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Variation between Self- and Mutual Assessment in Animal Contests

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ABSTRACT: Limited resources lead animals into conflicts of interest, which are resolved when an individual withdraws from a direct contest. Current theory suggests that the decision to withdraw can be based on a threshold derived from an individual's own state (self-assessment) or on a comparison between their own state and their opponent's (mutual assessment). The observed variation between these assessment strategies in nature does not conform to theory. Thus, we require theoretical developments that explain the functional significance of different assessment strategies. We consider a hawk-dove game with two discrete classes that differ in fighting ability, in which the players strategically decide on their investment toward mutual assessment. Analysis of the model indicates that there are simultaneous trade-offs relating to assessment strategies. First, weak individuals in a population must decide on whether to acquire information about their opponents at the cost of providing opponents with information about themselves. Secondly, all individuals must decide between investing in mutual assessment and being persistent in contests. Our analysis suggests that the potential for individuals to make errors during contests and differences in the consequences of sharing information within a population may serve as fundamental concepts for explaining variation in assessment strategy.

Keywords: contest, self-assessment, mutual assessment, signaling, information, strategic error.

Introduction

Animals can have conflicts of interest over access to resources that can be decided by a contest (Maynard Smith 1974; Kokko 2013). Individuals engaged in a contest are faced with a trade-off between gaining the benefits of resource access and minimizing the cost of interactions with rivals, which is resolved by a strategic decision to withdraw from the interaction (Arnott and Elwood 2008, 2009). The decision to withdraw from a contest, rather than risk further costs by persistence, can be made more effective by

responding to information that can predict the outcome (Giraldeau 1997; Dall et al. 2005).

One potential source of information is the resource holding potential (RHP) of each individual: each contestant's ability to physically overcome its opponent or pay the costs of contesting resource ownership (Parker 1974; Parker and Rubenstein 1981). An individual's RHP is dependent on the particulars of resource competition for its species; common factors include size, mass, and resource stores, which provide the ability to inflict damage, suffer blows, and metabolize energy (Clutton-Brock and Albon 1979; Hsu et al. 2006; Arnott and Elwood 2009). RHP can also correlate with morphological structures or signals (e.g., Stuart-Fox et al. 2006), although the links between these traits and fighting ability is not always clear. In any case, factors that influence RHP are typically able to be measured or estimated by researchers and are thus potentially assessable by the species in question as well. In this regard, studies have supported a role for RHP in contests and suggest that animals can improve their decision making in contests by perceiving and responding to information on RHP asymmetries (Arnott and Elwood 2009). Theoretical models have been used to consider optimal responses to this information, yet they typically assume that individuals are either completely ignorant or in complete possession of information on RHP asymmetries (Crowley 2000). By contrast, little is known about how individuals may behave when they have only partial information on the RHP asymmetry, especially when they have the option to improve on this information via a costly investment.

There are at least two sources of information (sensu Wagner and Danchin 2010) on RHP: private information on an individual's own RHP and public information regarding the RHP of an opponent. Furthermore, there are at least two sources of public information on opponent RHP. Individuals may first have access to information on the distribution of RHP within the population (general

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information) and second to cues or signals that indicate the RHP of a given opponent (specific information). Provided that an individual has some private and public information, it can compare its own RHP to its opponent's RHP (based on either general or specific information) in order to assess whether there is an RHP asymmetry that can influence the outcome of the contest. That is, an individual can assess the likely payoffs involved with fighting by using general information to compare its own RHP to the expected frequencies of opponents with different RHP. Individuals can then improve on this estimate by gathering specific information from their current opponent and can benefit by basing their decision of whether to withdraw or persist in an encounter on this assessment (Parker and Rubenstein 1981).

Whether general or specific information is used in an RHP comparison can determine the process of RHP assessment in a contest and the withdrawal strategy that results from this assessment. Theory suggests that individuals can respond to general information by assessing their own RHP—a self-assessment strategy (Mesterton-Gibbons et al. 1996; Payne and Pagel 1996, 1997; Payne 1998). For instance, individuals may persist or withdraw from contests according to the probability of encountering an individual of lower or higher RHP, respectively. More specifically, models that consider the structure of contests suggest that animals can be involved in a war of attrition in which they persist until reaching a personal threshold that is determined by their own RHP and the distribution of RHP in the population (Mesterton-Gibbons et al. 1996). In contrast, access to specific information allows animals to directly compare their own RHP against the RHP of their current opponent and withdraw only if they are certain that they are outmatched. Contests based on this mechanism use a mutual assessment strategy (Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983; Enquist et al. 1990).

Although animals can benefit from responding to the RHP asymmetry, the information that reflects the asymmetry is inherently uncertain and not completely reliable. Thus, there is always the potential for an individual to make a strategic error in its decision of whether or not to withdraw (Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983). That is, individuals may persist when they would benefit more from withdrawing or withdraw when it would have been better to persist. These errors can result in unnecessary costs incurred through fruitless persistence and lost opportunities to access a resource, respectively. The potential for these errors to be made has a strong influence on adaptive withdrawal strategies (Crowley 2000). Theoretical and empirical evidence has suggested that it can be adaptive to reduce the risk of strategic error by gathering specific information

(Enquist and Leimar 1983), which led to the proposition that mutual assessment processes predominate in animal contests.

Recent work has brought the validity of empirical studies that detect mutual assessment into question (Bridge et al. 2000; Taylor et al. 2001; Taylor and Elwood 2003; Briffa and Elwood 2009). Such studies suggest that assessment strategy is variable between and within species (e.g., Hsu et al. 2008; Prenter et al. 2008; Kasumovic et al. 2010). Furthermore, the intensified scrutiny of recent studies has uncovered a variety of assessment modes that were not predicted by theory (Arnott and Elwood 2009), and there are multiple cases of inconclusive results concerning the assessment strategies being used within a population (Jennings et al. 2005; Morrell et al. 2005; Stuart-Fox 2006). Therefore, it is clear that a functional understanding of the basis of withdrawal decisions in contests is lacking.

It has been suggested that variation in assessment strategy occurs as the result of a trade-off between the costs of reliably gathering specific information and the benefits of shorter and less intense contests provided by acting on this information (Taylor and Elwood 2003; Prenter et al. 2006; Elias et al. 2008; Arnott and Elwood 2009). However, this hypothesis has not been empirically tested or formally examined. We thus developed a model in an effort to initiate a general theory for explaining variation in assessment strategy. As current models of contest behavior do not consider variation in assessment strategy, we used the argument for partial mutual assessment as the theoretical basis for our model (Prenter et al. 2006). This hypothesis suggests that individuals have reliable information on their own RHP but can gather some degree of information on a specific opponent's RHP. Although Prenter et al.'s (2006) verbal model of variable assessment strategy has yet to receive any formal validation, it does have some empirical support (Kelly 2006; Smallegange et al. 2007; Elias et al. 2008). The model presented in this article formalizes the concept of variable assessment to understand how the costs and benefits of gathering specific information determine the adaptive use of self- or mutual assessment strategies. Furthermore, by considering information that varies in its cost and ability to predict outcomes, it is able to account for the effect of uncertainty and the potential to make strategic errors during contests.

