

Volatile Chemical Emission as a Weapon of Rearguard Action: A Game-Theoretic Model of Contest Behavior

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Abstract We use a game-theoretic model to explore whether volatile chemical (spiroacetal) emissions can serve as a weapon of rearguard action. Our basic model explores whether such emissions serve as a means of temporary withdrawal, preventing the winner of the current round of a contest from translating its victory into permanent possession of a contested resource. A variant of this model explores an alternative possibility, namely, that such emissions serve as a means of permanent retreat, attempting to prevent a winner from inflicting costs on a fleeing loser. Our results confirm that the underlying logic of either interpretation of weapons of rearguard action is sound; however, empirical observations on parasitoid wasp contests suggest that the more likely function of chemical weapons is to serve as a means of temporary withdrawal. While our work is centered around the particular biology of contest behavior in parasitoid wasps, it also provides the first contest model to explicitly consider self-inflicted damage costs, as called for recently by Lane and Briffa (2017).

Keywords spiroacetal · *Goniozus* · self-inflicted damage

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1 Introduction

Contests were among the first aspects of animal behavior to be explored by game-theoretic modelling (Maynard Smith and Price 1973; Parker 2013). Subsequent developments of theory have been stimulated by reciprocal interactions with empirical studies, leading to a refined understanding of the evolutionary forces that shape adaptive behavior during contest interactions and to a framework for predicting contest outcomes (Briffa and Hardy 2013; Kokko 2013; Sherratt and Mesterton-Gibbons 2013). Thus, game-theoretic analyses can be useful for providing a general expectation for how strategies will evolve and spread (Maynard Smith and Price 1973; Maynard Smith 1982) or may focus on understanding a particular type of contest situation (Sherratt and Mesterton-Gibbons 2013), including being attuned to the biological details of a given species (Hammerstein and Riechert 1988).

Females of the parasitoid wasp species *Goniozus legneri* and *Goniozus nephantidis* have been observed to release a volatile chemical, a spiroacetal, during multi-stage contests over a valuable resource, specifically, a host caterpillar (Goubault et al. 2006, 2008). In these experiments, any animal that released the chemical was invariably the loser of the contest bout preceding the release, and in most cases was also the ultimate loser of the contest overall. Release did not occur in every contest, and was more common when contests were more aggressive.

The function of such volatile chemical release remains unclear. Two suggestions have been that the chemical acts as a damaging weapon of rearguard action and that the chemical serves as a non-damaging signal of submission (Goubault et al. 2006, 2008; Hardy et al. 2013). Distinguishing between these two possibilities has proven difficult (Briffa et al. 2013, p. 68). Because contests are frequently resolved without any chemical emission, however, any signalling function is at least not a necessary component of contest termination. Moreover, the chemical concerned can act as an insecticide against some other species, leading Goubault et al. (2006, p. 2858) to favor the first possibility, for which as yet there exists no formal theory. Accordingly, our purpose here is to initiate a theory for weapons of rearguard action by developing a basic game-theoretic model. In so doing, we also develop the first model to follow the suggestion by Lane and Briffa (2017) that self-damage should be explicitly incorporated into contest theory.

What precisely is meant by a weapon of rearguard action? There appear to be subtle differences of usage. On the one hand, Goubault et al. (2006, p. 2858) state that it is “used by losers during tactical withdrawals.” This interpretation suggests that the weapon is primarily a means of preventing the winner of the current round from translating its victory into permanent possession of the resource. On the other hand, Briffa et al. (2013, p. 68) imply that a weapon of rearguard action creates “an opportunity for the releaser to retreat from a contest.” This interpretation suggests that the contest is no longer to be won, and that the weapon is primarily a means of creating an opportunity for escape (analogous to using Mace

or pepper spray). Our primary focus here is on developing a model that embodies the first interpretation. We refer to it as Model A (§2). Nevertheless, in a later section we also develop a variant of this model that instead embodies the second interpretation; we refer to it as Model B (§5). We use these models to explore why the volatile chemical is not released during all aggressive encounters, and what particular assumptions or parameter values would be expected to lead to patterns of behavior similar to those that have been observed.

2 Model A: Rearguard action as a means of contest extension

We consider contests over a valuable and indivisible resource between pairs of animals drawn randomly from a large population. These animals vary in resource holding potential (RHP, Parker 1974), which we regard as a measure of physical condition or strength: the stronger an animal is, the more likely it is that the animal will win. However, a contestant's probability of winning can also be augmented by advantages of ownership (Hardy et al. 2013; Kokko 2013; Petersen and Hardy 1996).

In order to obtain a tractable model, we idealize a contest that could involve multiple rounds of fighting by considering a contest with at most two rounds. One of the two contestants is the current owner of a contested resource, the other is an intruder challenging for use of that resource, and their roles are randomly assigned. The value of the resource is V to the prior owner and αV to the prior intruder; we will refer to α as the intruder premium, especially when $\alpha > 1$. In *Goniozus*, however, owners may place higher value on hosts than do intruders by virtue of being more ready to exploit them (Stokkebo and Hardy 2000), corresponding to $\alpha < 1$. Note that the meanings of V , α and all other parameters for Model A are listed in Table 1 for ease of reference.

Table 1 Model A parameters

Parameter	Meaning	Bounds
V	Value of resource to prior owner	$0 < V < \infty$
α	Value of resource to prior intruder, scaled with respect to V	$0 < \alpha < \infty$
γ	Maximum cost per round of fighting, scaled with respect to V	$0 < \gamma \leq 1$
k	Insensitivity of cost with respect to RHP, in the sense that a small increase in RHP implies a large cost reduction when k is very low but virtually no cost reduction when k is very high	$0 < k < \infty$
r	Reliability of RHP difference as a predictor of fight outcome	$0 < r < \infty$
μ	Owner advantage, in the sense that an owner wins against an opponent of equal RHP with probability $\frac{1}{2}(1 + \mu)$	$0 \leq \mu \leq 1$
θ_l	Toxicity of chemical to releaser: reduces first-round loser's RHP by factor $1 - \theta_l$	$0 \leq \theta_l \leq \theta_w$
θ_w	Toxicity of chemical to non-releaser: reduces first-round winner's RHP by factor $1 - \theta_w$	$\theta_l \leq \theta_w < 1$

We assume that each contestant knows its own fighting ability or RHP, but not that of its opponent (as in, e.g., Mesterton-Gibbons et al. 1996; Mesterton-Gibbons and Sherratt 2011). Let the focal indi-

vidual (Player 1) have RHP X , and let the non-focal individual (Player 2) have RHP Y . These RHPs are random variables drawn independently from the same continuous distribution on $[0, 1]$. We will denote its probability density function by g and its cumulative distribution function by G . Thus for $S = X$ or $S = Y$ we have

$$\text{Prob}(0 \leq S \leq s) = \int_0^s g(\xi) d\xi \quad (1)$$

for all $s \in [0, 1]$ with $G(0) = 0$ and $G(1) = 1$.

We assume that fighting is inevitable whenever two individuals encounter one another at an indivisible resource, so that whether to fight is not part of an animal's strategy. What is strategic, however, is whether to accept a first-round defeat as decisive or to force the contest to a second—and, in our idealized model, final—round. In this regard, we explore the possibility that the function of volatile chemical emission is to prevent a first-round winner from converting that victory into permanent ownership of the resource: the contest goes to a second round because the first-round loser is using chemical release as a weapon to prevent defeat in the first round from equating to permanent defeat. We assume throughout that the cost of releasing the chemical is negligible compared to that of fighting.

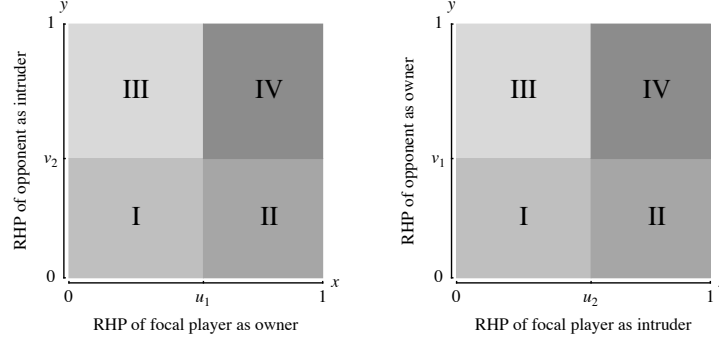
We make the following additional assumptions: An animal's strategy consists of a pair of RHP thresholds, one for accepting a first-round defeat as decisive when the animal is an owner, another for accepting a first-round defeat as decisive when the animal is an intruder. Let $u = (u_1, u_2) \in [0, 1] \times [0, 1]$ denote this strategy for Player 1, and let $v = (v_1, v_2) \in [0, 1] \times [0, 1]$ be the corresponding strategy for Player 2. That is, if Player 1 loses the first round when in role j , then it will accept its defeat as decisive if $X \leq u_j$ but emit the volatile chemical to instigate a second round if $X > u_j$, where $j = 1$ for the role of owner and $j = 2$ for the role of intruder; and likewise, if Player 2 loses the first round when in role j , then it will accept its defeat as decisive if $Y \leq v_j$ but emit the volatile chemical to instigate a second round if $Y > v_j$.

For a first-round loser, emission of the chemical not only guarantees that the contest progresses to a second round, but also may increase the emitter's chances of winning it. Although there is no direct evidence that the spiroacetal has a damaging effect on *Goniozus*, it is known to be lethal to *Drosophila* flies (Francke and Kitching 2001). We should therefore allow for the possibility that release of this chemical may impair an animal's physical condition, which in our model corresponds to reducing its RHP (Lane and Briffa 2017). Let emission of the chemical by a first-round loser with RHP S reduce its RHP to

$$S_l = (1 - \theta_l)S \quad (2a)$$

where $\theta_l \in [0, 1]$ and S is either X or Y . Let the concomitant effect on a first-round winner with RHP S be to reduce its RHP to

$$S_w = (1 - \theta_w)S \quad (2b)$$

Fig. 1 The sample space of pairs of strengths.

where $\theta_w \in [0, 1]$ and S is either Y or X , according to whether S is X or Y in (2a). It will be convenient to refer to θ_l or θ_w as the toxicity of the chemical to the loser or winner, respectively. If indeed $\theta_l > 0$, then release of the chemical corresponds to self-inflicted damage in the sense of Lane and Briffa (2017). Because the first-round loser is withdrawing from the site of maximum concentration of chemical as it releases it, however, we expect such self-inflicted damage to be at least matched by a concomitant reduction in the RHP of the first-round winner, that is, $\theta_w \geq \theta_l$.

We assume that an animal's probability of victory, denoted by p_o for an owner and by p_i for an intruder, increases with the difference in RHP between itself and its opponent in either round (as in, e.g., Mesterton-Gibbons and Sherratt 2009). We denote this difference in RHP by Δ , with $\Delta = X - Y$ for Player 1 and $\Delta = Y - X$ for Player 2 in such a way that

$$p'_o(\Delta) > 0, \quad p'_i(\Delta) > 0 \quad (3)$$

with

$$p_o(\Delta) + p_i(-\Delta) = 1 \quad (4)$$

for all $\Delta \in [-1, 1]$, where a prime denotes differentiation with respect to argument.

We assume that the cost per round of fighting is either independent of RHP, or else depends only on an animal's own RHP and is higher for weaker animals (as in, e.g., Mesterton-Gibbons and Adams 2003). It is convenient to scale cost with respect to value. We therefore denote the cost per round of fighting by $Vc(S)$ with

$$c'(S) \leq 0, \quad c(0) = \gamma \quad (5)$$

where S denotes RHP, so that γ denotes maximum cost. We assume the resource to be sufficiently valuable that its value exceeds the maximum cost per round of fighting. Hence

$$\gamma \leq 1. \quad (6)$$

Regardless of whether Player 1's role is that of owner or intruder, the acceptance thresholds partition the sample space into four rectangular regions, which we denote by I, II, III and IV, as indicated in

Figure 1. Having already scaled fighting cost with respect to value, for consistency we must also scale fitness with respect to value. Accordingly, for $K = \text{I}, \dots, \text{IV}$, let $Vf_K^o(X, Y)$ denote the payoff to the focal individual if $(X, Y) \in K$ when Player 1 is the owner, and let $Vf_K^i(X, Y)$ denote the corresponding payoff when Player 1 is the intruder.

