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From Hawks and Doves to Self-Consistent
Games of Territorial Behavior

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ABSTRACT: Explaining the "prior-residence effect" (automatic owner status of individuals who arrived first in an area) was one of the very first applications of game theory in animal behavior. These models, however, predict paradoxical solutions where intruders always win, with no satisfactory explanation for the absence of such cases in nature. We propose a solution based on new developments in evolutionary game theory. A self-consistent model with feedbacks between individual behavior and population dynamics produces qualitatively different frequency-dependent selection on intruders (floaters) than on territory owners. Starting with an ancestral population with no respect for ownership, the most likely evolutionary end point is complete or partial respect. Conventional rules of conflict resolution thus can rely on "uncorrelated asymmetries" without differences in resource-holding power or territory value, although they will be strengthened by such differences. We also review the empirical literature on animal contests, testing whether asymmetries in resource-holding power are required to explain the observations. Despite much empirical effort, results remain inconclusive, because experiments are often unable to distinguish between the motivation

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of individuals to fight and the behavioral outcome of a contest. To help arrive at conclusive answers, we suggest a standardized empirical approach to quantify prior-residence effects.

The animal kingdom provides countless examples of the "prior-residence effect," the fact that individuals who arrived somewhere first appear to have a "psychological" advantage when competing over resources in that area. First-arrived individuals are more likely to win fights (some recent studies are Kemp and Wiklund 2004; Lefevre and Muehter 2004; Okada and Miyatake 2004; Switzer 2004; see table A1 in the online edition of the *American Naturalist* for a complete list), or alternatively, their ownership of the resources may go completely uncontested (e.g., Davies 1978; Baugh and Forester 1994; Turner 1994). Taxa in which prior-residence effects have been found range from sea urchins to mammals (see table A1), and the effect offers a powerful explanation of territorial contest resolution. In a situation where other individuals respect ownership, the owner can concentrate on more useful activities than resource defense, such as breeding.

But why should respect for ownership evolve? This question was one of the first applications of game theory to investigate animal behavior. Early hawk-dove games predicted that aggression (playing "hawk") can be selected against, given sufficient costs of fighting (Maynard Smith and Price 1973). Applying the hawk-dove idea to territorial behavior requires defining a role asymmetry: one of the individuals is an owner, the other an intruder. Consequently, the list of strategies (hawk, dove) gains a new addition, the "bourgeois" strategy, in which an individual behaves aggressively only when in the owning role (Maynard Smith and Parker 1976). Indeed, the bourgeois strategy can be stable, and the outcome is termed an "uncorrelated asymmetry" (Maynard Smith and Parker 1976; Maynard Smith 1982): the difference between the players (owner vs. intruder) is sufficient to resolve the conflict despite the lack of correlation with fighting ability, value

of the resource to the individual, or any other effect that could bias the game in favor of one of the players. The uncorrelated-asymmetry hypothesis hence proposes that fights are settled based on purely conventional roles: it is cheaper for both players to adopt the convention that owners are respected simply because they are owners than to challenge the convention and end up in numerous fights as a consequence.

But the analysis of the ownership game reveals a strange feature, once one notices that the roles are mere arbitrary labels that allow settling the contest. There is nothing about the labels "owner" and "intruder" that make the owner the one more likely to adopt the role of the more aggressive player: the contest could be equally well settled by any other easily observable asymmetry, for example, "the player who is facing the sun plays dove." To make matters worse, there are reasons why intruders in particular could be expected to be aggressive: if they cannot reproduce at all without a territory, they have very little to lose (Grafen 1987). For these reasons, it is essential to include the anti-bourgeois strategy, where owners always retreat (play "dove") and intruders take their place (through playing hawk), in the set of possible strategies. The outcome is startling: antibourgeois is an evolutionarily stable strategy (ESS) exactly when bourgeois is too (Maynard Smith 1982; see table A2 in the online edition of the *American Naturalist*). Because the behavior predicted by this alternative appears counterintuitive, this solution is called the "paradoxical ESS," as opposed to the "commonsense" nature of the bourgeois strategy (Maynard Smith and Parker 1976; Maynard Smith 1982).