Model Description

A summary of the model is given in figure 1, and its parameters—which we introduce in this and the following section—are listed in table 1 for ease of reference. We consider a population of individuals in which access to a fitness-enhancing resource of value V is determined through direct interactions among pairs (players 1 and 2).

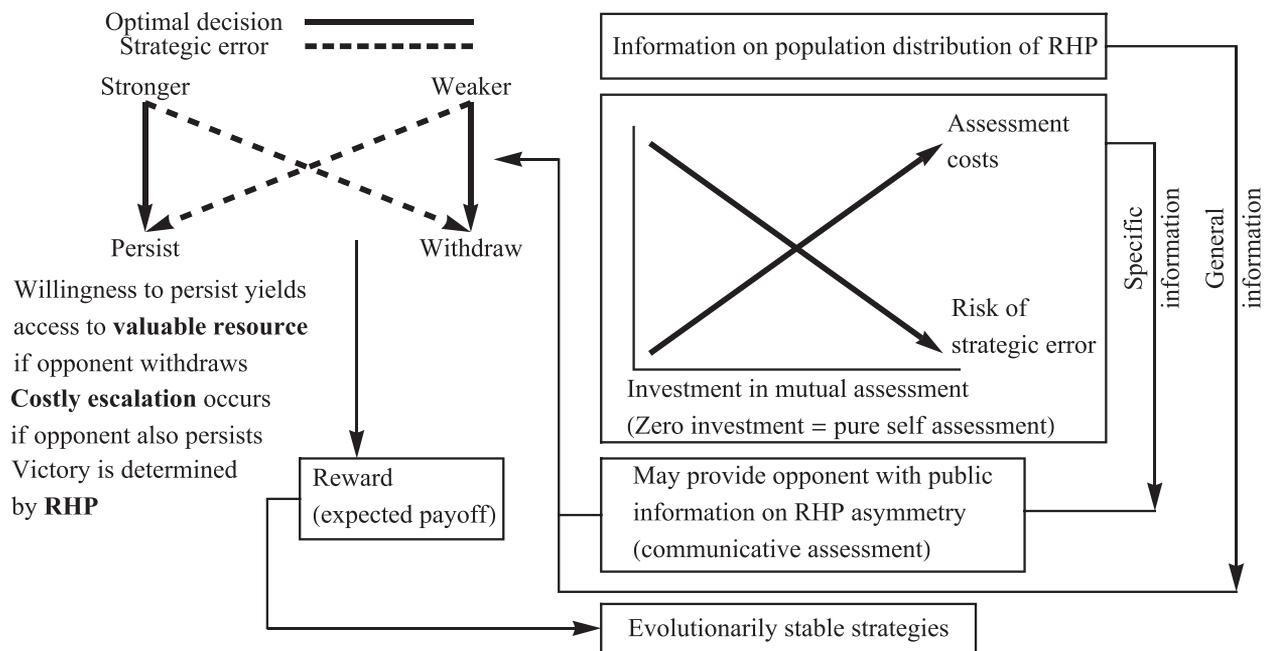


Figure 1: Pictorial representation of model's major components

This resource could represent anything that improves fitness, including food, mating opportunities, or an advantageous social position. We assume that the value of the resource is symmetrical in that each individual would receive equivalent benefits on winning a contest. Within these interactions, individuals use a withdrawal strategy that corresponds to a hawk-dove game (Maynard Smith and Parker 1976), in which they have the option to withdraw from the contest by playing dove or persist by playing hawk. The two individuals are assumed to make their decisions simultaneously, and the result of the interaction determines the fitness consequences for each individual. If both individuals play hawk, then the interaction escalates: both individuals suffer a fight cost C , and one individual gains access to the resource. Fight costs can include the time and energy devoted to the contest (Clutton-Brock and Albon 1979; Hack 1997a, 1997b; Briffa and Sneddon 2007), the buildup of metabolic wastes (Briffa and Sneddon 2007; Copeland et al. 2011), increased predation risk (Jakobsson et al. 1995), physical damage, or the risk of fatality (Enquist et al. 1990; Murray 1990; Haley 1994; Payne 1998; West et al. 2001). We assume that the winner of any fight is determined solely by RHP. For simplicity, we assume that individuals can either be weak, W , or strong, S , with strong individuals always winning against weak individuals and evenly matched opponents having an equal chance of winning. If only one individual plays hawk, then it will gain access to the resource without

a fight; and if both individuals play dove, then the resource is assumed to be shared or randomly allocated (i.e., payoff = $1/2 V$).

We assume that the proportions of individuals in the population having weak and strong RHP are λ and $1 - \lambda$, respectively, with at least some individuals of each type, that is,

$$0 < \lambda < 1. \tag{1}$$

Additionally, we assume that individuals have perfect knowledge of their own RHP, but not the RHP of their opponent.

From the perspective of a given individual, the world has four potential RHP combinations, which we have labeled $i = 1-4$, namely, WW (weak self, weak opponent; $i = 1$), WS (weak self, strong opponent; $i = 2$), SW (strong self, weak opponent; $i = 3$), and SS (strong self, strong opponent; $i = 4$). The probability of any one of these states occurring is simply a function of the distribution of RHP in the population; specifically, if p_i denotes the probability of state i , then

$$p_1 = \lambda^2, p_2 = \lambda(1 - \lambda) = p_3, p_4 = (1 - \lambda)^2. \tag{2}$$

The RHP combination that an individual actually perceives is determined by its strategic investment toward acquiring information about its current opponent (i.e., self- or mutual assessment). Because the information in equation (2) is a facet of the RHP distribution in the population, it

Table 1: Model parameters

Parameter	Meaning	Range	Key?
V	Value of fitness-enhancing resource	$V > 0$	
C	Cost of (winning or losing) a fight	$C > 0$	
λ	Proportion of individuals with weak (W) RHP in population	$0 < \lambda < 1$	Yes
r	Receptivity, i.e., the degree to which investment toward mutual assessment communicates information to the opponent as well as to the investor (with assessment being noncommunicative if $r = 0$)	$0 \leq r \leq 1$	Yes
α	Efficacy of assessment, i.e., the capacity for effort invested toward mutual assessment to correctly determine an opponent's RHP	$\alpha > 0$	
Γ	Cost per unit effort of assessment	$\Gamma > 0$	
$\beta = V/C$	Relative resource value, i.e., value of resource relative to cost of escalation	$\beta > 0$	Yes
Γ/α	Effective assessment cost, i.e., the assessment cost of the effort required to achieve a specific relative reduction in the probability of perception error, as described at the end of app. A, available online	$\Gamma/\alpha > 0$	
$\gamma = \Gamma/\alpha C$	Relative assessment cost, i.e., effective assessment cost Γ/α relative to cost of escalation C	$\gamma > 0$	Yes

Note: In the first instance, the model is defined in terms of the six parameters in the first six rows of the table. However, Γ and α appear only in the combination Γ/α , which reduces the number to five; and scaling fitness with respect to escalation cost C further reduces the number to four. These four dimensionless parameters are the only ones on which the ESS depends and in this sense are the key parameters, as indicated by the right-most column. RHP = resource holding potential.

is public, and so all individuals are assumed to be initially able to perceive their opponent as weak with probability λ and strong with probability $1 - \lambda$. Thus, individuals have both perfect private (own RHP) and general (distribution of RHP in the population) information, allowing them to assess the average RHP asymmetry that they will encounter. This information could have been gathered over generations, in the form of genes, or over an individual's lifetime as a result of learning from personal experience (Whitehouse 1997; Maynard Smith 2000; Dall et al. 2005; Hsu et al. 2006; Arnott and Elwood 2009; Wagner and Danchin 2010). By having only two discrete RHP classes, making RHP a perfect predictor of fight outcome and making the additional assumption that RHP is reliably communicated (i.e., with no possibility for bluff), we can keep the model as simple as possible. Furthermore, coupled with the assumption that private and general information is perfect, we can focus attention on the importance of strategic error as a result of incorrect assessment, including the influence of these errors on individuals with different RHP, with as few complicating factors as possible.