We allow for two alternative interpretations of the relationship between victory and ownership in the event that the contest goes to a second round. The first interpretation is that ownership is not transferred until the contest has been decided; in this case, we term the contest a contest with final possession. The second interpretation is that the first-round winner is the second-round owner and acquires the tactical advantages of ownership for the second round regardless of whether it was the prior owner (even though ownership is not permanently settled until the contest ends and the ultimate winner is decided); in this case, we term the contest a contest with intermediate possession. Accordingly, in the event that the contest goes to a second round, let W or L denote the second-round role of the first-round owner according to whether it wins or loses, respectively, and let w or l denote the second-round role of the first-round intruder according to whether it wins or loses; thus W is invariably the opposite role to l , and likewise for L and w , with

$$p_W(\Delta) + p_l(-\Delta) = 1 = p_L(\Delta) + p_w(-\Delta) \quad (7)$$

for all $\Delta \in [-1, 1]$ by (4). Then

$$W = L = o \quad \text{and} \quad w = l = i \quad (8a)$$

with final possession, whereas

$$W = w = o \quad \text{and} \quad L = l = i \quad (8b)$$

with intermediate possession. Note that the value assigned to the resource by a contestant is assumed to be determined by the contestant's prior role and to remain unchanged throughout the contest.

Let us first suppose that Player 1 is the owner while Player 2 is the intruder. Region I is where either animal would accept defeat after losing Round 1, and so the payoff to the focal individual is $V - Vc(X)$ with probability $p_o(X - Y)$ and $0 - Vc(X)$ with probability $p_i(Y - X)$, or $\{V - Vc(X)\}p_o(X - Y) - Vc(X)p_i(Y - X) = V\{p_o(X - Y) - c(X)\}$ by (4), so that

$$f_1^o(X, Y) = p_o(X - Y) - c(X). \quad (9)$$

Region II is where Player 1 instigates a second round after losing the first one, whereas Player 2 does not. So the payoff to the focal individual remains $V\{1 - c(X)\}$ if Player 1 wins the first round, that is, with probability $p_o(X - Y)$. If, however, Player 2 wins the first round, which happens with probability $p_i(Y - X)$, then the payoff to Player 1 is $V - Vc(X) - Vc(X_l)$ with probability $p_L(X_l - Y_w)$ and $0 - Vc(X) - Vc(X_l)$ with probability $p_w(Y_w - X_l)$, or $V\{p_L(X_l - Y_w) - c(X) - c(X_l)\}$ by (7) with $\Delta = X_l - Y_w$,

where X_l and Y_w are defined by (2). Multiplying the above conditional payoff by $p_i(Y - X)$, multiplying $V\{1 - c(X)\}$ by $p_o(X - Y)$, adding and using (4) with $\Delta = X - Y$, we obtain

$$f_{\text{II}}^o(X, Y) = p_o(X - Y) + \{p_L(X_l - Y_w) - c(X_l)\}p_i(Y - X) - c(X). \quad (10)$$

Correspondingly, Region III is where Player 2 instigates a second round after losing the first one, whereas Player 1 does not. So the payoff to the focal individual is $0 - Vc(X)$ if Player 2 wins the first round, that is, with probability $p_i(Y - X)$. If, however, Player 1 wins the first round, which happens with probability $p_o(X - Y)$, then the payoff to Player 1 is $V - Vc(X) - Vc(X_w)$ with probability $p_W(X_w - Y_l)$ and $0 - Vc(X) - Vc(X_w)$ with probability $p_l(Y_l - X_w)$, or $V\{p_W(X_w - Y_l) - c(X) - c(X_w)\}$ by (7) with $\Delta = X_w - Y_l$, where X_w and Y_l are defined by (2). Multiplying the above conditional payoff by $p_o(X - Y)$, $0 - Vc(X)$ by $p_i(Y - X)$, adding and again using (4), we obtain, in lieu of (10),

$$f_{\text{III}}^o(X, Y) = \{p_W(X_w - Y_l) - c(X_w)\}p_o(X - Y) - c(X). \quad (11)$$

Finally, Region IV is where either animal instigates a second round after losing the first one. So the payoff to the focal individual is $V\{p_W(X_w - Y_l) - c(X) - c(X_w)\}$ with probability $p_o(X - Y)$ or $V\{p_L(X_l - Y_w) - c(X) - c(X_l)\}$ with probability $p_i(Y - X)$. That is,

$$f_{\text{IV}}^o(X, Y) = \{p_W(X_w - Y_l) - c(X_w)\}p_o(X - Y) + \{p_L(X_l - Y_w) - c(X_l)\}p_i(Y - X) - c(X). \quad (12)$$

Let $f^o(u_1, v_2)$ denote the reward to a u -strategist in the role of owner against a v -strategist in the role of intruder, scaled with respect to value. Then

$$Vf^o(u_1, v_2) = \sum_{K=1}^{\text{IV}} \iint_K V f_K^o(x, y) g(x) g(y) dx dy \quad (13)$$

where g is the probability density function, implying

$$\begin{aligned} f^o(u_1, v_2) &= \int_0^{u_1} \int_0^{v_2} f_{\text{I}}^o(x, y) g(y) g(x) dy dx + \int_{u_1}^1 \int_0^{v_2} f_{\text{II}}^o(x, y) g(y) g(x) dy dx \\ &\quad + \int_0^{u_1} \int_{v_2}^1 f_{\text{III}}^o(x, y) g(y) g(x) dy dx + \int_{u_1}^1 \int_{v_2}^1 f_{\text{IV}}^o(x, y) g(y) g(x) dy dx. \end{aligned} \quad (14)$$

Considering cases when Player 1 is the intruder while Player 2 is the owner, the payoff to the focal individual in Region I becomes $\alpha V - Vc(X)$ with probability $p_i(X - Y)$ and $0 - Vc(X)$ with probability $p_o(Y - X)$, so that, by (4),

$$f_{\text{I}}^i(X, Y) = \alpha p_i(X - Y) - c(X). \quad (15)$$

Continuing in this manner, (10)–(12) and (14) become modified to

$$f_{\text{II}}^i(X, Y) = \alpha p_i(X - Y) + \{\alpha p_l(X_l - Y_w) - c(X_l)\} p_o(Y - X) - c(X), \quad (16)$$

$$f_{\text{III}}^i(X, Y) = \{\alpha p_w(X_w - Y_l) - c(X_w)\} p_i(X - Y) - c(X), \quad (17)$$

$$f_{\text{IV}}^o(X, Y) = \{\alpha p_w(X_w - Y_l) - c(X_w)\} p_i(X - Y) + \{\alpha p_l(X_l - Y_w) - c(X_l)\} p_o(Y - X) - c(X) \quad (18)$$

and

$$\begin{aligned} f^i(u_2, v_1) = & \int_0^{u_2} \int_0^{v_1} f_{\text{I}}^i(x, y) g(y) g(x) dy dx + \int_{u_2}^1 \int_0^{v_1} f_{\text{II}}^i(x, y) g(y) g(x) dy dx \\ & + \int_0^{u_2} \int_{v_1}^1 f_{\text{III}}^i(x, y) g(y) g(x) dy dx + \int_{u_2}^1 \int_{v_1}^1 f_{\text{IV}}^i(x, y) g(y) g(x) dy dx \end{aligned} \quad (19)$$

where $f^i(u_2, v_1)$ denotes the reward to a u -strategist in the role of intruder against a v -strategist in the role of owner, scaled with respect to value. Let $f(u, v)$ denote the unconditional reward to a u -strategist against a v -strategist, scaled with respect to value. Then assuming the roles of prior owner and intruder to be equally likely, we obtain

$$f(u, v) = \frac{1}{2} f^o(u_1, v_2) + \frac{1}{2} f^i(u_2, v_1). \quad (20)$$

Straightforward partial differentiation shows that

$$\frac{\partial f}{\partial u_1} = \frac{1}{2} \int_0^{v_2} \{f_{\text{I}}^o(u_1, y) - f_{\text{II}}^o(u_1, y)\} g(u_1) g(y) dy + \frac{1}{2} \int_{v_2}^1 \{f_{\text{III}}^o(u_1, y) - f_{\text{IV}}^o(u_1, y)\} g(u_1) g(y) dy \quad (21a)$$

$$= \frac{1}{2} g(u_1) \int_0^1 \{c(\{1 - \theta_l\}u_1) - p_L(\{1 - \theta_l\}u_1 - \{1 - \theta_w\}y)\} p_i(y - u_1) g(y) dy \quad (21b)$$

with

$$\begin{aligned} \frac{\partial^2 f}{\partial u_1^2} = & \frac{1}{2} \{1 - \theta_l\} \int_0^1 \{c'(\{1 - \theta_l\}u_1) - p'_L(\{1 - \theta_l\}u_1 - \{1 - \theta_w\}y)\} p_i(y - u_1) g(u_1) g(y) dy \\ & + \frac{1}{2} \int_0^1 \{c(\{1 - \theta_l\}u_1) - p_L(\{1 - \theta_l\}u_1 - \{1 - \theta_w\}y)\} \{p_i(y - u_1) g'(u_1) - p'_i(y - u_1) g(u_1)\} g(y) dy \end{aligned} \quad (22)$$

and

$$\frac{\partial f}{\partial u_2} = \frac{1}{2} \int_0^{v_1} \{f_{\text{I}}^i(u_2, y) - f_{\text{II}}^i(u_2, y)\} g(u_2) g(y) dy + \frac{1}{2} \int_{v_1}^1 \{f_{\text{III}}^i(u_2, y) - f_{\text{IV}}^i(u_2, y)\} g(u_2) g(y) dy \quad (23a)$$

$$= \frac{1}{2} g(u_2) \int_0^1 \{c(\{1 - \theta_l\}u_2) - \alpha p_l(\{1 - \theta_l\}u_2 - \{1 - \theta_w\}y)\} p_o(y - u_2) g(y) dy \quad (23b)$$

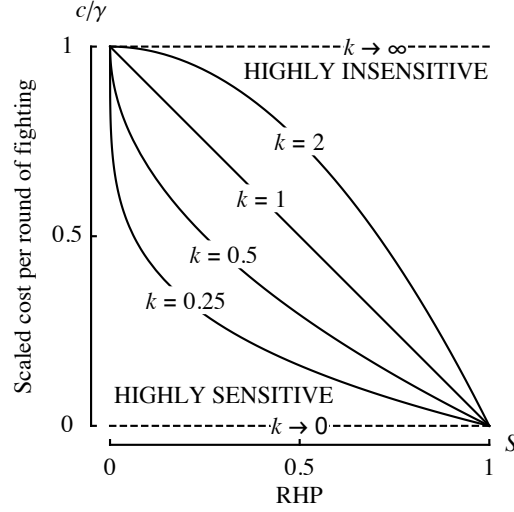


Fig. 2 Dependence of cost per round of fighting on resource holding potential according to equation (27) for five different values of the insensitivity parameter k . A small RHP increase implies a large cost reduction when k is very low but virtually no cost reduction when k is very high. Although the limiting curves for zero and infinite insensitivity are shown (dashed) for completeness, we assume that k is both positive and finite whenever costs are differential. Constant costs are treated as a separate case (according to equation (26)).

with

$$\begin{aligned} \frac{\partial^2 f}{\partial u_2^2} &= \frac{1}{2}\{1 - \theta_l\} \int_0^1 \{c'(\{1 - \theta_l\}u_2) - \alpha p_l'(\{1 - \theta_l\}u_2 - \{1 - \theta_w\}y)\} p_o(y - u_2) g(u_2) g(y) dy \\ &+ \frac{1}{2} \int_0^1 \{c(\{1 - \theta_l\}u_2) - \alpha p_l(\{1 - \theta_l\}u_2 - \{1 - \theta_w\}y)\} \{p_o(y - u_2) g'(u_2) - p_o'(y - u_2) g(u_2)\} g(y) dy. \end{aligned} \quad (24)$$

Note that the first terms of (22) and (24) are invariably negative, by (3) and (5).