The current consensus is that the uncorrelated-asymmetry hypothesis does not perform well as an explanation of territorial behavior (e.g., Hardy 1998). This is not only because of the strange duality it predicts between paradoxical and commonsense strategies. When looking closely, one usually finds some feature of individuals that is consistently different between resource owners and intruders, be it resource-holding power (RHP; e.g., Lindström 1992; Lozano 1994; Kemp and Wiklund 2001; Pryke and Andersson 2003)—which sometimes is causally enhanced through ownership, for example, when basking butterflies warm up in the sun (Stutt and Willmer 1998; but see Kemp and Wiklund 2004)—or the value of a territory, which again can increase with time spent as a territory owner (as argued by, e.g., Krebs [1982]; Tobias [1997]; Stokkebo and Hardy [2000]). This means that one does not have to rely on uncorrelated asymmetries as a solution.

On the other hand, some theoretical work aims to show that uncorrelated asymmetries do not necessarily predict this strange duality, but certain mechanisms ensure that the commonsense strategy prevails, for example, repeated interactions (Mesterton-Gibbons 1992), errors in decision making (Morrell and Kokko 2003), or physiological correlations between ways of responding to draws versus losses (Morrell and Kokko 2005). However, a closer look reveals that these cases always include some a priori assumption that makes owners more likely to win fights: Mesterton-Gibbons (1992) predefines a probability >1/2 that owners win, Morrell and Kokko (2003) assume that errors make fight outcomes correlate with true fighting ability, and the physiological correlations assumed by Morrell and Kokko (2005) have a similar effect. Thus, one could conclude—as, for example, Mesterton-Gibbons (1992) has done—that ownership as a pure convention does not work, in the sense of being able to predict commonsense solutions of ownership respect; some correlated asymmetries are always needed, perhaps together with cognitive mechanisms that allow assessment of the opponent's strength (Parker and Rubenstein 1981).

Here our aim is to challenge this consensus, based on theoretical considerations as well as an investigation of the way empirical tests are conducted. Regarding theoretical developments, we will show that game theory can, after all, produce models based on uncorrelated asymmetries that produce respect for ownership. The key is to make models self-consistent (Houston et al. 2005; Houston and McNamara 2006); self-consistent models are also called "ecogenetic" models (Eshel and Sansone 1995) or models with eco-evolutionary feedback (Le Galliard et al. 2005). The rationale is as follows. It is not logically consistent to analyze a game where the value of a territory and costs of fighting are constants V and C, respectively. For example, if fights are frequent, the value of a territory must necessarily decline, because challenges occur more often (Eshel and Sansone 1995; Houston and McNamara 2006). Likewise, the same costs of fighting must lead to a shorter life span if fights are very frequent; and if mortality is high in the population as a whole, a nonaggressive strategy that simply waits for a vacancy must perform relatively better, since territorial turnover is high.

By explicitly investigating all the options awaiting individuals throughout their lifetime, our models are made self-consistent, but they also incorporate Maynard Smith's (1982, p. 96) idea of "infinite regress." This argument has been used to explain away paradoxical strategies: if such a strategy really did prevail, there would be no time left for breeding because population members keep moving around, finding new places to settle only to be soon replaced by another individual. However, the exact consequences of an infinite regress have never been formally quantified; thus, its ability to remove paradoxical solutions has not been put under test. Here we provide a model that allows an infinite regress to take place (within the limits of the lifetime of individuals and their mobility) and calculates the consequent reproductive rates, using the as-

sumption that individuals can reproduce until they are displaced by another. After developing self-consistent models of territory ownership with and without resource-holding power differences, we comment on the empirical literature on correlated and uncorrelated asymmetries and give recommendations for future research.

Modeling Territorial Behavior with Population-Level Feedbacks

Our aim is to provide a self-consistent account of the aggressiveness of owners and intruders and to see if we can predict respect for ownership such that intruders are less aggressive than owners upon encounter. Grafen (1987) pointed out that when predicting the behavior of an intruder, one should consider how "desperate" it might be: what are the options available if it does not fight for the contested resource? However, Grafen's argument does not immediately predict a difference in the aggression of owners and intruders. Being desperate merely increases the payoff difference between having or not having the resource, but this applies to owners who might lose the resource as well as to intruders who might gain it (table A2).