In addition to using purely general information, individuals have the option to improve their information on a specific opponent's RHP through mutual assessment. Individuals strategically decide on how much effort to invest in assessing their opponent; this effort is u_1 for player 1 and v_1 for player 2, where $u_1, v_1 \geq 0$. Furthermore, we

distinguish between communicative and noncommunicative assessment behaviors, as assessment is not necessarily passive or unilateral and can depend on the actions taken by each contestant (Hack 1997*b*). Under noncommunicative assessment, assessing an opponent provides an individual with information, but provides no information to its opponent (e.g., a visual assessment). In contrast, individuals either advertently or inadvertently provide their opponent with information on the RHP asymmetry if assessment is communicative (e.g., a tug of war or comparison of signal strength). We establish the degree of communicative assessment by assuming that a given investment toward mutual assessment is as effective at yielding information to the opponent as to the investor according to how receptive individuals are to each other's behavior. We represent receptivity by r , with assessment being noncommunicative when $r = 0$ and communicative when $r > 0$. Accordingly, let E denote the total effective effort directed at judging the other's RHP correctly. Then for player 1 we set

$$E = X = u_1 + rv_1, \quad (3)$$

while for player 2 we set

$$E = Y = ru_1 + v_1. \quad (4)$$

Let $\phi_w(E)$ be the probability that an animal perceives the other contestant correctly if the other animal is weak,

and let $\phi_s(E)$ be the probability that an animal perceives the other contestant correctly if the other animal is strong. Then, from above, it is reasonable to assume that

$$\phi_w(0) = \lambda, \phi_s(0) = 1 - \lambda, \tag{5}$$

and $\phi_w(\infty) = \phi_s(\infty) = 1$ (i.e., infinite effort is required for perfect perception). To model the nature of how assessment accuracy changes in response to increasing effort (independently of opponent RHP), we first consider the potential for being incorrect using mutual assessment (when $E > 0$) relative to the potential for being incorrect using self-assessment (when $E = 0$). Specifically, the probability of making an assessment error decreases with total effort (E) according to

$$\frac{1 - \phi_w(E)}{1 - \phi_w(0)} = \frac{1 - \phi_s(E)}{1 - \phi_s(0)} = e^{-\alpha E}. \tag{6}$$

Here, the probability of making an incorrect perception (given effort toward assessment) relative to the initial probability of being incorrect (i.e., pure self-assessment) is determined by an exponential rate parameter, α (fig. 2). The rate parameter α represents the efficacy of assessment (i.e., the capacity for effort invested toward mutual assessment to correctly determine the opponent’s RHP). This could reflect the sensory and cognitive abilities of the assessor, the reliability of signaling, or previous experience with the opponent. Thus, from equations (5) and (6), the respective probabilities of perceiving a weak or strong opponent correctly increase with total effective effort according to

$$\begin{aligned} \phi_w(E) &= 1 - \{1 - \phi_w(0)\}e^{-\alpha E} = 1 - (1 - \lambda)e^{-\alpha E}, \\ \phi_s(E) &= 1 - \{1 - \phi_s(0)\}e^{-\alpha E} = 1 - \lambda e^{-\alpha E}. \end{aligned} \tag{7}$$

These equations simply state that the probability of being correct ($\phi_w(E)$ or $\phi_s(E)$) can be calculated as the complementary probability of the probability of making an incorrect assessment using only self-assessment ($1 - \phi_w(0)$ or $1 - \phi_s(0)$), discounted by the effect of mutual assessment.

Additionally, mutual assessment is not free: it incurs a cost Γ per unit of effort u_1 or v_1 . Such assessment costs can arise from a number of sources, although few studies have explicitly considered them. For instance, individuals may need to produce signals that are costly in time or energy in order to receive honest information from their opponent (Dawkins and Guilford 1991), with the cost of signaling increasing as the information content of the signal increases (Enquist et al. 1990; Hack 1997b). Additionally, receiving information from an opponent may expose an individual to predation risk (Dawkins and Guilford 1991) or may involve being damaged by an opponent’s

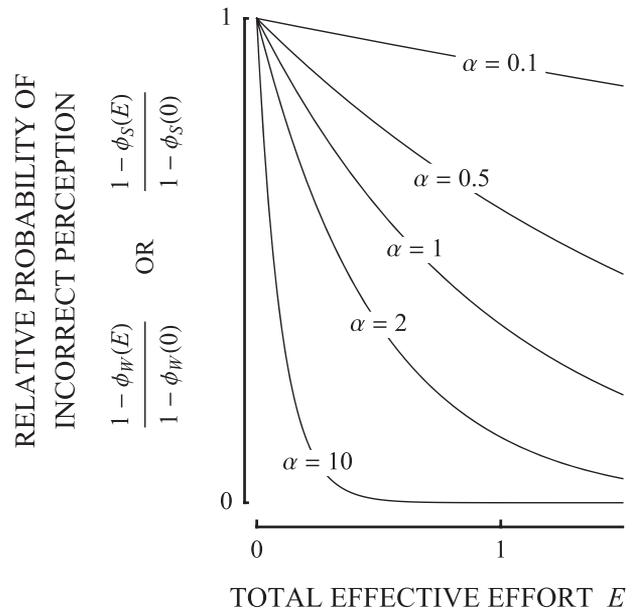


Figure 2: Probability of an incorrect perception relative to the initial probability of an incorrect perception as a function of total effort toward assessing an opponent’s resource holding potential (RHP), for various values of the efficacy α . This parameter measures the capacity for effort invested toward mutual assessment to correctly determine the opponent’s RHP, in the sense that a small investment greatly reduces the probability of error when α is high but has comparatively little effect when α is low.

attack (Enquist and Leimar 1983; Payne 1998). There may also be costs associated with the development of cognitive or perceptive abilities required for making assessments (Taylor and Elwood 2003; Prenter et al. 2006; Elias et al. 2008; Arnott and Elwood 2009; Elwood and Arnott 2012).