Further progress towards a tractable model requires the choice of specific forms for p , c and g . Accordingly, we idealize high variation in physical condition by assuming that RHP is uniformly distributed between 0 and 1 as in Adams and Mesterton-Gibbons (1995), so that

$$g(\xi) = 1 \quad (25)$$

in (1). Moreover, and again for simplicity, we satisfy (5) by choosing either

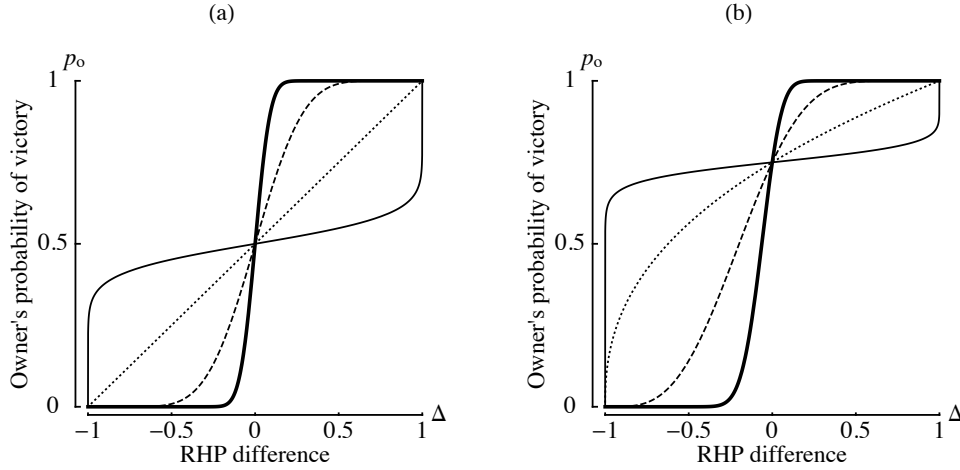
$$c(S) = \gamma, \quad (26)$$

so that costs are independent of physical condition, or

$$c(S) = \gamma(1 - S^k) \quad (27)$$

with $0 < k < \infty$, so that costs are higher at lower physical condition. Here k measures the insensitivity of cost with respect to RHP, in the sense that a small increase in RHP implies a large cost reduction

Fig. 3 The effect of difference in resource holding potential on the owner's probability of victory. Probability of victory is defined by equation (28). Results are shown for four different values of reliability, namely, $r = 0.1$ (thin solid curve), $r = 1$ (dotted), $r = 10$ (dashed) and $r = 100$ (thick solid curve) and for two different values of ownership advantage, namely, (a) $\mu = 0$ and (b) $\mu = 0.5$.



when k is very low but virtually no cost reduction when k is very high, as illustrated by Figure 2. We distinguish these alternatives by stating that costs are constant or differential according to whether (26) or (27) applies.

We have yet to specify the probability of victory, p_o for an owner and p_i for an intruder. We satisfy (3) and (4) by choosing

$$p_o(\Delta) = \left\{ \frac{\Gamma(2r)}{\Gamma(r)^2} B\left(\frac{1}{2} + \frac{1}{2}\Delta, r, r\right) \right\}^{1 - \frac{\ln(1+\mu)}{\ln(2)}} \quad (28)$$

where B is the incomplete Beta function, i.e., $B(w, p_1, p_2) = \int_0^w \xi^{p_1-1} (1-\xi)^{p_2-1} d\xi$. Here r is a measure of the reliability of RHP difference as a predictor of fight outcome, as illustrated by Figure 3(a); intuitively, RHP difference is a very weak predictor if r is small, a moderately reliable predictor if r is close to 1 and a strong predictor if r is very large. Because

$$p_o(0) = \frac{1}{2}(1 + \mu) \quad (29)$$

with $p_i(0) = \frac{1}{2}(1 - \mu)$, we see that μ represents the advantage of ownership, i.e., degree to which an owner's probability of winning is increased beyond $\frac{1}{2}$ toward 1 in a contest between evenly matched opponents. The effect of this parameter is illustrated by comparing Figures 3(a) and 3(b).

3 ESS analysis for Model A

A population strategy $v = (v_1, v_2)$ is a strong evolutionarily stable strategy or ESS *sensu* Maynard Smith (1982) when it is uniquely the best reply to itself, that is when $f(v, v) > f(u, v)$ for any potential mutant

strategy $u \neq v$, which for $j = 1$ or $j = 2$ requires

$$\left. \frac{\partial f}{\partial u_j} \right|_{u=v} = 0 \quad (30)$$

with

$$\left. \frac{\partial^2 f}{\partial u_j^2} \right|_{u=v} < 0 \quad (31)$$

for $0 < v_j < 1$ at the ESS, but instead

$$\left. \frac{\partial f}{\partial u_j} \right|_{u=v} < 0 \quad (32)$$

for $v_j = 0$ at the ESS and

$$\left. \frac{\partial f}{\partial u_j} \right|_{u=v} > 0 \quad (33)$$

for $v_j = 1$ at the ESS (see, e.g. Broom and Rychtář 2013).

3.1 Differential costs

It follows from (5), (21b), (23b), (25), (27), (32) and (33) that $v_1 = 0$ at the ESS for $\gamma < \underline{\gamma}_c^o$ and $v_2 = 0$ at the ESS for $\gamma < \underline{\gamma}_c^i$, where

$$\underline{\gamma}_c^o = \frac{\int_0^1 p_L(-\{1 - \theta_w\}y) p_i(y) dy}{\int_0^1 p_i(y) dy} \quad (34a)$$

and

$$\underline{\gamma}_c^i = \frac{\alpha \int_0^1 p_i(-\{1 - \theta_w\}y) p_o(y) dy}{\int_0^1 p_o(y) dy} = \frac{\alpha \int_0^1 p_i(-\{1 - \theta_w\}y) p_o(y) dy}{\int_0^1 p_o(y) dy}, \quad (34b)$$

on using (8). Note that these expressions are independent of both k and θ_l , and that $\underline{\gamma}_c^o < \frac{1}{2}$ and $\underline{\gamma}_c^i < \frac{1}{2}\alpha$ (although these values are approached in the limit as $\theta_w \rightarrow 1$). Furthermore, $v_1 = 1$ at the ESS for $\gamma > \bar{\gamma}_c^o$ and $v_2 = 1$ at the ESS for $\gamma > \bar{\gamma}_c^i$, where

$$\bar{\gamma}_c^o = \frac{\int_0^1 p_L(1 - \theta_l - \{1 - \theta_w\}y) p_i(y-1) dy}{(1 - \{1 - \theta_l\}^k) \int_0^1 p_i(y-1) dy} \quad (35a)$$

and

$$\bar{\gamma}_c^i = \frac{\alpha \int_0^1 p_i(1 - \theta_l - \{1 - \theta_w\}y) p_o(y-1) dy}{(1 - \{1 - \theta_l\}^k) \int_0^1 p_o(y-1) dy}. \quad (35b)$$

Note that if $\theta_l = 0$, implying $c(1 - \theta_l) = 0$ by (27), then $v_j = 1$ can hold at the ESS neither for $j = 1$ nor for $j = 2$, because (21b) or (23b) implies $\left. \frac{\partial f}{\partial u_j} \right|_{u=v=1} < 0$, contradicting (33). Thus, because the RHP threshold for emission will always be less than its maximum value at the ESS when $\theta_l = 0$, it will always pay the strongest first-round losers to emit the chemical when the chemical is not toxic to the releaser. The very same result follows by noting that $\bar{\gamma}_c^o \rightarrow \infty$, $\bar{\gamma}_c^i \rightarrow \infty$ as $\theta_l \rightarrow 0$ in (35). When $\theta_l > 0$, on the other hand, both $\bar{\gamma}_c^o$ and $\bar{\gamma}_c^i$ are finite. If $\theta_l > 0$ is so large that $\bar{\gamma}_c^o$ and $\bar{\gamma}_c^i$ are not only finite but also less than 1, then it follows from (6) that there exists a range of values of the maximum cost γ so close to its

upper limit of 1 that even the strongest first-round losers would refrain from chemical emission; hence no first-round loser would emit the chemical, which is contrary to empirical evidence (Goubault et al. 2006, 2008). It therefore seems likely that self-toxicity θ_l is low enough to ensure $\bar{\gamma}_c^o, \bar{\gamma}_c^i > 1$ or γ is never so close to its maximum, or both.

For values of γ between the lower and upper critical values, it follows from (5), (21b), (23b), (25) and (30) that $v_1 = v_1^*$ at the ESS for $\underline{\gamma}_c^o < \gamma < \bar{\gamma}_c^o$ and $v_2 = v_2^*$ at the ESS for $\underline{\gamma}_c^i < \gamma < \bar{\gamma}_c^i$, where $v_1 = v_1^*$ and $v_2 = v_2^*$ are the only roots of the equations

$$\int_0^1 \{c(\{1 - \theta_l\}v_1) - p_L(\{1 - \theta_l\}v_1 - \{1 - \theta_w\}y)\} p_i(y - v_1) dy = 0 \quad (36a)$$

and

$$\int_0^1 \{c(\{1 - \theta_l\}v_2) - \alpha p_l(\{1 - \theta_l\}v_2 - \{1 - \theta_w\}y)\} p_o(y - v_2) dy = 0, \quad (36b)$$

respectively. Note from (8a) and (8b) that (34a), (35a) and (36a) differ between contests with final ($p_L = p_o$, prior owner retains owner advantage for the second round) or with intermediate ($p_L = p_i$, prior owner loses owner advantage for the second round) possession, whereas (34b), (35b) and (36b) are unaffected ($p_l = p_i$ in either case, a losing intruder lacks owner advantage).

We find that inequality (31) is invariably satisfied with $j = 1$ for $v_1 = v_1^*$ defined by (36a) and with $j = 2$ for $v_2 = v_2^*$ defined by (36b), thus confirming that $v^* = (v_1^*, v_2^*)$ is indeed an ESS. In some special cases we can verify these results analytically (see Appendix A, in particular (A.11)), although in general we can verify them only numerically. Nevertheless, inspection shows that (31) holds for $j = 1$ because (22) and (25) imply

$$\begin{aligned} \frac{\partial^2 f}{\partial u_1^2} \Big|_{u=v} &= \frac{1}{2} \{1 - \theta_l\} \int_0^1 \{c'(\{1 - \theta_l\}v_1) - p'_L(\{1 - \theta_l\}v_1 - \{1 - \theta_w\}y)\} p_i(y - v_1) dy \\ &\quad - \frac{1}{2} \int_0^1 \{c(\{1 - \theta_l\}v_1) - p_L(\{1 - \theta_l\}v_1 - \{1 - \theta_w\}y)\} p'_i(y - v_1) dy \quad (37) \end{aligned}$$

The first term must be negative by (3) and (5), and (3) implies that the second integral could be sufficiently negative to make (37) positive only if $c(\{1 - \theta_l\}v_1) - p_L(\{1 - \theta_l\}v_1 - \{1 - \theta_w\}y)$ were substantially negative on $[0, 1]$, in which case (36a) could not hold. A very similar argument shows why (31) holds for $j = 2$.

The resultant ESS $v^* = (v_1^*, v_2^*)$ in general depends on seven parameters, namely, $\alpha, \gamma, k, r, \mu, \theta_l$ and θ_w . At this ESS, Player 1 wins the contest after losing the first round if $(X, Y) \in \text{II} \cup \text{IV}$ in Figure 1 and Player 2 wins the first round but Player 1 wins the second. With $\Delta = X - Y$ and $\Delta_{lw} = X_l - Y_w$ (defined by (2) with $S = X$ or Y), this event arises with probability $p_i(-\Delta)p_L(\Delta_{lw})$ if Player 1 is the prior owner

or $p_o(-\Delta)p_l(\Delta_{lw})$ if Player 2 is the prior owner, for $(X, Y) \in \text{II} \cup \text{IV}$. So, the overall probability that Player 1 wins the contest after losing the first round is

$$\begin{aligned} & \frac{1}{2} \int_{v_1^*}^1 \int_0^1 p_i(y-x)p_L(x_l-y_w)g(y)g(x)dydx + \frac{1}{2} \int_{v_2^*}^1 \int_0^1 p_o(y-x)p_l(x_l-y_w)g(y)g(x)dydx \\ &= \frac{1}{2} \int_{v_1^*}^1 \int_0^1 p_i(y-x)p_L(x_l-y_w)dydx + \frac{1}{2} \int_{v_2^*}^1 \int_0^1 p_o(y-x)p_i(x_l-y_w)dydx \end{aligned} \quad (38)$$

by (8) and (25), where $x_l = (1 - \theta_l)x$ and $y_w = (1 - \theta_w)y$; the first integral is the probability of winning after losing as owner and the second integral is the probability of winning after losing as intruder. The corresponding probability that Player 2 wins the contest after losing the first round, obtained by substituting III for II and interchanging x and y , equals the expression in (38). Hence, the probability that the contest is won by a first-round loser, denoted by p_{LW} , is just twice the above expression, or

$$p_{LW} = \int_{v_1^*}^1 \int_0^1 p_i(y-x)p_L(x_l-y_w)dydx + \int_{v_2^*}^1 \int_0^1 p_o(y-x)p_i(x_l-y_w)dydx. \quad (39)$$

Correspondingly, the probability that the volatile chemical is released—by either contestant, regardless of which individual ultimately wins, is

$$p_{VC} = \int_{v_1^*}^1 \int_0^1 p_i(y-x)dydx + \int_{v_2^*}^1 \int_0^1 p_o(y-x)dydx. \quad (40)$$

Another quantity of interest is the overall probability that the prior owner wins the contest, namely,

$$\begin{aligned} P_o &= \iint_{\text{I}} p_o(x-y)g(x)g(y)dx dy + \iint_{\text{II}} \{p_o(x-y) + p_i(y-x)p_L(x_l-y_w)\}g(x)g(y)dx dy \\ &+ \iint_{\text{III}} p_o(x-y)p_W(x_w-y_l)g(x)g(y)dx dy \\ &+ \iint_{\text{IV}} \{p_o(x-y)p_W(x_w-y_l) + p_i(y-x)p_L(x_l-y_w)\}g(x)g(y)dx dy \\ &= \int_0^1 \int_0^{v_2^*} p_o(x-y)dydx + \int_{v_1^*}^1 \int_0^1 p_i(y-x)p_L(x_l-y_w)dydx \\ &+ \int_0^1 \int_{v_2^*}^1 p_o(x-y)p_o(x_w-y_l)dydx \end{aligned} \quad (41)$$

by (8) and (25); except when $\mu = 0$, $p_i < p_o$. It follows from (8) and (41) that P_o is lower with intermediate than with final possession, as illustrated by the lowest two panels of Figure 6.