However, taking into account population dynamics could change the situation. A nonbreeding intruder (often called a "floater"; Zack and Stutchbury 1992) will find itself in a more relaxed situation if territory owners often succumb to death: simply waiting for a vacancy to arise might then be enough. This must be evaluated against the floater's own survival prospects during the appropriate time. More important still, variables such as the rates of finding vacancies will not be fixed for each species but will themselves evolve; for example, if many floaters kill themselves by fighting aggressively, it might become relatively better to wait, because the numbers of competitors will be lower.

Here we examine the dynamics of floating and breeding with population-level feedback. After solving the model with no RHP differences, we introduce variation in RHP, to see how differences in fighting ability influence the distribution of commonsense versus paradoxical outcomes. This allows us to examine theoretically the hypothesis that ownership is respected because strong individuals tend to accumulate as owners (Parker 1974; Leimar and Enquist 1984; Alcock and Bailey 1997; Kemp and Wiklund 2004).

Evolutionarily Stable Behavior with No Differences in RHP

We begin the description of the model by defining the possible strategies. We consider a population consisting of breeders (territorial owners) and nonterritorial floaters. If these meet (according to rules defined below), the owner and floater can each play "daring" or "careful." These

correspond to hawks and doves in older models. The strategy is described by the probabilities that an individual plays daring if it is a territorial owner or a floater. For brevity, we call the probability of playing daring the "aggressiveness" of an individual, denoted x for owners and y for floaters. A daring floater is an intruder willing to fight, while a daring owner defends his territory aggressively. If only one individual of the two plays daring, it takes over the territory. If neither is daring, either player obtains the territory with probability 1/2, and the other one leaves. If both are daring, a fight ensues. In this section, we assume no RHP asymmetry, so that one of the players (the winner) obtains the territory and the other one (the loser) leaves, again with probabilities 1/2.

We now define the parameters that are fixed for a population (Greek letters in table A3 in the online edition of the *American Naturalist*). We assume that breeding occurs continuously. Time units are scaled such that territory owners produce one offspring per time unit. Territory owners have a background mortality rate of μ_T; this rate excludes deaths associated with fights. Because owners produce offspring at a rate 1 and floaters do not produce offspring, $\mu_T < 1$ will be necessary to avoid population extinction. Newborn individuals become nonbreeding floaters, who can then either fill territories vacated by the death of the territory owner or obtain territories by usurping the current owner. The background mortality of floaters (excluding deaths associated with fights) equals μ_F.

If an owner dies, the nearest floater takes over the vacancy. We assume that in addition to encountering possible vacant territories, floaters sample θ occupied territories per time unit and that they meet the territory owner every time they sample such a territory. If both individuals then play daring, a fight ensues.

Fights can be lethal for the loser, who will die as a result of the fight with probability δ. The background mortality rates μ_T and μ_F, the lethal injury probability δ, and the rate of territory inspection θ are the only parameters that take fixed values for each population. There are additional population parameters whose values depend on the behavior of population members; we call these "feedback parameters." Such parameters are the number of floaters per territory owner (denoted n) and the total mortality rates of territory owners (m_T) and floaters (m_F). When necessary, we will use notations such as $n(x, y)$ to indicate dependence on population strategies. For brevity, however, we usually use the shorter notation n. To make it clear which parameters are fixed in a population and which ones evolve with the strategy played, we have used Greek letters to denote fixed values and Latin characters for parameters and variables that respond to the strategy in use in the population (see table A3 for a list of notation).

The total mortality rate of owners increases with the

relative number of potential intruders n and their rate of territory inspection θ, because intruders cause fights that can be lethal (with probability δ). Because an inspection causes a fight with probability xy and the probability of losing is $1/2$, the total mortality of owners equals

$$m_T = \mu_T + \frac{xyn\theta\delta}{2}. \tag{1}$$

The total mortality rate of floaters, m_F, is derived similarly, but the rate of territory inspection is θ per floater; thus,

$$m_F = \mu_F + \frac{xy\theta\delta}{2}. \tag{2}$$

The number of floaters per territory, n, increases at a rate of 1 per time unit through births and decreases at a rate $m_F n$ through deaths of floaters and at a rate m_T because of floaters either finding vacancies created by the death of the territorial or taking over territories of owners who died in the contest. Note that floaters can become territorials through usurpation of an owner, but in cases of no mortality, this does not change the net number of floaters, and the associated deaths are taken into account in the total mortality rates. At equilibrium, the number of floaters, n, does not change over time:

$$\frac{dn}{dt} = 1 - m_F n - m_T = 0. \tag{3}$$

This gives the equilibrium number of floaters per territory,

$$n = \frac{1 - m_T}{m_F} = \frac{1 - \mu_T}{\mu_F + \theta xy\delta}. \tag{4}$$

The rate at which an individual floater finds and occupies vacant territories is again a feedback parameter,

$$v = \frac{\mu_T}{n}. \tag{5}$$

Evolutionary Equilibria and Their Stability Conditions. We can derive the following results (the derivation and the exact values for all criteria are detailed in app. B in the online edition of the *American Naturalist*):