For each of the four possible actual states i in the model, there are four possible perceptual states, which we label $j = 1$ –4: CC (both animals perceive their opponent’s RHP correctly; $j = 1$), CI (only player 1 perceives correctly; $j = 2$), IC (only player 2 perceives correctly; $j = 3$), and II (neither animal perceives the other’s RHP correctly; $j = 4$).

Each contestant is assumed to respond to its perception of the RHP combination by playing hawk if it perceives SW and dove if it perceives WS. That is, weak individuals will always withdraw from an interaction if they perceive themselves to be outmatched, and strong individuals will always be willing to press their perceived advantage. However, individuals that perceive themselves to be matched with their opponent have a range of strategic withdrawal options available to them, because individuals may escalate with any probability between 0 (pure dove) and 1 (pure hawk). Individuals that perceive the RHP combination as WW play hawk with strategic probability u_2 for player 1 and v_2 for player 2, hence, dove with probability $1 - u_2$

Table 2: Evolutionarily stable strategies (ESSs) with self- or mutual assessment classified according to the strategic withdrawal components of the ESS

Case	v_2^*	v_3^*	Self-assessment type	Mutual-assessment type	Character
a	1	1	IA: strong (sect. B.1.1)	IIa: strong (sect. B.2.1)	Daring
b	•	1	IB: weak (sect. B.1.9)	IIb: weak (sect. B.2.9)	Daring
c	0	1	IC: strong (sect. B.1.3)	No such ESS (sect. B.2.3)	Conventional
d	0	•	ID: weak (sect. B.1.5)	IIc: weak (sect. B.2.5)	Careful
e	0	0	IE: strong (sect. B.1.2)	IId: strong (sect. B.2.2)	Careful
f	•	•	No such ESS (sect. B.1.6)	IIf: weak (sect. B.2.6)	Mixed
g	•	0	No such ESS (sect. B.1.8)	IIg: weak (sect. B.2.8)	Anomalous

Note: $v^* = (v_1^*, v_2^*, v_3^*)$ with $v_1^* = 0$ for self-assessment and $v_1^* > 0$ for mutual assessment; v_2^* and v_3^* are the probabilities of persisting when perceiving WW and SS, respectively; and a dot denotes a positive number less than 1. Also, “strong” or “weak” refers to type of evolutionarily stable strategy, as opposed to resource holding potential type: mutant strategies are always selected against at a strong ESS, whereas mutant strategies can spread initially before being selected against at a weak ESS. The sections named in the table are available online.

or $1 - v_2$. Those that perceive SS play hawk with strategic probability u_3 for player 1 and v_3 for player 2, hence, dove with probability $1 - u_3$ or $1 - v_3$. An individual that has an incorrect perception of the RHP combination makes a strategic error in terms of its withdrawal strategy: responding to a weak opponent as if it were strong, or to a strong opponent as if it were weak.

From all of the above, we can assign a behavioral strategy to each individual in the population. Specifically, the strategy consists of a three-dimensional vector comprising (i) how much to invest in acquiring specific information and how often to play hawk on perceiving a matched opponent when (ii) weak or (iii) strong. This strategy is formally represented by $u = (u_1, u_2, u_3)$ for player 1 and $v = (v_1, v_2, v_3)$ for player 2. The components of the strategy are constrained according to $u_i, v_i \geq 0$, and $0 \leq u_i, v_i \leq 1$ for $i = 2, 3$; in particular, all are nonnegative numbers. This simply means that investment toward mutual assessment can be zero (i.e., self-assessment) or limitlessly greater (although increasing investment comes at greater cost), and that the withdrawal strategy against a matched opponent can vary from always withdraw ($u_i = 0$ or $v_i = 0$ for $i \geq 2$) to always persist ($u_i, v_i = 1, i \geq 2$).

We explore the model by assigning player 1 a mutant strategy and having it interact with a population of individuals all using the same strategy and in the role of player 2. The resultant fitness to a mutant u -strategist in a population of v -strategists, denoted by $f(u, v)$, is now readily calculated as the expected value—over all possible combinations of actual and perceived RHP—of the payoff to strategy u minus the costs of assessment. Details of this computation are given in appendix A; appendixes A–D available online.

Evolutionarily Stable Strategy Analysis

Population strategy $v^* = (v_1^*, v_2^*, v_3^*)$ is an evolutionarily stable strategy (ESS) in the sense of Maynard Smith (1982)

if it does not pay a potential mutant to adopt an alternative strategy $u = (u_1, u_2, u_3)$. The asterisk is used to distinguish the ESS v^* from an arbitrary population strategy v (see app. B). The stable population strategy is a strong ESS if it is also uniquely the best reply to itself, so that no alternative strategy can invade. The ESS is weak if there is at least one alternative strategy that does equally well against the ESS but is outperformed by the ESS in any subpopulation that adopts the alternative strategy. Intuitively, in a population at a strong ESS, any mutant strategy is immediately selected against, whereas, at a weak ESS, a strategy that is an alternative best reply can gain an initial toehold but cannot spread before being selected against. For the sake of simplicity, we assume throughout that each component of strategy is independent of the other two, so that a potential mutant strategy u differs from an ESS v^* only in one component of the vector.

Detailed ESS calculations are presented in appendix B and can be summarized as follows. First, we distinguish an ESS as type I or type II according to whether it involves pure self-assessment ($v_1^* = 0$) or some form of mutual assessment ($v_1^* > 0$). Second, a strategy comprises not only assessment behavior but also the conditions of withdrawal in contests. While an individual’s withdrawal behavior is fixed if it perceives an RHP asymmetry, there is the potential for different withdrawal behaviors when no asymmetry is perceived. Because a contest can be perceived as matched in two different ways (WW or SS) and there are three kinds of behavior for each (pure hawk, pure dove, or mixed), either type of ESS could have up to $3 \times 3 = 9$ subtypes. However, only five of the possible type I subtypes and only six of the type II subtypes can arise (table 2, figs. 3, B5, app. B; figs. B1–B5 available online).

The different subtypes for the withdrawal component of strategy can be grouped to characterize one of five different types of population. First, there are “daring” populations in which strong individuals fight unconditionally