3.2 Constant costs

The above analysis is largely unaltered when costs are constant; in particular, (34) is still correct for $\underline{\gamma}_c^o$ and $\underline{\gamma}_c^i$. With c now given by (26), however, we obtain

$$\bar{\gamma}_c^o = \frac{\int_0^1 p_L(1 - \theta_l - \{1 - \theta_w\}y)p_i(y-1)dy}{\int_0^1 p_i(y-1)dy} \quad (42a)$$

$$\bar{\gamma}_c^i = \frac{\alpha \int_0^1 p_i(1 - \theta_l - \{1 - \theta_w\}y)p_o(y-1)dy}{\int_0^1 p_o(y-1)dy} \quad (42b)$$

in place of (35) and

$$\int_0^1 \{\gamma - p_L(\{1 - \theta_l\}v_1 - \{1 - \theta_w\}y)\}p_i(y - v_1)dy = 0 \quad (43a)$$

$$\int_0^1 \{\gamma - \alpha p_i(\{1 - \theta_l\}v_2 - \{1 - \theta_w\}y)\}p_o(y - v_2)dy = 0 \quad (43b)$$

in place of (36). Moreover, $\bar{\gamma}_c^o$ and $\bar{\gamma}_c^i$ are now both finite even if $\theta_l = 0$, whereas $\bar{\gamma}_c^o \rightarrow \infty$, $\bar{\gamma}_c^i \rightarrow \infty$ as $\theta_l \rightarrow 0$ in the case of differential costs, by (35). Indeed $\bar{\gamma}_c^o < 1$ and $\bar{\gamma}_c^i < \alpha$ (although these values are approached in the limit as both $\theta_L \rightarrow 0$ and $\theta_W \rightarrow 1$). Thus, if the cost per round of fighting is sufficiently high, then it does not pay even the strongest first-round losers to emit the chemical, even when it has no toxicity to the releaser.

4 Results for Model A

With differential costs, the ESS $v^* = (v_1^*, v_2^*)$ depends in general on seven parameters, namely, α (value of resource to prior intruder, scaled with respect to prior owner's value), γ (maximum cost per round of fighting), k (insensitivity of cost to RHP), r (reliability of RHP difference as a predictor of fight outcome), μ (owner advantage), θ_l (toxicity to the first-round loser) and θ_w (toxicity to the first-round winner); whereas, with constant costs, the ESS depends only on six parameters, being independent of k . Because α and γ are scaled with respect to the fitness value of the resource to a prior owner, all seven parameters are dimensionless (and are listed in Table 1 for ease of reference).

We now discuss how the ESS depends on these parameters. For greatest clarity, we describe this dependence by dealing in turn with various special cases. From these results the general picture can then be extrapolated, and we describe it in §7. It has been confirmed by extensive computations, not all of which are presented in this paper.

4.1 Differential costs in the absence of toxicity

In this section we use differential costs to describe the dependence of the ESS on α , γ , k , r and μ in the absence of toxicity; accordingly, we set $\theta_l = 0 = \theta_w$. (We explore the effect of toxicity in §4.2 below.)

4.1.1 Neither owner advantage nor value asymmetry: $\mu = 0$, $\alpha = 1$

Without owner advantage, the distinction between final and intermediate possession becomes irrelevant. So $p_o = p_i$ and, since $\alpha = 1$, $v_1^* = v_2^*$ at the ESS, which—absent toxicity—now depends only on r , k and γ . It will be convenient in this section to use v^* in place of v_1^* or v_2^* for their common value. Figures 4(a) and 5(a) illustrate by showing the ESS as a function of γ with $r = 1$ for three different values of k and with $k = 1$ for three different values of r (so that the bottom curve in Figure 4(a) and the second-to-bottom curve in Figure 5(a) are identical). The corresponding probabilities p_{LW} and p_{VC} , defined by (39) and (40), are shown in Figures 4(b) and 5(b).

These figures illustrate several points. First, the critical maximum-cost threshold $\underline{\gamma}_c^o = \underline{\gamma}_c^i = \underline{\gamma}_c$, below which all first-round losers release the chemical, is independent of k , as illustrated by Figure 4(a); however, $\underline{\gamma}_c$ decreases with r , as illustrated by Figure 5(a). It decreases with r because the higher the reliability of RHP difference as a predictor of outcome, the likelier it is that a first-round winner would win again if there were a second round, and so the less it pays a first-round loser to release the chemical. Second, when $\gamma > \underline{\gamma}_c$, the ESS threshold for chemical emission, v^* , increases with k because the lower the sensitivity of fighting cost to RHP, the lower the cost reduction from being in good physical condition for a second round, and so the less it pays to precipitate one (Figure 4(a)); correspondingly, the probability p_{VC} that the volatile chemical is released by a first-round loser and the smaller probability p_{LW} that a releaser wins the overall contest both decrease with k (Figure 4(b)). Third, when $\gamma > \underline{\gamma}_c$, v^* increases with r for the same reason that $\underline{\gamma}_c$ decreases with r (Figure 5(a)); correspondingly, p_{VC} and p_{LW} both decrease with r (Figure 5(b)). Fourth, because $\theta_l = 0$, $v^* < 1$ for all $\gamma \leq 1$, and so it will always pay the strongest first-round losers to release the chemical.

4.1.2 Owner advantage without value asymmetry: $\mu > 0$, $\alpha = 1$

Here the critical maximum-cost threshold $\underline{\gamma}_c^o$, below which all prior owners release the chemical on losing the first round, increases with μ for contests with final possession ($L = o$), as illustrated by Figure 6(a), but decreases with μ for contests with intermediate possession ($L = i$), as illustrated by Figure 6(c); whereas the critical threshold $\underline{\gamma}_c^i$, below which all prior intruders release the chemical on losing the first round, decreases with μ for either kind of contest, as illustrated by Figure 6(b). Correspondingly, when $\gamma > \underline{\gamma}_c^o$, the RHP threshold v_1^* , above which losing owners release the chemical at the ESS, decreases with μ under final possession (Figure 6(a)) but increases with μ under intermediate possession (Figure

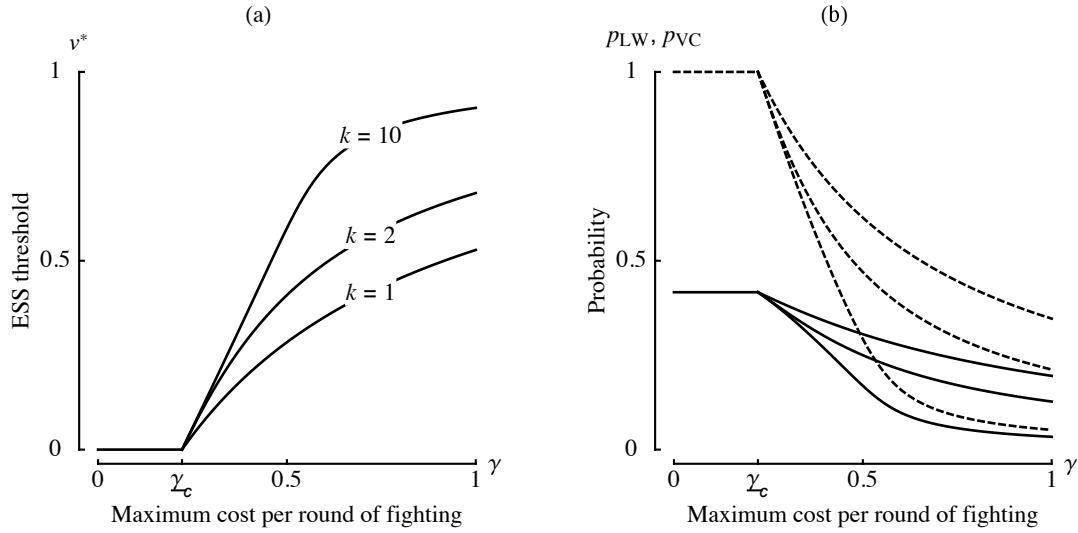


Fig. 4 (a) The evolutionarily stable RHP threshold, above which first-round losers release the chemical to force a second round, as a function of γ for $r = 1, \mu = 0, \alpha = 1, \theta_l = 0 = \theta_w$ and three different values of the parameter k , which measures insensitivity of fighting cost to RHP. (b) The corresponding probability p_{LW} that a first-round loser wins the contest (solid) and the larger probability p_{VC} that a first-round loser releases the volatile chemical (dashed) for $k = 1$ (top), $k = 2$ (middle) and $k = 10$ (bottom). The maximum-cost threshold below which all first-round losers emit the chemical, $\underline{\gamma}_c = \frac{2}{3}$, is independent of k .

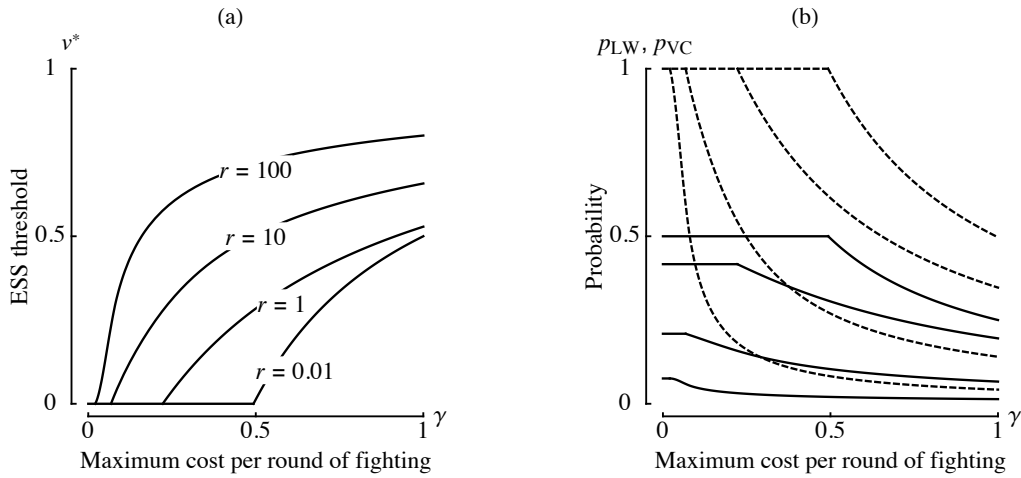


Fig. 5 (a) The evolutionarily stable RHP threshold, above which first-round losers release the chemical to force a second round, as a function of γ for $k = 1, \mu = 0, \alpha = 1, \theta_l = 0 = \theta_w$ and three different values of the parameter r , which measures reliability of RHP difference as a predictor of fight outcome. (b) The corresponding probability p_{LW} that a first-round loser wins the contest (solid) and the larger probability p_{VC} that a first-round loser releases the volatile chemical (dashed) for $r = 0.01$ (top), $r = 1$ (upper middle), $r = 10$ (lower middle) and $r = 100$ (bottom).