1. No ESS exists where owners play a mixed strategy ($0 < x^* < 1$).

2. The only possible ESS of the form $\{0, y^*\}$ is the pure paradoxical strategy $\{0, 1\}$.

From results 1 and 2, it follows that the only possible equilibria are the paradoxical equilibrium $\{0, 1\}$, a "no respect" equilibrium (i.e., all individuals always fight) $\{1,$

$1\}$, the commonsense "complete-respect" equilibrium $\{1, 0\}$, and a semimixed "partial-respect" strategy where owners always defend, and floaters sometimes challenge them: $\{1, y^*\}$ with $0 < y^* < 1$. While the partial-respect strategy does not show full respect for ownership, it still has commonsense features: owners always defend their property, and intruders at least sometimes retreat without challenging them. It is noteworthy that the "hippie world" solution $\{0, 0\}$, where resources are shared without aggression, is never stable.

3. The commonsense complete-respect solution, where owners defend their territories and intruders respect ownership, is an ESS when the background mortality of territory owners is large and fighting is risky.

4. The paradoxical solution, where owners retreat and intruders replace them without fights, is an ESS when the background mortality of breeders is high, that of floaters is low, the number of territories they can inspect per unit time θ is high, and fight costs are high. In this case, reproductive values of owners and floaters do not differ from each other hugely: an owner does not lose as much from stepping down as it would under different circumstances.

5. As in solution 3, the no-respect solution, where individuals always fight when meeting each other ($x = y = 1$), is an ESS when the background mortality of floaters is high, breeder mortality is low, and floaters do not encounter new territories quickly. These conditions imply that floaters are "desperadoes": breeding possibilities are rarely encountered, and floaters are short-lived and thus in a hurry. This equilibrium also becomes more likely if fight costs δ are low.

6. The semimixed partial-respect ESS with $x^* = 1$, $0 < y^* < 1$ can be stable, and the value of y^* is given in appendix B. The degree of respect increases (i.e., floater aggression decreases) with the costs of fighting, the rate of territory encounter, and the background mortality of breeders. When the mixed equilibrium exists, it always coexists with the paradoxical equilibrium.

We also show (app. B) that the conditions that stabilize the commonsense equilibrium are also sufficient to make the paradoxical ESS exist. The converse is not true.

Evolutionary Trajectories with or without Variation in RHP. The previous section showed that full or partial respect can be evolutionarily stable, but such solutions always coexist with the paradoxical equilibrium: introducing population feedback does not destroy the paradoxical strategy. The paradoxical strategy, on the other hand, can exist without coexisting with a "respectful" strategy. This seems to suggest that population feedback is of little use when explaining the prevalence of respect for ownership in nature. However, it is clearly of interest to ask which ESS is reached from various starting conditions: the basins

of attraction—that is, the regions of initial values (x, y) from which evolution proceeds to each equilibrium—are not necessarily equally large for the various ESSs. One must additionally evaluate how biologically likely each starting point $\{x, y\}$ is for the initial evolution of territoriality. It makes little sense to consider starting values that can never be stable and are thus unlikely to be reached at any point during evolution (such as hippie world, $\{0, 0\}$).

Our numerical procedure for calculating evolutionary trajectories is outlined in appendix B. In this section, we also provide an extension of the ESS analysis by relaxing the assumption that there are no differences in individuals' fighting abilities. The possibility that high-RHP individuals tend to accumulate as owners was already proposed by Parker (1974) to explain ownership respect, but to our knowledge it has not been properly developed theoretically. In that case, residency itself will convey information about relative RHP. We include this in our model by assuming that individuals can fall into two categories: they are either strong or weak fighters. This trait is randomly determined at birth (we assume no heritability of the character), with a proportion π of individuals born strong.

