kin Blackmail

If all players can rationally assess the outcomes for their inclusive fitness and respond with full flexibility (fig. 2), kin would be blackmailed into altruism under the appropriate parameter values (the subgame-perfect outcome *D* in fig. 1*a*). In this scenario, player 1 would rely on player 2 making the rational choice to maximize its inclusive fitness at any node in the game tree. However, it is not guaranteed that a blind process of natural selection will inevitably lead to subgame-perfect equilibria (Binmore 2010).

We first consider whether blackmail can invade from rarity in the simple game in figure 1*a*. In figure 3*a*, we plot the conditions for selection to favor changes in unconditional helping (*x*, probability that player 2 helps) and blackmail (*m*, probability that player 1 puts itself at risk) in a simple neighbor-modulated model (Taylor and Frank 1996; see the supplemental PDF, available online). A mutant blackmailer (player 1) is effectively assuming that player 2 will recognize that the best choice to maximize its inclusive fitness is to switch to helping (outcome *D*). However, player 2 here lacks flexibility to make the rational response, which has not had an opportunity to evolve under blackmail. In this scenario, the mutant player 1 would harm itself for no benefit (outcome *C*), and blackmail would fail to invade. Despite this, there are two broad reasons why populations may, in principle, evolve kin blackmail (outcome *D* in fig. 1*a*).

In general, subgame-perfect strategies are expected to evolve as a result of Selten's (1983) "trembling hand" argument: if every decision carries a small probability of error, partners are occasionally exposed to other pathways on the game tree and evolve rational conditional responses to each move they may find their partner has made (Selten 1983; McNamara 2013). However, invoking trembling hands means assuming that players can evolve sufficient flexibility to make best responses in each subgame, despite encountering some subgames only rarely because of infrequent errors, which is unlikely in general (McNamara and Houston 2002).

In an alternative route to kin blackmail, organisms may have already evolved an ability to respond to a naturally occurring risk before the invasion of blackmailers. For instance, in the ambrosia beetle *Xyleborinus saxeseni*, offspring are more likely to stay as helpers if the mother


a
$\lambda = 0.2, \delta = 3$
Blackmail by brinkmanship (m)
Unconditional helping (x)
0.0
0.2
0.4
0.6
0.8
1.0
b
First mover not exposed to risk
Risk arises naturally
Do not escalate
Escalate risk
Do not help
Help
A
B
C
D
E
F
Higher benefit ($\delta = 3$)
Lower benefit ($\delta = 2$)
Stronger blackmail ($\lambda = 0.2$)
Weaker blackmail ($\lambda = 0.5$)
c
d
e
f
Blackmail by brinkmanship (m)
Risk–sensitive helping (v)
Frequency of altruism expressed in population

lays more eggs (Peer and Taborsky 2007) or if the colony is exposed to pathogen risks (Nuotclà et al. 2019). In this context, player 1 may choose to escalate the risk (e.g., laying too many eggs for the nest to remain viable without helpers or allowing pathogen risk to rise). In the kin selection model in the supplemental PDF, a given player 1 is exposed to a chance risk with probability k (fig. 3*b*). We allow player 2 a strategy of risk-sensitive helping (v). If player 1 is at risk, player 2 helps with probability $v + (1 - v)x$, where x is the probability of unconditional helping. In figure 3*c*–3*f*, we plot the dynamics of selection on blackmail (m) and v at $x = 0$. In the absence of blackmail ($m = 0$), actors who increase their helping effort when the recipient's fitness is at risk ($v > 0$) can evolve (fig. 3*c*). This allows the invasion of a recipient strategy that deliberately generates risk ($m > 0$). When encountering risk-sensitive second movers, blackmail is no longer initially deleterious. As m rises, higher levels of altruism are favored (fig. 3*c*). Blackmail cannot invade when the benefits to the recipient's fitness are insufficient to allow the initial invasion of risk-sensitive helping, which occurs when the benefit provided is too small (fig. 3*d*, 3*f*) or the risk is not sufficiently severe (fig. 3*e*, 3*f*). Unlike figure 3*a*, the outcome that arises in figure 3*c*–3*f* is the outcome that would be predicted as subgame perfect at these parameter values in the simpler game in figure 1.

Discussion

In social evolution, organisms can coerce others into providing help (Ågren et al. 2019). Most strategies of coercion involve manipulating options available to actors, such as eliminating the possibility of worker-laid eggs surviving in social insect colonies (Wenseleers et al. 2004; Wenseleers and Ratnieks 2006). By contrast, kin blackmail can involve a recipient manipulating its own options. We suggest that kin blackmail offers a coercive route to altruism among alloparental relatives, causing actors to help voluntarily at payoff values that would ordinarily be against their inclusive fitness interests. By forcing control over its own reproduction or survival onto an actor, a recipient credibly threatens to impose sanctions on a relative's indirect fitness if the relative fails to cooperate.

Our results highlight that kin blackmail by brinkmanship requires four components:

Leverage. Blackmailers must have sufficient resources (A_1) to put at risk (a current clutch or expectation of future fitness).

Opportunity. Blackmailers must be able to force high dependency of otherwise safe components of their baseline fitness A_1 onto actors (lower λ), strategically reducing their ability to recover the jeopardized fitness themselves (without exorbitant costs).

Targeted risk. Risk λ must be such that a blackmailed actor would have a high chance of eliminating the risk if it helps (high z). This may arise, for instance, if the simple presence of a second individual in the nest prevents the loss of the jeopardized fitness by reducing the brood's exposure to predation or parasitism. If blackmailed actors evolve to be better at defusing risk (higher z), they inadvertently increase their own range of susceptibility to blackmail (fig. 2).