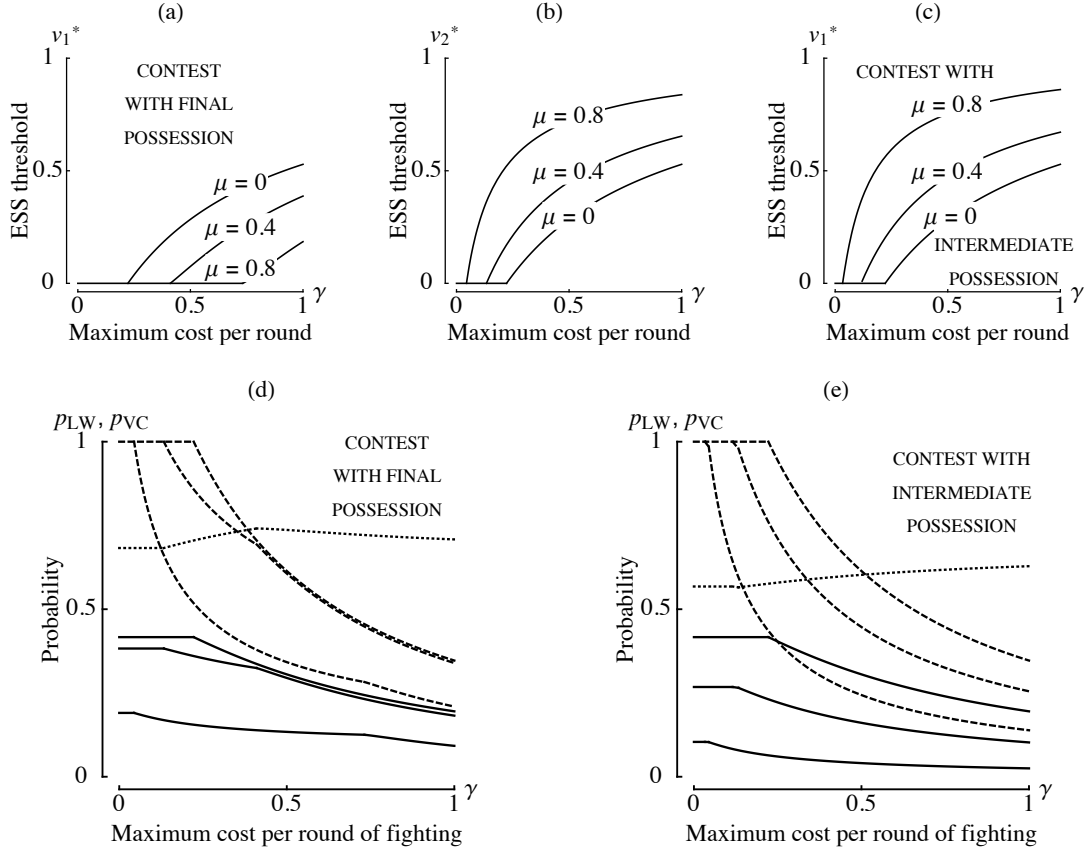


Fig. 6 The evolutionarily stable RHP threshold, above which first-round losers release the chemical to force a second round, as a function of γ for $k = \alpha = r = 1$, $\theta_l = 0 = \theta_w$ and three different values of the parameter μ , which measures owner advantage. (a) Owner's threshold in a contest with final possession. (b) Intruder's threshold in a contest with either final or intermediate possession. (c) Owner's threshold in a contest with intermediate possession. (d) The corresponding probability p_{LW} that a first-round loser wins the contest (solid) and probability p_{VC} that a first-round loser releases the volatile chemical (dashed) for $\mu = 0$ (top), $\mu = 0.4$ (middle) and $\mu = 0.8$ (bottom) in a contest with final possession. Also shown dotted is the probability P_0 that the prior owner wins the contest for $\mu = 0.4$. (e) Same as (d) for a contest with intermediate possession.

6(c)); whereas, when $\gamma > \gamma_c^i$, the RHP threshold v_2^* , above which losing intruders release the chemical at the ESS, increases with μ for either type of contest (Figure 6(b)). The probability p_{VC} that the volatile chemical is released by a first-round loser and the probability p_{LW} that a releaser wins the overall contest are illustrated by (d) and (e) of Figure 6. Also shown for $\mu = 0.4$ is the probability P_0 that the prior owner wins the contest, illustrating that P_0 is always lower with intermediate than with final possession.

These results reflect that a losing owner's probability of winning a second round increases with owner advantage μ only in contests with final possession; whereas in contests with intermediate possession, the same probability decreases with μ , as it does for a losing intruder. Under final possession, a prior owner wins the contest after releasing the chemical by losing and then winning with owner advantage, whereas a prior intruder wins the contest after releasing the chemical by losing and then winning against owner

advantage. By contrast, under intermediate possession, a prior owner wins the contest after releasing the chemical by losing with owner advantage and then winning against it, whereas a prior intruder still wins the contest after releasing the chemical by losing and then winning against owner advantage. As a consequence, with final possession, v_2^* always exceeds v_1^* , and the difference between these two thresholds increases with μ , as illustrated by comparing Figure 6(a) to Figure 6(b); whereas, with intermediate possession, v_1^* exceeds v_2^* but the difference is small at any μ , as illustrated by comparing Figure 6(c) to Figure 6(b). Moreover, p_{VC} and p_{LW} both decrease with μ , and are lower under intermediate than under final possession.

4.1.3 Value asymmetry without owner advantage: $\alpha \neq 1$, $\mu = 0$

Here at the ESS for sufficiently large γ , $v_1^* < v_2^*$ if $\alpha < 1$ but $v_1^* > v_2^*$ if $\alpha > 1$. That is, at the ESS, the RHP threshold, above which a first-round loser releases the chemical to force a second round, is lower for the contestant that values the resource more highly: it decreases with the value placed on the resource by the intruder. Figure 7(a) illustrates by showing the ESS as a function of γ for $r = k = 1$, $\mu = 0$ and $\theta_l = 0 = \theta_w$ for three different values of α . The corresponding probability p_{LW} that a first-round loser wins the contest (solid), probability p_{VC} that a first-round loser releases the volatile chemical (dashed) and probability P_0 that the prior owner wins the contest are shown in Figure 7(b). Collectively, Figure 7 shows that the greater the value placed on the resource by the intruder, the lower the RHP threshold above which it releases the chemical at the ESS, the likelier the chemical is released, the likelier the first-round loser wins the contest and the likelier the contest winner is the intruder. Thus intruder premium and owner advantage are countervailing asymmetries, as illustrated with $\alpha = 1.5$ by the lowest dotted curve in Figure 7(b), for which $P_0 < \frac{1}{2}$ (where P_0 is the probability of success for the prior owner).

4.2 Constant costs with toxicity

We use constant costs to describe how the ESS depends on the toxicities θ_l and θ_w to a first-round loser and winner, respectively, when there is neither an owner advantage nor a value asymmetry. Accordingly, we set $\mu = 0$ and $\alpha = 1$. As in §4.1.1, $v_1^* = v_2^*$ at the ESS, and it is convenient to use v^* in place of v_1^* or v_2^* for their common value. Correspondingly, it is convenient to set $\underline{\gamma}_c = \underline{\gamma}_c^o = \underline{\gamma}_c^i$ and $\bar{\gamma}_c = \bar{\gamma}_c^o = \bar{\gamma}_c^i$ for the common values of the two critical cost thresholds, below which all first-round losers (no matter how weak) release the chemical and above which no first-round loser (no matter how strong) releases the chemical, respectively.

In this particular case, expressions for the ESS can be found analytically and are given in Appendix A. At low cost—specifically, $\gamma < \underline{\gamma}_c^i$ —all first-round losers release the volatile chemical; at intermediate cost—specifically, $\underline{\gamma}_c^i < \gamma < \bar{\gamma}_c^i$ —sufficiently strong first-round losers release the chemical; and at high

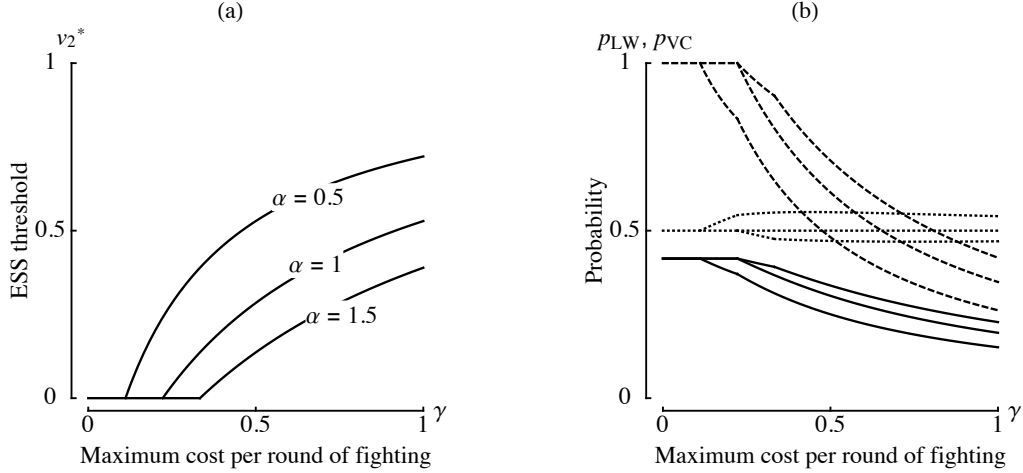


Fig. 7 The evolutionarily stable RHP threshold, above which first-round losers release the chemical to force a second round, as a function of γ for $\mu = 0$, $k = r = 1$, $\theta_l = 0 = \theta_w$, and three different values of the parameter α , which is the intruder-to-owner resource-value ratio. (a) Intruder's ESS threshold. The owner's threshold is not shown because it is independent of α , and always equal to the intruder's threshold for $\alpha = 1$. (b) The corresponding probability p_{LW} that a first-round loser wins the contest (solid) and probability p_{VC} that a first-round loser releases the volatile chemical (dashed) for $\alpha = 0.5$ (lowermost), $\alpha = 1$ and $\alpha = 1.5$ (uppermost) together with the probability p_o (dotted) that the prior owner wins the contest for $\alpha = 0.5$ (uppermost), $\alpha = 1$ and $\alpha = 1.5$ (lowermost). Here $\underline{\gamma}_c^0 = \frac{2}{9}$ is fixed, whereas $\underline{\gamma}_c^i$ increases with α . Note that the $\alpha = 1$ curve in (a) is identical to the curves labelled $k = 1$ and $r = 1$ in Figures 4(a) and 5(a), respectively.

cost—specifically, $\gamma > \bar{\gamma}_c^i$ —all animals accept that the first round determines the contest. The effects of varying θ_w and θ_l ($\leq \theta_w$) are illustrated by the upper and lower panels of Figure 8, respectively. Increased toxicity to the winner increases both the critical cost below which even the weakest first-round losers release the chemical and the critical cost above which even the strongest first-round losers refrain from releasing the chemical; and between these critical costs, it reduces the RHP threshold for releasing the chemical at any given cost (Figures 8(a) and (b)). Increased toxicity to the loser does not affect the critical cost below which even the weakest first-round losers release the chemical, but it reduces the critical cost above which even the strongest first-round losers refrain from releasing it; and between these critical costs, it increases the RHP threshold for releasing the chemical at any given cost (Figures 8(c) and (d)).

5 Model B: Rearguard action as a means of escape

Here we explore the second interpretation discussed in §1, namely, that the weapon of rearguard action is primarily a means of escape. In §2 we implicitly assumed that a first-round loser can withdraw without cost if it accepts the result of the first round as decisive, which it fails to do if sufficiently strong. Here we assume instead that all animals accept the first-round result as decisive, but a loser may sustain an additional cost in the process of withdrawing. We also assume that the weaker the loser, the more likely it is to sustain a withdrawal cost, and that the withdrawal cost increases with the strength of the winner.