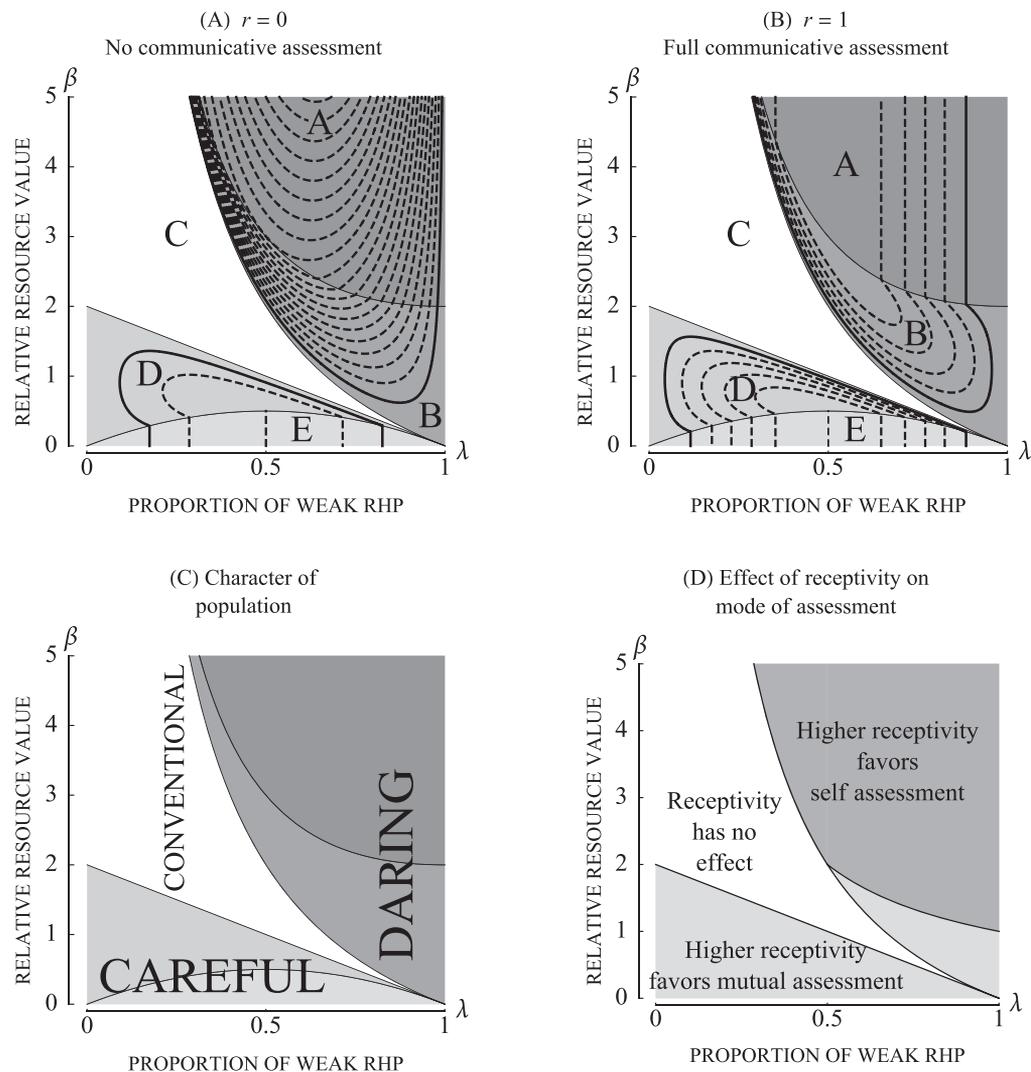


Figure 3: Five regions of the λ - β plane corresponding to five different types of pure self-assessment evolutionarily stable strategy, where λ denotes proportion of weak resource holding potential (RHP) and β denotes relative resource value (table 1). The regions are distinguished by their shading and are defined in table 2. Superimposed are contour maps of the surface of the critical relative cost threshold (γ_c) for $r = 0$ (A) and $r = 1$ (B), where r denotes receptivity. Increments of $1/48$ are used, with the first contour given as a solid line. C, Regions A and B correspond to a daring population, region C to a conventional one, and regions D and E to a careful one. D, How the effect of receptivity on mode of assessment varies with RHP proportion and relative resource value.

and weak individuals are willing to fight against opponents they assess as weak (table 2a, 2b). Second, there are “careful” populations in which weak individuals always withdraw from an interaction and strong individuals persist unconditionally only against perceived weak opponents (table 2d, 2e). Third, there are populations that have adopted a “convention” for deciding contests (table 2c). In these cases, strong individuals always persist, and weak individuals always withdraw. There can also be “mixed” populations, intermediate between careful and daring (table 2f). In such populations, neither strong nor weak in-

dividuals persist or withdraw unconditionally. Finally, there can be an “anomalous” population in which weak individuals may fight among each other but strong individuals persist only against weak individuals (table 2g). Such populations occur only when strong individuals are sufficiently rare and relative resource value is sufficiently low, allowing weak individuals to be more daring and strong individuals to be more careful. Note that in all cases, a weak individual will always withdraw if it assesses its opponent to be strong, and a strong individual will always be willing to persist if it assesses its opponent as weak.

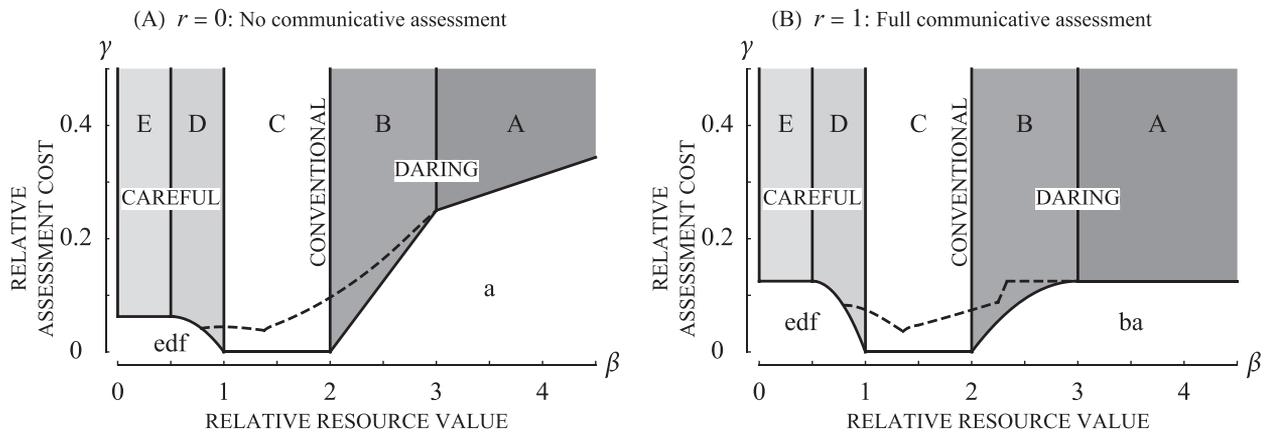


Figure 4: Effect of receptivity (r) on a self-assessment evolutionarily stable strategy (ESS) when variance in resource holding potential is maximal ($\lambda = 1/2$) for $r = 0$ (A) and $r = 1$ (B). Here, relative resource value (β ; table 1) increases horizontally, while relative assessment cost (γ ; table 1) increases vertically. There cannot exist a type I ESS in the unshaded regions below the solid boundary curve, that is, where γ is less than the critical threshold γ_c ; but there is always a type I ESS where γ exceeds γ_c , that is, in a shaded region or region C. A type II ESS can exist either below the solid curve or (above it and) below the dashed curve (corresponding to the shaded regions of fig. 5). The solid curve shows that the critical relative assessment cost, γ_c , varies with relative resource value β across different regions that represent different withdrawal strategies. Regions E and D characterize a careful population, in which only strong individuals are willing to persist. All individuals are willing to persist in regions A and B, which characterize a daring population. Region C typifies a conventional strategy in which strong individuals always persist and weak individuals always withdraw. Lowercase letters refer to corresponding withdrawal strategies that are part of the mutual assessment strategy (see fig. 5). For further details, see appendix C, available online.