Because we are interested in whether differences in fighting ability can lead to general respect for ownership such that ownership functions as the sole cue that settles conflicts, we assume that individuals know only their status as floater or owner. The status can, of course, correlate with fighting ability, and the evolutionary success of strategies is calculated accordingly. In contests between two individuals of the same fighting ability, the fight leads to victory or loss and possible death as in the previous section. If a strong and a weak individual fight, the strong one wins with probability $(1 + \alpha)/2$, where α describes fight predictability, that is, the degree to which strength gives an advantage in fights. If $\alpha = 0$, outcomes are randomly determined, and the model then becomes identical to the "no-RHP-difference" model developed in the previous section, whereas with $\alpha = 1$, the stronger contestant invariably wins.

When $\alpha = 0$ (i.e., no RHP differences), the numerical procedure shows that the various ESSs can be reached by evolution (fig. 1). If one considers that the most relevant starting point for an ancestral population is one in which respect for ownership has not yet evolved and resources are always contested (no respect; $x = y = 1$ in the upper right corner of both panels in fig. 1), evolution either stays at no respect (fig. 1A) or proceeds to the equilibrium with partial respect of ownership rather than the paradoxical equilibrium.

Figure 1 shows only the solutions for one particular choice of values of population parameters (mortalities and efficiency of territorial sampling). However, its results are not an isolated example. To obtain an overview of how commonly evolution can lead to paradoxical versus com-

monsense strategies when starting from no respect, we checked 1,000 random choices for parameter values: parameter values were randomly picked from an even distribution that ranged between 0 and 1 for the parameters μ_T, μ_F, and δ and between 0 and 10 for θ. Then we calculated the evolutionary trajectory, starting from $x = 1$, $y = 1$. In 398 cases, the population stayed at the no-respect equilibrium. In 592 cases, the evolutionary end point was commonsense or partially commonsense, and in a mere 10 cases, the paradoxical solution evolved. In these 10 paradoxical cases, mean floater mortality was only 0.0153, and the baseline mortality of owners was, on average, 44 times that of floaters (range 1.43–114.6). We may conclude that evolution can proceed from no respect toward the paradoxical ESS, but this appears to require an extremely unlikely mortality pattern where territory owners suffer vastly higher mortality than floaters.

Figure 2A depicts a typical result in the absence of RHP differences, while figure 2B (with $\alpha = 1$) adds these differences. It is clear that differences in fighting ability make intruders more careful: because strong owners have accumulated in the territorial population and weak fighters have often lost fights, floaters are more likely to be weak than owners. At the equilibrium $x^* = 1$ and $y^* = 0.23$, 94% of owners are strong, compared with 48% of floaters (calculations follow app. B). Floaters therefore enjoy smaller expected payoffs from engaging in a fight than they do in figure 2A, which explains their greater reluctance. However, the difference between figure 2A and figure 2B is quantitative rather than qualitative: in both cases, evolution proceeds toward a partial-respect equilibrium, and the only difference is in the value of y^*.

How powerful are RHP differences in producing qualitatively different outcomes? For example, can they switch the territorial system from the no-respect state to one with respect for ownership, either partial or complete? Figure 3 shows the effect of fight predictability α on the evolutionary end point when evolution begins in the no-respect state. In all cases of figure 3, owners always defend their property, and increasing α makes intruders less aggressive (i.e., decreases y^*). This includes qualitative changes; for example, when $\delta = 0.35$, no respect changes to partial respect, with $y^* = 0.78$, while α increases from 0 to 1 (fig. 3).