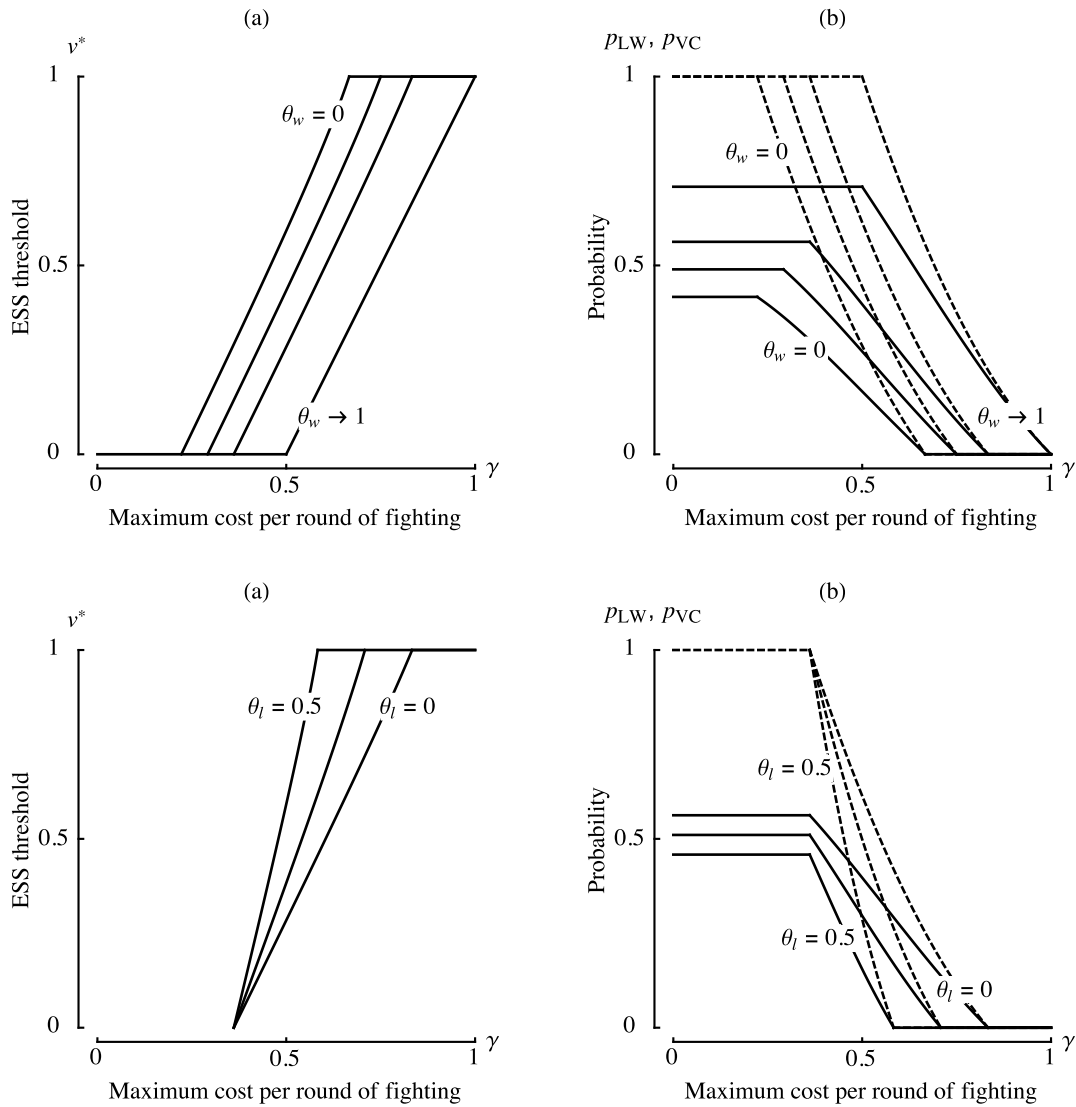


Fig. 8 The effect of toxicity on the ESS under constant costs. The evolutionarily stable RHP threshold v^* , above which first-round losers release the chemical to force a second round, is shown as a function of γ with $r = 1$, $\mu = 0$, $\alpha = 1$ for (a) $\theta_l = 0$ and (from left to right) $\theta_w = 0$, $\theta_w = 0.25$, $\theta_w = 0.5$, $\theta_w \rightarrow 1$ and for (c) $\theta_w = 0.5$ and (from left to right) $\theta_l = 0.5$, $\theta_l = 0.25$, $\theta_l = 0$. The corresponding probability p_{LW} that a first-round loser wins the contest (solid) and probability p_{VC} that a first-round loser releases the volatile chemical (dashed) are shown in (b) and (d), respectively. The cost threshold below which all first-round losers emit the chemical is independent of θ_l but increases with θ_w , according to (A.3). The cost threshold above which no first-round loser emits the chemical decreases with θ_l and increases with θ_w , again according to (A.3). Analytical expressions for v^* , p_{LW} and p_{VC} are given by (A.4) and (A.6).

Under this alternative scenario, a first-round loser accepts that the contest cannot be won: emission of the volatile chemical merely guarantees escape without further cost. If the cost of releasing the chemical were negligible compared to any withdrawal cost, then a loser would always release the chemical, which is contrary to empirical evidence (Goubault et al. 2006, 2008). We therefore introduce a cost of discharge and assume for simplicity that it is constant; after scaling as usual with respect to value V , we denote it

by δ . Consistently with §2, we may continue to assume that this discharge cost is negligible compared to the cost-per round of fighting, which in Model B has no strategic effect, because both contestants invariably bear the cost of fighting a single round—unlike in Model A, where the contest may be forced to a second round.

Let S_L and S_W denote the RHPs of loser and winner, respectively. For simplicity, we assume that the probability of sustaining a withdrawal cost decreases linearly with loser RHP according to $1 - S_L$; thus the weakest possible loser ($S_L = 0$) is guaranteed to sustain a withdrawal cost if it refrains from chemical emission, and the strongest possible loser ($S_L = 1$) is guaranteed to avoid a withdrawal cost. Again for simplicity, we assume that the withdrawal cost (scaled as usual with respect to value) increases with winner RHP according to $\eta(S_W)^\beta$. Thus the expected cost of withdrawal without emission—the withdrawal cost times the probability of sustaining it—is

$$\omega(S_L, S_W) = \eta(1 - S_L)(S_W)^\beta. \quad (44)$$

Here β measures the sensitivity of the withdrawal cost with respect to winner RHP. In economic jargon, β is the elasticity, that is, the ratio of the proportional increase in cost to the corresponding proportional increase in winner RHP. For our purposes, however, its effect is most readily apparent from a glance at Figure 9(a): the proportion of winners capable of inflicting a significant withdrawal cost is low or high according to whether β is high or low. For ease of reference, parameters new to Model B are listed in Table 2 (together with Model A parameters that remain relevant).

Table 2 Model B parameters

Parameter	Meaning	Bounds
δ	Cost of discharge, scaled with respect to V	$0 < \delta \leq 1$
η	Maximum withdrawal cost, scaled with respect to V	$0 < \eta \leq 1$
β	Sensitivity of withdrawal cost with respect to winner RHP	$0 < \beta < \infty$
r	Reliability of RHP difference as a predictor of fight outcome	$0 < r < \infty$
μ	Owner advantage, in the sense that an owner wins against an opponent of equal RHP with probability $\frac{1}{2}(1 + \mu)$	$0 \leq \mu \leq 1$

An animal's strategy still consists of a pair of RHP thresholds, one for the role of owner and one for that of intruder—specifically, $u = (u_1, u_2)$ for Player 1, and $v = (v_1, v_2)$ for Player 2—but because a loser's probability of escaping without cost increases with RHP, each threshold is now assumed to be an RHP *below* which the weapon is activated. That is, if Player 1 loses the first round when in role j , then it will emit the volatile chemical to guarantee escape without further cost if $X < u_j$ but attempt to escape without use of a volatile if $X \geq u_j$ (where $j = 1$ for an owner and $j = 2$ for an intruder); and likewise, if Player 2 loses the first round when in role j , then it will emit the volatile chemical if $Y < v_j$ but refrain from doing so if $Y \geq v_j$.

Several of the distinctions observed in §2 now disappear because there is no longer a second round of fighting, and the analysis must be modified accordingly. First, there is no longer a distinction between intermediate and final possession. Second, there is no longer a distinction between Regions I and III in Figure 1. In either case, the focal individual emits the chemical and pays the discharge cost upon withdrawing. Its payoff is therefore $V - Vc(X)$ with probability $p_o(X - Y)$ and $-Vc(X) - V\delta$ with probability $p_i(Y - X)$ if it is the owner or $\alpha V - Vc(X)$ with probability $p_i(X - Y)$ and $-Vc(X) - V\delta$ with probability $p_o(Y - X)$ if it is the intruder, so that (9), (11), (15) and (17) reduce to

$$f_I^o(X, Y) = f_{III}^o(X, Y) = p_o(X - Y) - \delta p_i(Y - X) - c(X) \quad (45)$$

$$f_I^i(X, Y) = f_{III}^i(X, Y) = \alpha p_i(X - Y) - \delta p_o(Y - X) - c(X). \quad (46)$$

Third, there is likewise no longer a distinction between Regions II and IV in Figure 1. In either case, the payoff to the focal individual is $V - Vc(X)$ with probability $p_o(X - Y)$ and $-Vc(X) - V\omega(X, Y)$ with probability $p_i(Y - X)$ for an owner and $\alpha V - Vc(X)$ with probability $p_i(X - Y)$ and $-Vc(X) - V\omega(X, Y)$ with probability $p_o(Y - X)$ for an intruder, so that (10), (12), (16) and (18) reduce to

$$f_{II}^o(X, Y) = f_{IV}^o(X, Y) = p_o(X - Y) - \omega(X, Y)p_i(Y - X) - c(X). \quad (47)$$

$$f_{II}^i(X, Y) = f_{IV}^i(X, Y) = \alpha p_i(X - Y) - \omega(X, Y)p_o(Y - X) - c(X). \quad (48)$$

Expressions (14), (19), (20), (21a) and (23a) all remain valid, reducing (21b) and (23b) to

$$\frac{\partial f}{\partial u_1} = \frac{1}{2} g(u_1) \int_0^1 \{ \omega(u_1, y) - \delta \} p_i(y - u_1) g(y) dy \quad (49)$$

and

$$\frac{\partial f}{\partial u_2} = \frac{1}{2} g(u_2) \int_0^1 \{ \omega(u_2, y) - \delta \} p_o(y - u_2) g(y) dy \quad (50)$$

respectively. Because $\omega(1, y) = 0$ by (44) and $\delta > 0$, it follows from (49) and (50) that $\frac{\partial f}{\partial u_j}$ is negative for $u_j = 1$ for both $j = 1$ and $j = 2$, and hence from (33) that we cannot have either $v_1 = 1$ or $v_2 = 1$ at the ESS. Thus the strongest losers should always refrain from releasing the chemical to guarantee their escape, regardless of whether they are owners or intruders.

From (25), (30), (32), (44) and (49), it now follows that $v_1 = 0$ at the ESS for $\delta > \delta_c^o$ and that $v_1 = v_1^*$ at the ESS for $\delta < \delta_c^o$, where

$$\delta_c^o = \frac{\int_0^1 \omega(0, y) p_i(y) dy}{\int_0^1 p_i(y) dy} = \frac{\eta \int_0^1 y^\beta p_i(y) dy}{\int_0^1 p_i(y) dy} \quad (51)$$

and $v_1 = v_1^*$ is the only root of the equation

$$\int_0^1 \{ \eta(1 - v_1) y^\beta - \delta \} p_i(y - v_1) dy = 0. \quad (52)$$

Note that δ_c^o decreases with β , with $\delta_c^o \rightarrow \eta$ as $\beta \rightarrow 0$ and $\delta_c^o \rightarrow 0$ as $\beta \rightarrow 1$ as illustrated by Figure 9. Likewise $v_2 = 0$ at the ESS for $\delta > \delta_c^i$ and $v_2 = v_2^*$ at the ESS for $\delta < \delta_c^i$, where

$$\delta_c^i = \frac{\int_0^1 \omega(0, y) p_o(y) dy}{\int_0^1 p_o(y) dy} = \frac{\eta \int_0^1 y^\beta p_o(y) dy}{\int_0^1 p_o(y) dy} \quad (53)$$

and $v_2 = v_2^*$ is the only root of the equation

$$\int_0^1 \{ \eta(1 - v_2)y^\beta - \delta \} p_o(y - v_2) dy = 0. \quad (54)$$

It is found that (31) always holds for either $j = 1$ or $j = 2$, for reasons analogous to those identified in the discussion immediately below (37). Note that the ESS for Model B depends on neither the cost of fighting nor the intruder premium. On the contrary, it merely reflects a balance between the relative costs of emission and withdrawal.

Under this alternative scenario, the contest cannot be won by a first-round loser: $p_{LW} = 0$ in place of (39). In place of (40), the probability that the volatile chemical is released, by either contestant, becomes

$$p_{VC} = \int_0^{v_1^*} \int_0^1 p_i(y - x) dy dx + \int_0^{v_2^*} \int_0^1 p_o(y - x) dy dx \quad (55)$$

and, in place of (41), the probability P_o that the prior owner wins the contest is simply the integral of $p_o(x - y)$ over the whole of the sample space in Figure 1.

6 Results for Model B

Given that ownership advantage yields no interesting effects in this case, we present results only for the symmetric case ($\mu = 0$), for which $p_o = p_i$ and hence $\delta_c^o = \delta_c^i = \delta_c$ with $v_1^* = v_2^* = v^*$ at the ESS, which now depends only on r , β and δ/η . Figure 9(b) illustrates by showing v^* (solid) (dashed) as a function of δ for $r = 1$ and various values of β . Figure 9(c) shows the corresponding probability p_{VC} that a loser releases the volatile chemical.

The lower the value of β , the greater the proportion of winners capable of inflicting a significant withdrawal cost (Figure 9(a)). Hence the critical discharge cost, above which no losers will release the chemical, decreases with β (Figure 9(b)): if β is so high that few winners are capable of inflicting a large withdrawal cost, then losers will release the chemical only if its discharge cost is very low (relative to maximum withdrawal cost). If, on the other hand, β is so low that most winners are capable of inflicting a large withdrawal cost (Figure 9(a)), then some losers will release the chemical even if its discharge cost is high (Figure 9(c)). Certainly, values of β and δ/η can always be found to match empirical observations of the frequency of release of the volatile chemical to Model B's prediction for the probability of release at the ESS. Nevertheless, because the contest can never be won by a first-round loser under this scenario, our results still appear to favor Model A.