To aid in analysis, we define two dimensionless parameters:

$$\beta = \frac{V}{C}, \quad \gamma = \frac{\Gamma}{\alpha C}. \quad (8)$$

The first parameter, β , which we call relative resource value, measures the value of the resource relative to the cost of escalation. The second parameter, γ , which we call relative assessment cost, measures the effective assessment cost, which is the cost of improving assessment accuracy (Γ/α ; see app. A), relative to the cost of escalation, C . Note that relative assessment costs may be small—and hence assessment cost-effective relative to escalation—either because information on opponents can be gained at low cost (low Γ) or because it has high efficacy rates (high α). Alternatively, relative assessment costs may improve the effectiveness of gathering information if fighting is sufficiently costly (high C). Smaller values of γ reflect more efficient information gain. Note that β and γ are also defined in table 1 for ease of reference.

Trade-Off between Mutual Assessment and Escalation

An individual that is behaving optimally can afford to bear only a certain amount of costs. It is in the allocation of these costs between mutual assessment and the capacity to escalate that determines whether self- or mutual assessment is the ESS for a given set of ecological conditions

defined by our parameters (table 1). Specifically, the assessment strategy used at the ESS is determined by the relative assessment cost γ . Mutual assessment is evolutionarily stable when the effective cost of mutual assessment is low relative to the cost of escalation, and self-assessment is evolutionarily stable when the effective cost of mutual assessment is relatively high. There is thus a critical threshold that the relative assessment cost (γ) must exceed for there to be self-assessment at the ESS; otherwise, there is mutual assessment at the ESS. This critical threshold is a function of the distribution of RHP in the population (λ), relative resource value (β), and the degree of receptivity for communicative assessment (r). We refer to the critical threshold as γ_c . For a given r , how γ_c varies with the RHP distribution (λ) and relative resource value (β) is most easily conceived as variation in the height of a surface: the lower the height, the more that self-assessment is favored. A contour map of this surface appears in figure 3A, 3B, and a cross section is in figures 4 and 5.

The shape of the surface for the critical threshold depends on the withdrawal strategy associated with the self-assessment ESS (app. B). As there are five possible withdrawal strategies that could be adopted for a self-assessment ESS, there are five regions of parameter space that define the relationship between the critical threshold, distribution of RHP, and relative resource value. These regions are independent of receptivity, r , and are presented visually in figure 3. Regions A and B reflect a daring population, while regions

avored in the daring region (A or B) than in the careful region (D or E). That is, mutual assessment must be more cost-effective (i.e., have lower effective cost Γ/α in relation to the costs of escalation C) to occur in the careful region than to occur in the daring region.

The contour maps in figure 3 and the boundary line in figure 4 also indicate that there is a complex relationship between γ_c and β . With reference to figure 4, it is apparent that the critical threshold can vary positively, negatively, or not at all as β increases. Furthermore, the slope of γ_c against β , if positive, is steeper when receptivity (r) is low than when receptivity is high. The implications of this relationship are that variation between self- and mutual assessment strategies in nature may depend on interactions between ecological conditions. For instance, a shift from mutual to self-assessment occurs with increasing resource value if fight costs are high (e.g., in the careful region), but if fight costs are low (e.g., in the daring region), then the same shift will occur with decreasing resource value. The case of the maximally varying population with respect to RHP ($\lambda = 1/2$) corresponds to figures 4 and 5 and is analyzed in detail in appendix C. The patterns regarding variation in the critical threshold are qualitatively identical across variation in λ . Appreciation of the patterns in figures 4 and 5 provides an understanding of how the assessment-strategy threshold can vary with relative resource value (β), which is a readily observable quantity in nature. Additionally, noting how the threshold varies with receptivity illustrates how information transfer affects adaptive strategies. Finally, a pictorial representation of the threshold aids in comprehending the trade-off between information and persistence (γ).

The Effect of Communication

The potential for mutual assessment to be communicative ($r > 0$) has contrasting effects on the critical relative assessment cost, γ_c (figs. 3–5). Specifically, there are regions in which increasing r increases the threshold γ_c , implying that individuals can sustain greater relative costs of mutual assessment when they are more receptive to opponent behavior. Additionally, there are regions in which increasing r decreases γ_c , implying that mutual assessment must be sufficiently cost-effective when individuals are receptive to one another for it to be adopted. These effects of communication can be appreciated by noticing how the critical relative cost threshold shifts as r increases from 0 to 1 in figures 3–5. In the careful region and the lowest portion of the daring region, the threshold (γ_c) increases as r increases, implying that higher receptivity favors mutual assessment (fig. 3D). By contrast, in most of the daring region, γ_c decreases as r increases. Thus, higher receptivity favors self-assessment in the daring region.

The effect of communicative assessment depends on RHP, owing to a difference in payoffs between strong and weak individuals when opponents make strategic errors. Specifically, strong individuals benefit when opponents make fewer strategic errors and weak individuals benefit when their opponents make more strategic errors (app. A, table A2; tables A1–A3 available online). The relative benefits of opponent error to weak individuals versus the costs to strong individuals then determine whether increasing receptivity r has a positive or a negative effect on the critical threshold γ_c . The benefits of opponent error to weak individuals are greater in the daring region, such that increasing r has a negative effect on γ_c (figs. 3–5). In such cases, weak individuals can benefit more from hiding information on their own RHP and investing toward mutual assessment only when it is very cost-effective in relation to the costs of escalation. On the other hand, the costs of opponent error to strong individuals are greater within the careful region, as contests are extremely costly; hence r has a positive effect on γ_c . This is equivalent to individuals sharing the costs of mutual assessment through communication, allowing them to invest in mutual assessment even when it is relatively costly in comparison to the cost of escalation.

Strategic Error Is Necessary for Assessment Strategy to Vary

Notably, the critical relative cost threshold is zero within the conventional region (region C; figs. 3, 4), implying that here a self-assessment ESS exists regardless of how cost-effective acquiring specific information is in relation to fight costs. At this ESS, weak individuals completely avoid fighting and strong individuals always fight. In those circumstances, as shown in appendix B, there cannot be a type II (mutual assessment) ESS: investment toward mutual assessment provides no benefits, because the optimal withdrawal strategy has no risk of strategic error. This risk is absent because the population has adopted a pure withdrawal strategy that depends on RHP, such that weak individuals always withdraw and strong individuals always persist. Thus, weak individuals will never escalate contests that cannot be won, and strong individuals will never withdraw when victory is guaranteed. Put simply, it is impossible for mutual assessment to exist as an ESS when using a withdrawal strategy that contains no element of strategic error. However, withdrawal strategies that incorporate strategic error allow for the existence of a mutual-assessment ESS. This can be clearly seen from the potential for both a self- and a mutual-assessment ESS in particular regions (see figs. 4, 5, app. D). In these cases, the mutual-assessment ESSs are those that involve withdrawal strategies associated

with greater strategic error (i.e., more aggression in weak individuals and less aggression in strong individuals).

Therefore, strategic error is necessary for there to be variation in assessment strategy. We further explore the relationship between withdrawal and assessment strategies in appendix D.