Nevertheless, partial respect in the above example is not very strong—78% of intruders still challenged the owner. Overall, figure 3 shows that the influence of RHP differences is fairly slight. Solutions are never paradoxical in figure 3, even if we assume no RHP differences (at $\alpha = 0$), and the lines delimiting different solutions are vertical or close to vertical in most parts of figure 3, which indicates that predictability of fight outcomes, α, merely slightly shifts regions of different solutions toward less frequent challenges by intruders; in other words, RHP differences
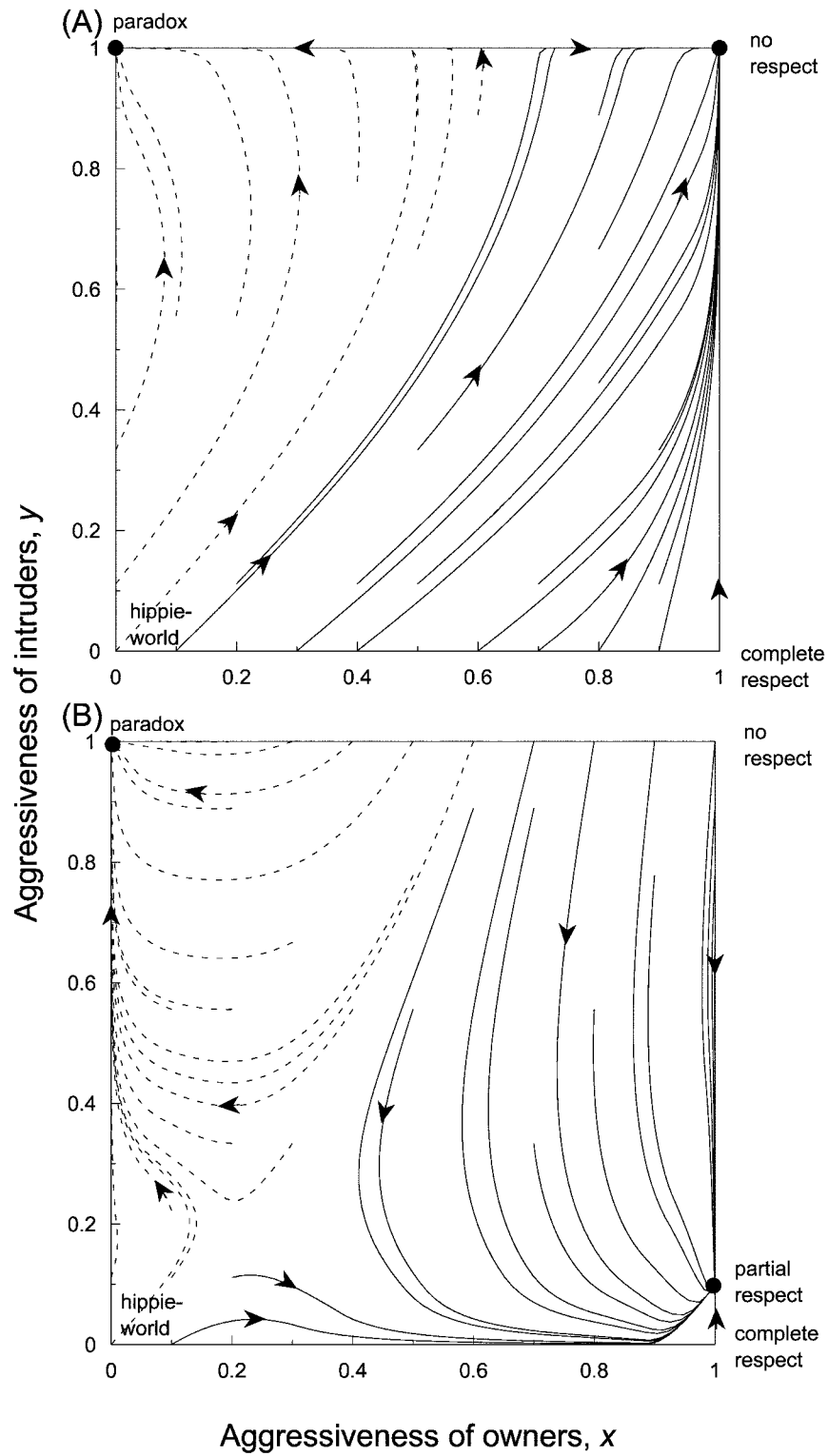
Figure 1: Evolutionary trajectories of the feedback model without RHP differences. Dots mark stable equilibria. Dotted lines describe evolution toward the paradoxical strategy, solid lines evolution toward any other kind. *A*, Fighting carries fairly low mortality risk ($\delta = 0.1$), leading to two