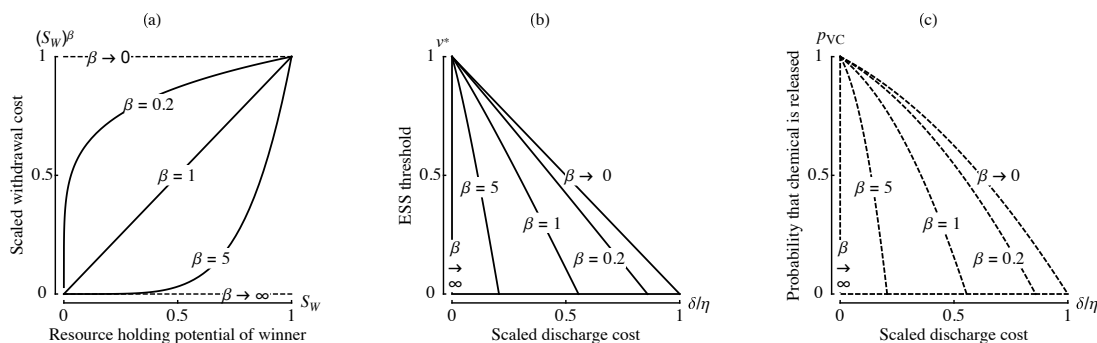


Fig. 9 (a) Withdrawal cost, scaled with respect to its maximum value, as a function of winner RHP for various values of β (elasticity of withdrawal cost with respect to winner RHP). (b) The evolutionarily stable RHP threshold, below which first-round losers release the chemical to guarantee escape without further cost, as a function of δ/η (discharge cost, scaled with respect to maximum withdrawal cost) for $\mu = 0$ (no owner advantage), $r = 1$ (moderate reliability of RHP as a predictor of contest outcome) and various values of β . Note that $v^* \rightarrow 1 - \delta/\eta$ as $\beta \rightarrow 0$ by (B.1)–(B.3). (c) The corresponding probability p_{VC} that a loser releases the volatile chemical. Note that $p_{VC} \rightarrow (1 - \delta/\eta)(2 + \delta/\eta)/2$ as $\beta \rightarrow 0$ by (B.4). For other values of r , the picture is very similar. Although v^* and p_{VC} increase with r , the dependence is weak, and in particular δ_c never differs much from $1/(1 + \beta)$, its value in the limit both as $r \rightarrow 0$ and as $r \rightarrow \infty$. Analytical expressions for v^* and p_{VC} are given by (B.3) and (B.4).

7 Discussion

We have used a pair of game-theoretic models to explore whether volatile chemical emissions can serve as a weapon of rearguard action, either as a means of temporary withdrawal or as a means of permanent retreat. These models allow a comparison between the alternative interpretations, and we discuss each in turn.

Our first model, Model A (§3), considers the possibility that chemical emission serves to facilitate a temporary withdrawal, so that a first-round loser retains a chance of ultimately prevailing in a second round of the same contest. Our results confirm that the underlying logic of this possible function is sound. Under differential costs (§3.1), that is, when fighting costs decrease with a contestant's physical condition or RHP, the chemical will be released by some, but not all, of the first-round losers; this proportion decreases as the (maximum) cost per round of fighting increases. Specifically, the chemical will be used by those whose RHP exceeds an evolutionarily stable threshold, and in particular will always be used by the strongest first-round losers, even when fighting is costly (Figures 4–7). Because a strong animal is most likely to lose to another strong animal, and because stronger animals are more likely to engage aggressively, this prediction tallies with the observation that chemical release was more common when contests were more aggressive. By contrast, under constant costs (§3.2), that is, when fighting costs are independent of RHP, the chemical will not be used by any first-round losers—even the strongest—if costs are sufficiently high (Figure 8). Here a caveat is in order: in principle, even under differential costs, first-round losers will likewise all refrain from releasing the chemical when costs are

sufficiently high if the chemical is very toxic to releasers, but in practice, self-toxicity is almost certainly very low, because the releaser withdraws from the vicinity of release.

When the maximum cost per round of fighting (γ , the cost paid by individuals in poorest condition) is sufficiently low, Model A predicts that all first-round losers will use the chemical. That losers of intermediate bouts in *Goniozus* contests use the chemical only at relatively low frequency suggests, however, that the maximum cost is never so low, but rather always exceeds the relevant critical value, namely, $\underline{\gamma}_c^o$ for owners and $\underline{\gamma}_c^i$ for intruders (§3.1), above which at least some first-round losers release the chemical. These critical values are necessarily equal in the absence of any owner advantage or value asymmetry, but otherwise either one may exceed the other, according to whether owner advantage (μ) or intruder premium (α) more significantly exceeds its symmetric value ($\mu = 0$ or $\alpha = 1$, respectively). Likewise, that losers of intermediate bouts in *Goniozus* contests do sometimes use the chemical suggests that maximum cost also lies below the relevant upper critical value, namely, $\bar{\gamma}_c^o$ for owners and $\bar{\gamma}_c^i$ for intruders (§3.1), beyond which it does not pay to release the chemical.

Assuming that both lower critical values are indeed exceeded ($\gamma > \underline{\gamma}_c^o, \gamma > \underline{\gamma}_c^i$), under differential costs the RHP threshold for using the chemical at the ESS increases with a parameter k measuring insensitivity of cost to RHP (Figure 4(a)). Correspondingly, the probability that a first-round loser will use the chemical (p_{VC}) and the probability that a first-round loser will win the contest (p_{LW}) both decrease with k (Figure 4(b)). Both probabilities also decrease with a parameter r measuring reliability of RHP difference as a predictor of fight outcome (Figure 5(b)), although the dependence on r of the ESS threshold is more nuanced: it increases with r only if γ is not too large (Figure 5(a)). The same two probabilities decrease with owner advantage μ (Figure 6) but increase with intruder premium α (Figure 7). Correspondingly, the RHP threshold decreases with α at the ESS for an intruder, but is independent of α for an owner (Figure 7); whereas the RHP threshold decreases with μ at the ESS for an owner under final possession, but increases with μ for an owner under intermediate possession (Figure 6). Thus intruder premium and owner advantage are countervailing asymmetries, as illustrated by Figure 7(b). These patterns persist under constant costs (except that k is no longer relevant, because fighting cost does not vary with RHP).

Continuing to assume $\gamma > \underline{\gamma}_c^o, \gamma > \underline{\gamma}_c^i$ but also $\gamma < \bar{\gamma}_c^o, \gamma < \bar{\gamma}_c^i$, under constant costs the RHP threshold for using the chemical at the ESS increases with toxicity θ_l to the releaser (Figure 8(c)), but decreases with toxicity θ_w to its opponent (Figure 8(a)). Correspondingly, the probability that a first-round loser will use the chemical (p_{VC}) and the probability that a first-round loser will win the contest (p_{LW}) decrease with θ_l (Figure 4(d)) and increase with θ_w (Figure 4(b)), respectively. This pattern persists under differential costs (except that, as noted already above, θ_l is likely so low that $\bar{\gamma}_c^o, \bar{\gamma}_c^i$ both exceed 1, and are therefore no longer relevant).

Our second model, Model B (§5), considers the alternative possibility that chemical emission serves to facilitate permanent withdrawal, preventing a winner from inflicting costs on a fleeing loser. Under this alternative scenario, a first-round loser accepts that the contest cannot be won: emission of the volatile chemical merely guarantees escape without further cost. Because both contestants invariably bear the cost of fighting a single round, the cost-per round of fighting now has no strategic effect. Thus, although the cost of discharging the chemical could be ignored in Model A as being negligible compared to the cost per round of fighting, in Model B it must be included. Indeed the model reflects a balance between the relative costs of emission and withdrawal. If the chemical is released, a discharge cost is paid but there is no withdrawal cost; if the chemical is not released, a discharge cost is avoided, but the expected cost of withdrawal without emission decreases with the RHP of the loser and increases with that of the winner. At the ESS, there is a critical discharge cost, above which no losers release the chemical; below this critical threshold, which decreases with the sensitivity β of the withdrawal cost to the winner's RHP, the chemical is released by the weakest losers, and for any given discharge cost, the proportion of releasers likewise decreases with β .

There exist some intriguing points of contact with results obtained by Goubault et al. (2006). Most importantly, there appear to exist parameter values that can produce values of p_{VC} and p_{LW} close to their observed values, namely, $\frac{40}{189} \approx 0.21164$ and $\frac{3}{47} \approx 0.0638298$, respectively. For example, with $k = \alpha = 1$, $\mu = 0$ and $r = 25$ in Model A (so that $\underline{\gamma}_c^o = \underline{\gamma}_c^i \approx 0.0419512$), we obtain $p_{VC} \approx 0.212635$ and $p_{LW} \approx 0.0633558$ when $\gamma = 0.39$; and it is clear from Figure 9(b) that numerous pairs of values for β and δ/η yield $p_{VC} \approx 0.21$ for Model B. However, no pair of values for β and δ/η in Model B will ever yield $p_{LW} \approx \frac{3}{47}$: the first-round loser can never win the contest if the purpose of the chemical emission is to withdraw from it entirely. This qualitative difference between the models suggest to us that volatile chemical emissions as weapons of rearguard action are more likely to function as a means of temporary withdrawal than as a means of permanent retreat.

Our modelling was explicitly motivated to explore possible functions of the emission of a volatile chemical during agonistic contests between parasitoid wasps. As the chemical in question is known to have insecticidal properties (Francke and Kitching 2001), we included consideration of self-damage. As such, our model is the first to adopt the recent suggestion of Lane and Briffa (2017) that self-inflicted damage costs should be incorporated into contest models. We find that, even though our main conclusion continues to hold in the absence of such costs, incorporating them refines our model's predictions; specifically, the probability that the chemical will be released and the probability that a first-round loser will subsequently win the contest both decrease with toxicity to the releaser (and increase with toxicity to its opponent, Figure 8). Thus a more general conclusion from this study is that in the field of animal contests, self-inflicted damage is a useful additional consideration.

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Appendix A: Some analytical results for Model A

In two special cases we have found purely analytical expressions for the ESS. Both obtain when $\mu = 0$ (no owner advantage, hence no distinction between intermediate and final possession), $r = 1$ (moderate reliability of RHP) and $\alpha = 1$ (no intruder premium). Because of the symmetry implied by $\mu = 0$ with $\alpha = 1$, we use (u, v) in place of both (u_1, v_2) and (u_2, v_1) in (20).

In the first of the two special cases, costs are constant, so that (26) reduces (20) to

$$f(u, v) = \frac{1}{12}\{1 - \theta_l\}u^3 - \frac{1}{16}\{2(1 + 2\gamma) - 3\theta_l - \theta_w\}u^2 - \frac{1}{24}\{2(2 - 9\gamma) + 5\theta_w\}u + \frac{1}{48}\{24(1 - 4\gamma) + 2(2\{2 + 9\gamma\} + 5\theta_w)v + 3(2\{1 - 2\gamma\} - 3\theta_l - \theta_w)v^2 - 4(1 - \theta_l)v^3\} \quad (\text{A.1})$$

with $\gamma \leq 1$ and $\theta_l \leq \theta_w < 1$, so that

$$\frac{\partial f}{\partial u} = \frac{1}{4}\{1 - \theta_l\}u^2 - \frac{1}{8}\{2(1 + 2\gamma) - 3\theta_l - \theta_w\}u - \frac{1}{24}\{2(2 - 9\gamma) + 5\theta_w\}. \quad (\text{A.2})$$

Let us define $\underline{\gamma}$ and $\bar{\gamma}_c$ by

$$\underline{\gamma} = \frac{2}{9} + \frac{5}{18}\theta_w, \quad \bar{\gamma}_c = \frac{2}{3} - \frac{1}{2}\theta_l + \frac{1}{3}\theta_w. \quad (\text{A.3})$$

Then it is readily shown that (A.2) is negative on $[0, 1]$ for $\gamma < \underline{\gamma}$ and positive on $[0, 1]$ for $\gamma > \bar{\gamma}_c$; whereas, for $\underline{\gamma} < \gamma < \bar{\gamma}_c$, (A.2) is positive at $u = 0$, negative at $u = 1$ and approaches ∞ as $u \rightarrow \infty$. The partial derivative therefore changes sign from positive to negative precisely once on $(\underline{\gamma}, \bar{\gamma}_c)$, implying that f has a unique maximum on $[0, 1]$ at $u = v^*(\gamma)$, where

$$v^*(\gamma) = \begin{cases} 0 & \text{if } 0 < \gamma \leq \underline{\gamma} \\ \phi(\gamma) & \text{if } \underline{\gamma} < \gamma \leq \bar{\gamma}_c \\ 1 & \text{if } \bar{\gamma}_c < \gamma \leq 1 \end{cases} \quad (\text{A.4})$$

with

$$\phi(\gamma) = \frac{12(\gamma - \underline{\gamma})}{4\gamma - 3\theta_l - \theta_w + 2 + \sqrt{(4\gamma - 3\theta_l - \theta_w + 2)^2 + 48(1 - \theta_l)(\underline{\gamma} - \gamma)}}. \quad (\text{A.5})$$