Discussion

There are two pertinent and simultaneous trade-offs relating to the assessment of opponents during contests. First, all individuals must decide between reducing the risks of strategic error by investing in mutual assessment, or increasing the capacity to persist in contests over resources. Second, weak individuals in a population must decide whether to acquire information about their opponents at the cost of revealing their own inferiority. Theoretically, the selection pressure underlying these trade-offs is the use of withdrawal strategies that, due to incomplete information, carry an inherent risk of responding inappropriately to an opponent but can otherwise increase access to limited resources.

Our model also demonstrates that a difference in payoffs between weak and strong individuals can significantly affect the benefits of mutual assessment. First, the group that benefits from gathering information can vary. When contests are costly in relation to the benefits of winning, weak individuals avoid fighting altogether, but strong individuals benefit from some aggression. Thus, mutual assessment is not beneficial to weak individuals, but it can allow strong individuals to avoid costly escalation against matched opponents. In contrast, when contests are relatively inexpensive, all individuals benefit by being aggressive, at least to some extent. However, weak individuals benefit by avoiding contests that they cannot win and hence benefit from mutual assessment. Strong individuals, on the other hand, can potentially win any fight and gathering information is not beneficial since they are willing to escalate unconditionally. Second, the difference between weak and strong fighters can establish a conflict over the quality of information that is transferred when assessment is communicative, which is discussed in detail below. Third, the need for mutual assessment can be avoided if individuals adopt a pure withdrawal strategy according to their RHP, which could imply that conventional solutions to contests can sufficiently reduce the costs associated with both mutual assessment and escalation. However, the use of such a strategy is restricted to particular ecological conditions.

Variation between Self- and Mutual Assessment

The trade-off between gathering information and persisting in contests can explain why self-assessment is more common in nature than previous models predict. In order for an individual to maximize the resources it can gain from contests, it may need to adopt a withdrawal strategy that inherently carries the risk of making a strategic error. This risk can be lowered by adopting a mutual assessment strategy, but doing so reduces the individual's capacity to bear the costs associated with escalation. That is, although escalation is costly, animals may need to fight to access resources, and effort spent assessing opponents can reduce their ability to persist in a fight (e.g., Elwood and Arnott 2012). Thus individuals must compromise between reducing the risk of strategic error and maintaining the ability to engage in escalated interactions. It is the relative costs of these alternatives that determine whether there is self- or mutual assessment at the ESS. In other words, the foregone ability to afford involvement in escalated contests is the opportunity cost of mutual assessment. This can be observed in jumping spiders (*Phidippus clarus*) attempting to usurp a territory. Intruders appear to first assess the RHP of the resident and then switch to a self-assessment-based war of attrition if they assess themselves to have the RHP advantage (Kasumovic et al. 2010). This behavior implies that the intruder has reduced its investment toward obtaining specific information in favor of being able to persist in the war of attrition for longer. Our results thus contrast with the hypothesis that variation in assessment strategy is based purely on the trade-off between the costs and benefits of mutual assessment (Taylor and Elwood 2003; Prenter et al. 2006; Elias et al. 2008; Arnott and Elwood 2009). Specifically, although the costs and benefits of mutual assessment are important, it may be the comparison of this ratio to the costs of escalation that determines the stable assessment strategy rather than the ratio on its own.

Our model predicts that assessment strategy will vary according to the value of contested resources, the costs of escalation, and the cost-effectiveness of assessment. A comparison of assessment strategies used among fig wasp species suggests that assessment strategy varies with the value of resources in a fashion consistent with our model (Pereira and Prado 2005; Moore et al. 2008). In particular, male fig wasps often use self-assessment in fights over access to females in species for which females are extremely limited and hence valuable (Enquist and Leimar 1987; Murray 1987; Colegrave 1994). In contrast, mutual assessment appears to be used in species for which a given mating opportunity is less valuable, although the structure of the fig is also likely to be important (Pereira and Prado 2005; Moore et al. 2008). A shift from self- to mutual

assessment with decreasing resource value is expected under our model when contests are excessively costly, which conforms to fig wasp contests that carry the risk of serious injury and fatalities. Our model also predicts that assessment strategy can shift from mutual to self-assessment with an increase in escalation costs when relative resource value is high and individuals are typically aggressive against matched opponents. This prediction is supported by numerous observations of switching assessment strategies from mutual to self-assessment as the contest escalates from pure display to—presumably more costly—physical interactions (Morrell et al. 2005; Elias et al. 2008; Hsu et al. 2008; Kasumovic et al. 2010). Finally, Elias et al. (2008) showed that mutual assessment appeared to increase in contests between jumping spiders (*P. clarus*) that had previous experience with one another when compared to the first contest between the same individuals. This result is consistent with our model if experience improves the efficacy, and hence the cost-effectiveness, of mutual assessment.

The Effect of Communicative Assessment

The degree to which mutual assessment behavior provides opponents with information may have an important influence on the opportunity costs faced by an individual. Specifically, our model predicts that the transfer of specific information as a result of making an assessment (i.e., communicative assessment) can either increase or decrease the critical threshold that determines assessment strategy. The root of this differential effect comes from our assumptions regarding variation in the RHP of the population and the payoffs of interactions. Specifically, weak individuals receive greater expected payoffs if their opponents make a strategic error, while strong individuals benefit more if their opponents make correct decisions. This assumption is supported by observations of contests in convict cichlids (*Amatitlania nigrofasciata*): opponents that assess an individual to be weak are more likely to escalate than opponents that assess an individual to be strong (Leiser et al. 2004). Thus, weak individuals may suffer, and strong individuals benefit, from sharing information on their RHP with their opponent. Consequently, weaker individuals benefit from hiding information on their own RHP and may thus avoid communicative mutual assessment. On the other hand, stronger individuals benefit from sharing information on their own RHP, and thus, communicative assessment discounts their investment toward mutual assessment. In other words, if assessment is communicative, weak individuals face a trade-off between gaining information on opponents and providing opponents with information, while strong individuals do not. This information conflict can then influence the functional

significance of self- and mutual assessment strategies, assuming that assessment strategy is independent of RHP.

Communication of RHP between contesting individuals has traditionally been considered as a cooperative behavior that allows contestants to resolve a conflict without resorting to excessively costly outcomes (Clutton-Brock and Albon 1979; Crespi 1986; Rubenstein and Hack 1992; Keeley and Grant 1993; Hurd 1997). For instance, the sequential assessment model predicts that contestants should fully cooperate on sharing information on RHP asymmetries during contests and that information transfer is independent of RHP (Enquist and Leimar 1983; Enquist et al. 1990). However, our results suggest that, while individuals may share a common interest in avoiding costly outcomes, there can be conflicts of interest over the quality of information being transferred that depend on RHP and the evolution of cooperative mutual assessment will be limited by this conflict. While this is a novel interpretation of our model, it can offer explanations for some puzzling behaviors. For example, Enquist et al. (1990) observed contests in the cichlid *Nannacara anomala* and found that, although both contestants signaled their RHP to their opponents, the smaller contestant of a pair performed fewer signals that gave accurate information than the larger contestant. This hypothesis can also provide an explanation for theoretically confusing hyperaggression in smaller individuals, termed “Napoleons” (Just et al. 2007; Svensson et al. 2012): weak individuals may rapidly escalate in order to prevent their opponents from making an accurate assessment of the RHP asymmetry and force their stronger opponents into making a premature withdrawal decision.