Meaningful benefit. For an actor's help to be useful, the investment in help cannot simply restore the jeopardized fitness A_1 but must also provide a meaningful benefit ($D_1 - A_1$). For instance, meaningful benefits can occur when relatively little effort is required by the actor to eliminate the risk λ or where actors choosing help must do so by making longer-term commitments.

The actor must respond to the risk that the recipient has placed itself in, requiring an ability to alter behavior on the basis of environmental or social cues (context-dependent behavior similar to dispersal and conditional helping decisions; El Mouden and Gardner 2008; Holman 2014; Johnstone and Savage 2019).

In principle, the high-risk brinkmanship strategy of the recipient may be used only at critical periods in social relationships. If helping reduces future direct fitness options for helpers (e.g., physiological loss of fertility; Hunt 2007), risky kin blackmail could be relaxed once it is no longer in the helper's interests to leave. Alternatively, some forms of kin blackmail may be permanent, especially if achieved through a physical change. For instance, a social

Figure 3: Selection for blackmail. *a*, Dynamics of selection on blackmail (m) and unconditional helping (x). Here, blackmail fails to invade: victims have not had opportunities to evolve flexible responses. *b*, Game tree when player 1 can be exposed to a naturally occurring risk. Dice denote a move "by nature" (chance exposure to risk). Player 1 is shown in green, and player 2 is shown in blue. The rational move at each node to maximize the player's inclusive fitness by backwards induction is shown in bold. Stable kin blackmail is shown in red. *c*–*f*, Dynamics of selection on blackmail (m) and risk-sensitive helping (v). Blackmail can invade by exploiting the willingness of altruists to help when the recipient is in need (risk-sensitive helping; *c*). Blackmail cannot invade under lower benefit but strong blackmail (lower λ; *d*), weak blackmail but high benefit (*e*), or weak blackmail and low benefit (*f*). In plots *a* and *c*–*f*, the benefit of altruism to the recipient's personal fitness is $\delta = B_1 - A_1$, with certain defusing ($z = 1$). Relatedness is $r = 0.5$. The probability of a naturally arising risk in *c*–*f* is $k = 0.1$. Total frequency of altruism in the population is shown in blue. Circles show evolutionarily stable equilibria. Arrows point in the direction of selection. The payoffs are $A_1 = A_2 = 4$, $C_1 = \lambda A_1 = E_1$, $C_2 = A_2 = E_2$, $D_1 = B_1 = F_1$, $D_2 = B_2 = F_2$, and $B_2 = 1$. In *a*, we assume risk-sensitive helping is absent ($\bar{v} = 0$) and $k = 0$. In *c*–*f*, we assume $\bar{x} = 0$.

insect foundress may build a nest architecture that strategically increases the vulnerability of the brood. A foundress must leave her larvae unattended to forage, compelling a helper (a sister or first-emerging daughter) to join the nest and help to raise the brood.

A potentially widespread opportunity for kin blackmail involves energy allocation. An analogous strategic use of energy has been explored in parental care. For instance, Barta et al. (2002) and McNamara and Houston (2002) model mothers manipulating their reserves so that they become incapable of caring for their brood alone, making desertion a credible threat if unrelated fathers desert. Because a father has a direct fitness interest in his offspring, he is forced to shoulder the burden of continued care. In a corresponding kin blackmail context, a mother may overinvest her energy budget in one task (e.g., egg laying), deliberately impairing her ability to perform a second task (e.g., foraging). Because a relative (such as a son in a cooperatively breeding bird) has an indirect fitness interest in the mother's reproductive success, increasing risks of brood failure may incentivize the relative to perform the second task at higher levels.

Kin blackmail involves coercing active helping effort by adopting risks. Analogous effects may arise in reproductive skew games without helping. For instance, Cant (1998) finds that dominant reproductives may overinvest in clutch size to disincentivize egg laying by nonhelping subordinates (strategically raising subordinates' indirect fitness costs of egg laying through local resource competition). Kin blackmail may also arise in human interactions. For instance, Hagen's (1999) bargaining hypothesis (Hagen 2003; Syme et al. 2016) views depression as a (nonintentional) attempt to motivate social partners into increased help by threatening valued resources (e.g., the focal individual's contribution to collective foraging). In the illustrative case of postpartum depression, the "resource" can be a mother's reproductive success, in principle allowing mothers to threaten the indirect fitness interests of kin (Hagen 1999).

When strategic commitment devices succeed, it may be easy to overlook coercion. For example, in the African paper wasp *Belonogaster juncea*, a foundress needs helpers to raise the brood: a lone foundress has an extremely low chance of success (Tindo et al. 2008). A standard interpretation is that high failure rates are an ecological constraint (Tindo et al. 2002; Tibbetts and Reeve 2003). By contrast, a kin blackmail hypothesis predicts that single foundresses would be capable of brood rearing if they were to adopt less risky strategies (such as laying only modest clutches). Faced with a large number of brood with an increased risk of total failure in the absence of help, sisters may then be blackmailed into helping to rear the brood.

In conclusion, we suggest that recipients may be able to coerce higher levels of altruism by making their own fitness overly dependent on kin. Much as the deterrent threat of nuclear war has shaped international relations without the use of nuclear weapons since 1945 (Schelling 2006; Rauchhaus 2009), seemingly harmonious cooperation may sometimes be a product of inclusive-fitness deterrents that—because of their strategic success—are rarely seen to be carried out.

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Statement of Authorship

P.K. conceived the original idea, which both authors developed together; P.K. conducted the modeling; and both authors wrote the manuscript.

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Two *Ropalidia* wasps cooperating to build a new nest on a banana frond in Ghana. Photo: Patrick Kennedy.