Because $v^*(\gamma)$ is the best reply to any v , it must also be the best reply to itself. So $v^*(\gamma)$ is the ESS, and it is plotted in Figures 8(a) and 8(c) for specific values of θ_l and θ_w . We note in passing that the above results agree with the more general analysis in §3: by (26) and (28) with $\mu = 0$ and $r = 1 = \alpha$, (34) and (42) reduce to (A.3), while (43) reduces $6(1 - \theta_l)v^2 - 3(4\gamma - 3\theta_l - \theta_w + 2)v - 4 - 5\theta_w + 18\gamma = 0$ (with

$v_1 = v_2 = v$), whose only solution between 0 and 1 is $v = \phi(\gamma)$. At this ESS, the overall probability that the contest is won by a first-round loser is

$$\begin{aligned}
 p_{LW} &= 2 \int_{v^*(\gamma)}^1 \int_0^1 p(y-x)p(x_l - y_w) dy dx \\
 &= \begin{cases} \frac{5}{12} + \frac{1}{24}(7\theta_w - 5\theta_l) & \text{if } 0 < \gamma \leq \underline{\gamma}_c \\ \frac{1}{24}\{1 - \phi(\gamma)\}\{(10 - 5\theta_l + 7\theta_w + (2 - 5\theta_l - 3\theta_w)\phi(\gamma) - 4(1 - \theta_l)\phi(\gamma)^2)\} & \text{if } \underline{\gamma}_c < \gamma \leq \bar{\gamma}_c \\ 0 & \text{if } \bar{\gamma}_c < \gamma \leq 1 \end{cases} \quad (\text{A.6a})
 \end{aligned}$$

and the probability that the volatile chemical is released is

$$\begin{aligned}
 p_{VC} &= 2 \int_{v^*(\gamma)}^1 \int_0^1 p(y-x) dy dx \\
 &= \begin{cases} 1 & \text{if } 0 < \gamma \leq \underline{\gamma}_c \\ \frac{1}{2}\{1 - \phi(\gamma)\}\{2 - \phi(\gamma)\} & \text{if } \underline{\gamma}_c < \gamma \leq \bar{\gamma}_c \\ 0 & \text{if } \bar{\gamma}_c < \gamma \leq 1 \end{cases} \quad (\text{A.6b})
 \end{aligned}$$

by (39) and (40), respectively, with $p_L = p_o = p_i = p$. Both probabilities are plotted in Figures 8(b) and 8(d) for specific values of θ_l and θ_w .

In the second of the two special cases, costs are differential but linear, that is, $k = 1$ in (27). In place of (A.1) we obtain

$$\begin{aligned}
 f(u, v) &= \frac{1}{12}\{1 - \theta_l\}(1 + 2\gamma)u^3 - \frac{1}{16}\{2 - 3\theta_l - \theta_w + 2(5 - 3\theta_l)\gamma\}u^2 - \frac{1}{24}\{2(2 - 9\gamma) + 5\theta_w\}u \\
 &\quad + \frac{1}{48}\{24(1 - 2\gamma) - 2(5\theta_l + 7\theta_w)\gamma + 2(4 + 5\theta_w)(1 + 2\gamma)v \\
 &\quad + 3(2 - 3\theta_l - \theta_w - 2\{1 + \theta_w\}\gamma)v^2 - 4(1 - \theta_l)v^3\} \quad (\text{A.7})
 \end{aligned}$$

(again with $\gamma \leq 1$ and $\theta_l \leq \theta_w < 1$), so that

$$\frac{\partial f}{\partial u} = \frac{1}{4}\{1 - \theta_l\}(1 + 2\gamma)u^2 - \frac{1}{8}\{2 - 3\theta_l - \theta_w + 2(5 - 3\theta_l)\gamma\}u - \frac{1}{24}\{2(2 - 9\gamma) + 5\theta_w\} \quad (\text{A.8})$$

in place of (A.2). We retain the definition of $\underline{\gamma}_c$ in (A.3), but redefine $\bar{\gamma}_c$ as

$$\bar{\gamma}_c = \frac{2(2 + \theta_w) - 3\theta_l}{6\theta_l}. \quad (\text{A.9})$$

Then, proceeding as above, we find that the ESS is still given by (A.4) and that (A.6) still holds, but with

$$\phi(\gamma) = \frac{12(\gamma - \underline{\gamma}_c)}{2(5 - 3\theta_l)\gamma - 3\theta_l - \theta_w + 2 + \sqrt{\{2(5 - 3\theta_l)\gamma - 3\theta_l - \theta_w + 2\}^2 + 48(1 - \theta_l)(1 + 2\gamma)(\underline{\gamma}_c - \gamma)}}. \quad (\text{A.10})$$

in place of (A.5). Moreover,

$$\frac{\partial^2 f}{\partial u^2} \Big|_{u=v=\phi(\gamma)} = -\frac{1}{8} \sqrt{\{2(5-3\theta_l)\gamma - 3\theta_l - \theta_w + 2\}^2 + 48(1-\theta_l)(1+2\gamma)(\underline{\gamma} - \gamma)} \quad (\text{A.11})$$

confirms that (31) holds. Note, however, that $\bar{\gamma}_c < 1$ will be satisfied only if θ_l exceeds $\frac{2}{9}(1 + \theta_w)$ and hence in particular exceeds $\frac{4}{9}$, an improbably large value. Thus we expect that the chemical will invariably be released by the strongest losers. In the case where there is no toxicity ($\theta_l = 0 = \theta_w$), the ESS is plotted in Figure 4(a) as the lowest curve, and the corresponding probability p_{LW} that the contest is won by a first-round loser and probability p_{VC} that the chemical is released are plotted in Figure 4(b) as the uppermost solid and dashed curves, respectively. This diagram illustrates that when costs are differential (as opposed to constant) and there is no toxicity, the probability that a first-round loser wins the contest never falls to zero, because the RHP threshold for release of the volatile chemical is exceeded by the RHPs of the strongest first-round losers.

Appendix B: Some analytical results for Model B

When $r = 1$ and $\mu = 0$ as in Figure 9, so that $p_o = p_i = p$ and $v_1 = v_2 = v$, (51) and (53) reduce to $\delta_c^o = \delta_c^i = \delta_c$ where

$$\delta_c = \frac{2}{3} \left(\frac{1}{1+\beta} + \frac{1}{2+\beta} \right) \eta, \quad (\text{B.1})$$

while (52) and (54) reduce to $2\eta(1-v)\{(2+\beta)(1-v) + 1 + \beta\} = \delta(1+\beta)(2+\beta)(3-2v)$ or $2(1-v)\{(2+\beta)(1-v) + 1 + \beta\} = \hat{\delta}(1+\beta)(2+\beta)(3-2v)$ where $\hat{\delta} = \delta/\eta$, with solution $v = \psi(\hat{\delta})$ where

$$\psi(\hat{\delta}) = \frac{3(1+\beta)(2+\beta)(\hat{\delta}_c - \hat{\delta})}{5 + 3\beta - (1+\beta)(2+\beta)\hat{\delta} + \sqrt{(1+\beta)\{(5+\beta)\beta^2\hat{\delta}^2 + (1+2\hat{\delta})^2 + \beta(1+2\hat{\delta} + 8\hat{\delta}^2)\}}}, \quad (\text{B.2})$$

so that the ESS becomes

$$v^*(\hat{\delta}) = \begin{cases} \psi(\hat{\delta}) & \text{if } 0 \leq \hat{\delta} \leq \hat{\delta}_c \\ 0 & \text{if } \hat{\delta}_c < \hat{\delta} \leq 1. \end{cases} \quad (\text{B.3})$$

It is plotted in Figure 9(a) for specific values of β . At this ESS, the probability that the volatile chemical is released is

$$\begin{aligned} p_{VC} &= 2 \int_0^{v^*(\hat{\delta})} \int_0^1 p(y-x) dy dx \\ &= \begin{cases} \frac{1}{2} \psi(\hat{\delta}) \{3 - \psi(\hat{\delta})\} & \text{if } 0 \leq \hat{\delta} \leq \hat{\delta}_c \\ 0 & \text{if } \hat{\delta}_c < \hat{\delta} \leq 1 \end{cases} \end{aligned} \quad (\text{B.4})$$

by (55), and is plotted in Figure 9(b) for specific values of β .

References

- Adams, E. S., Mesterton-Gibbons, M., 1995. The cost of threat displays and the stability of deceptive communication. *Journal of Theoretical Biology* 175, 405–421.
- Briffa, M., Hardy, I. C. W., 2013. Introduction to animal contests. In: Hardy, I. C. W., Briffa, M. (Eds.), *Animal Contests*. Cambridge University Press, Cambridge, pp. 1–4.
- Briffa, M., Hardy, I. C. W., Gammell, M. P., Jennings, D. J., Clarke, D. D., Goubault, M., 2013. Analysis of animal contest data. In: Hardy, I. C. W., Briffa, M. (Eds.), *Animal Contests*. Cambridge University Press, Cambridge, pp. 47–85.
- Broom, M., Rychtář, J., 2013. *Game-Theoretical Models in Biology*. CRC Press, Boca Raton, Florida.
- Francke, W., Kitching, W., 2001. Spiroacetals in insects. *Current Organic Chemistry* 5 (2), 233–251.
- Goubault, M., Batchelor, T. P., Linforth, R. S. T., Taylor, A. J., Hardy, I. C. W., 2006. Volatile emission by contest losers revealed by real-time chemical analysis. *Proceedings of the Royal Society of London B* 273, 2853–2859.
- Goubault, M., Batchelor, T. P., Romani, R., Linforth, R. S. T., Fritzsche, M., Francke, W., Hardy, I. C. W., 2008. Volatile chemical release by bethylid wasps: identity, phylogeny, anatomy and behaviour. *Biological Journal of the Linnean Society* 94, 837–852.
- Hammerstein, P., Riechert, S. E., 1988. Payoffs and strategies in territorial contests: ESS analyses of two ecotypes of the spider, *Agelenopsis aperta*. *Evolutionary Ecology* 2, 115–138.
- Hardy, I. C. W., Goubault, M., Batchelor, T. P., 2013. Hymenopteran contests and agonistic behaviour. In: Hardy, I. C. W., Briffa, M. (Eds.), *Animal Contests*. Cambridge University Press, Cambridge, pp. 147–177.
- Kokko, H., 2013. Dyadic contests: modelling fights between two individuals. In: Hardy, I. C. W., Briffa, M. (Eds.), *Animal Contests*. Cambridge University Press, Cambridge, pp. 5–32.
- Lane, S. M., Briffa, M., 2017. The price of attack: Rethinking damage costs in animal contests. *Animal Behaviour* 126, 23–29.
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Maynard Smith, J., Price, G., 1973. The logic of animal conflict. *Nature* 246, 15–18.
- Mesterton-Gibbons, M., Adams, E. S., 2003. Landmarks in territory partitioning: a strategically stable convention? *American Naturalist* 161, 685–697.
- Mesterton-Gibbons, M., Marden, J. H., Dugatkin, L. A., 1996. On wars of attrition without assessment. *Journal of Theoretical Biology* 181, 65–83.
- Mesterton-Gibbons, M., Sherratt, T. N., 2009. Neighbor intervention: a game-theoretic model. *Journal of Theoretical Biology* 256, 263–275.
- Mesterton-Gibbons, M., Sherratt, T. N., 2011. Information, variance and cooperation: minimal models. *Dynamic Games and Applications* 1, 419–439.
- Parker, G. A., 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology* 47, 223–243.
- Parker, G. A., 2013. Foreword. In: Hardy, I. C. W., Briffa, M. (Eds.), *Animal Contests*. Cambridge University Press, Cambridge, pp. xi–xx.
- Petersen, G., Hardy, I. C. W., 1996. The importance of being larger: parasitoid intruder-owner contests and their implications for clutch size. *Animal Behaviour* 51, 1363–1373.
- Sherratt, T. N., Mesterton-Gibbons, M., 2013. Models of group or multi-party contests. In: Hardy, I. C. W., Briffa, M. (Eds.), *Animal Contests*. Cambridge University Press, Cambridge, pp. 33–46.
- Stokkebo, S., Hardy, I. C. W., 2000. The importance of being gravid: egg load and contest outcome in a parasitoid wasp. *Animal Behaviour* 59, 1111–1118.