Testing the Assumptions and Predictions of the Model

Although the model conforms to our current observations and can even resolve some points of contention, there is much that remains purely theoretical. In this respect, our model can provide testable hypotheses for further experimentation on natural cases where assessment strategy has been observed to vary (e.g., Morrell et al. 2005; Elias et al. 2008; Hsu et al. 2008; Kasumovic et al. 2010). Specifically, we predict that contestants will switch from mutual to self-assessment in high-cost contests as resource value increases or contest costs decrease. In contrast, we expect the opposite pattern in low-cost contests. A switch from mutual to self-assessment is expected whenever the cost-effectiveness of assessment decreases, regardless of resource value and contest costs.

Our assumption that weak individuals benefit from opponent error and strong individuals do not also requires experimental tests. We predict that weak individuals will attempt to limit information transfer (e.g., by performing fewer or less informative communicative behaviors). Ad-

ditionally, attempts by weak individuals to hide information will increase with the value of the contested resource and decrease with the costs of persistence. The information-conflict hypothesis also predicts that the performance of communicative assessment behaviors will be associated with the absolute RHP of a given individual, rather than the relative RHP of the contestants. Finally, contests that rely on communicative assessment (e.g., sequential assessment) may be less likely in populations where the RHP distribution is skewed toward weaker individuals.

Mutual Assessment and Withdrawal Strategies

From a theoretical standpoint, there are some notable differences between the results of our model and Crowley (2000) that could indicate the influence of obtaining specific information on withdrawal strategies. Specifically, Crowley (2000) shows that the ESS withdrawal strategy is an RHP-dependent pure strategy if individuals have access to only general information, there are only two RHP categories that are equally prevalent in the population, and strong individuals always defeat weak individuals. That is, strong individuals always play hawk, and weak individuals always play dove. However, we find that mixed strategies, in which individuals play a mixture of hawk and dove, can exist under the same conditions, although this outcome depends on relative resource value. Thus, the option to invest in obtaining specific information may result in the adoption of a mixed ESS for withdrawal strategies even if specific information is not used. Alternatively, this difference may be due to Crowley's (2000) inclusion of an escalation cost asymmetry between winners and losers, or the costs of sharing when both individuals play dove. The implication of our result is that the potential to invest in obtaining specific information (even if it is not obtained) can disrupt the use of a strategy in which individuals fight if they are above an RHP threshold and withdraw if they are below, in favor of a strategy in which withdrawal decisions are made on the basis of probability.

Conclusions and Future Developments

Our model can be expanded to explore the implications of continuous variation in RHP and the importance of RHP in determining contest outcomes (Crowley 2000; McNamara and Houston 2005). Furthermore, the costs of contests can be made to vary depending on the assessment strategy being used, the outcome of the contest, and the RHP of the contestants (e.g., the cost of a contest may increase as RHP asymmetry decreases for mutual assessment; losers may pay greater escalation costs; high-RHP individuals may inflict, and be able to receive, more costs;

Enquist et al. 1990; Crowley 2000; Leiser et al. 2004; Hsu et al. 2008). Similarly, the costs of assessment could vary with an individual's RHP or the asymmetry between contestants (Enquist and Leimar 1983; Enquist et al. 1990; Leiser et al. 2004). The implications of such alternative RHP conditions and cost structures must be explored to account for a more accurate representation of nature and to improve our understanding of assessment strategies.

In this article, we proposed that variation in assessment strategy is the result of a balance between investment toward mutual assessment and the capacity to escalate. However, there may be other important limitations on mutual assessment (Whitehouse 1997; Taylor et al. 2001; Taylor and Elwood 2003; Prenter et al. 2006; Elias et al. 2008; Arnott and Elwood 2009). First, there may be constraints to information processing—from cognitive abilities, available information, and sensory acuity—that limit mutual assessment (Taylor and Elwood 2003; Prenter et al. 2006; Elias et al. 2008; Arnott and Elwood 2009). For instance, a comparison of RHP may be too cognitively complex for many animals, and private and public information on RHP may instead be assessed independently and combined rather than directly compared (Elwood and Arnott 2012). However, there has been little work in terms of identifying the cognitive requirements for different ways of assessing RHP in contests. Second, investment toward mutual assessment may reduce an individual's RHP, or individuals may have to initially gather experience in contests before being able to make an accurate assessment (Arnott and Elwood 2009). Third, there is even the potential for no role assessment (neither self- nor mutual) to occur in contests, such as if individuals fight indiscriminately (Colegrave 1994; Cook and Bean 2006; Moore et al. 2008) or are able to adjust their withdrawal strategy according to experience (Whitehouse 1997). Finally, most contest models assume that individuals compare information on their own RHP to public information on opponent RHP. However, some animals appear to compete in a way that suggests private information is ignored and withdrawal decisions are made entirely on the basis of specific information without the comparative process of mutual assessment (Wise and Jaeger 1998; Rillich et al. 2007; Prenter et al. 2008; Arnott and Elwood 2009). Thus, future theoretical developments may need to consider the use of general and specific information independently of a comparison with private information (e.g., Elwood and Arnott 2012). Overall, it is clear that we must consider a wide range of processes that extend beyond the scope and capabilities of this model in order to understand assessment strategies.

The adaptive value of information-gathering strategies like mutual assessment depends on the costs of assessment. While our model considers the costs of gathering specific

information on opponent RHP, we assumed that individuals possess perfect private and general information without cost. However, specialized strategies that ignore information can be adaptive over strategies that gather information (Stephens 1989). Indeed, we predict this strategy here with respect to the evolution of gathering specific information. Thus, we may expect individuals to ignore private and general information of RHP in some cases. Generally, previous theoretical work has demonstrated that withdrawal strategies approach the solution to the original, symmetrical case of the hawk-dove game as the information in the system decreases (Crowley 2000; McNamara and Houston 2005). That is, all individuals play hawk if the value of the contest outweighs the costs of fighting and otherwise the same mixed strategy (Crowley 2000). Given that we are already familiar with the case of no private information in contests, future theoretical work must develop models that determine the conditions in which it is adaptive to ignore or gather information on own RHP. The results can then be compared to the case covered by our model, in which it is information on opponent RHP that is costly to gather. Empirical studies can then focus on finding support for any of these models.

Despite the broad scope concerning assessment strategies, our model supports an important role for strategic error at the heart of contest behavior through its influence on withdrawal strategies (Parker and Rubenstein 1981), aggressiveness (Just et al. 2007), and opponent assessment (Enquist and Leimar 1983; Just et al. 2007; this study). Furthermore, asymmetries in the payoffs of sharing information between contestants may lead to conflicts of information sharing, which could have important implications for any model that considers the use of public information. Together, these factors may serve as central components of future models that attempt to provide a general explanation of variation in assessment strategies.

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