evolutionary end points: the paradoxical strategy or the no-respect equilibrium. Other parameters: $\theta = 10$, $\mu_T = \mu_F = 0.5$. *B*, Fighting carries high mortality risk ($\delta = 0.5$), which makes no respect unstable and partial respect stable. Other parameters are as in *A*.
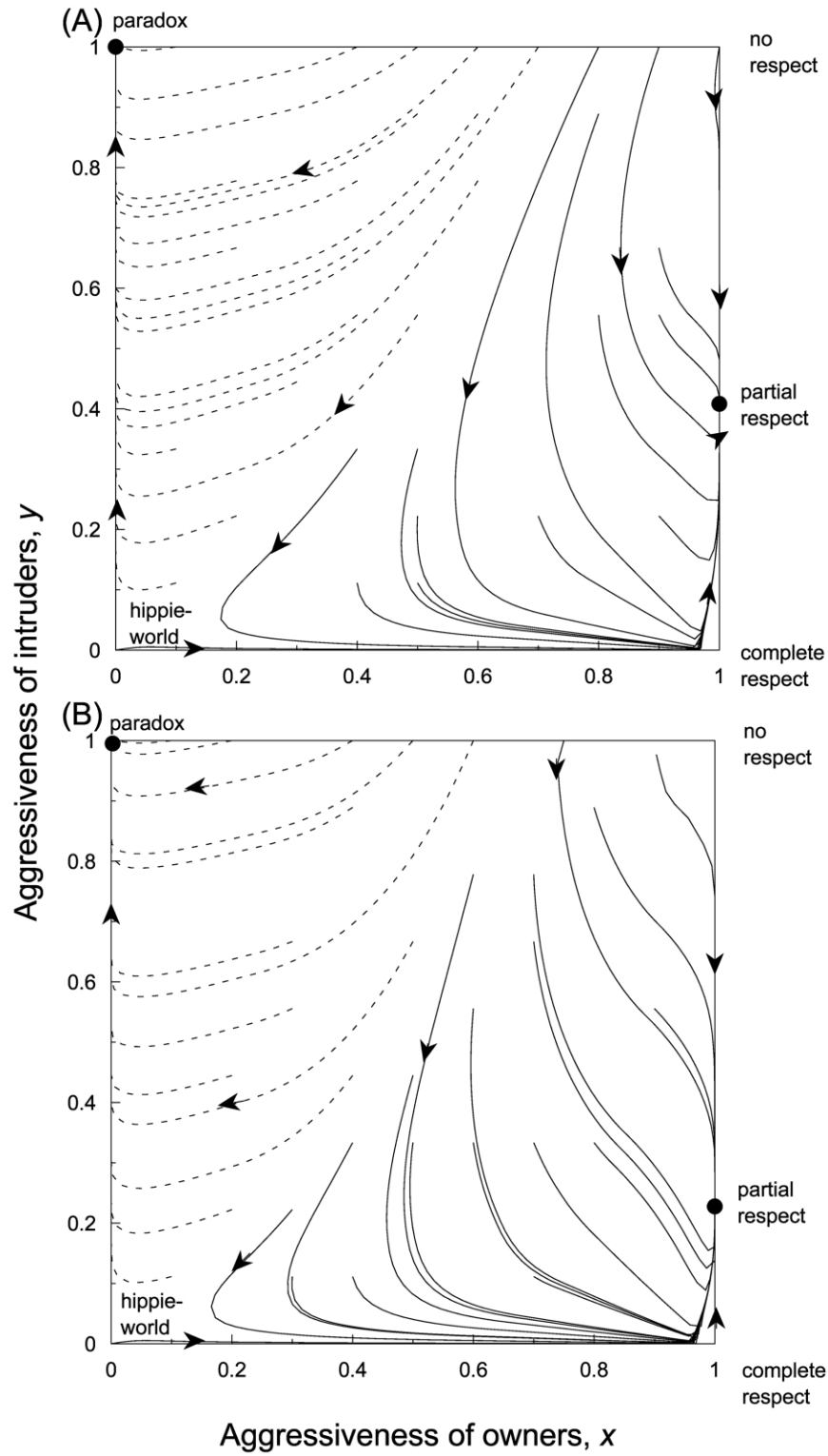
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Figure 2: Comparison of model with and without RHP differences. *A*, No RHP differences and parameters $\theta = 10$, $\mu_T = 1.0$, and $\mu_F = 1.2$ lead to partial respect being stable in a similar vein as in figure 1. At this equilibrium, intruders challenge owners in approximately 40% of encounters. *B*, Assuming RHP differences with $\alpha = 1$, $\pi = 0.5$ leads to similar evolutionary trajectories, but there is now more respect: intruders challenge owners less often, in approximately 23% of encounters, than in *A*. Other parameters are as in *A*.
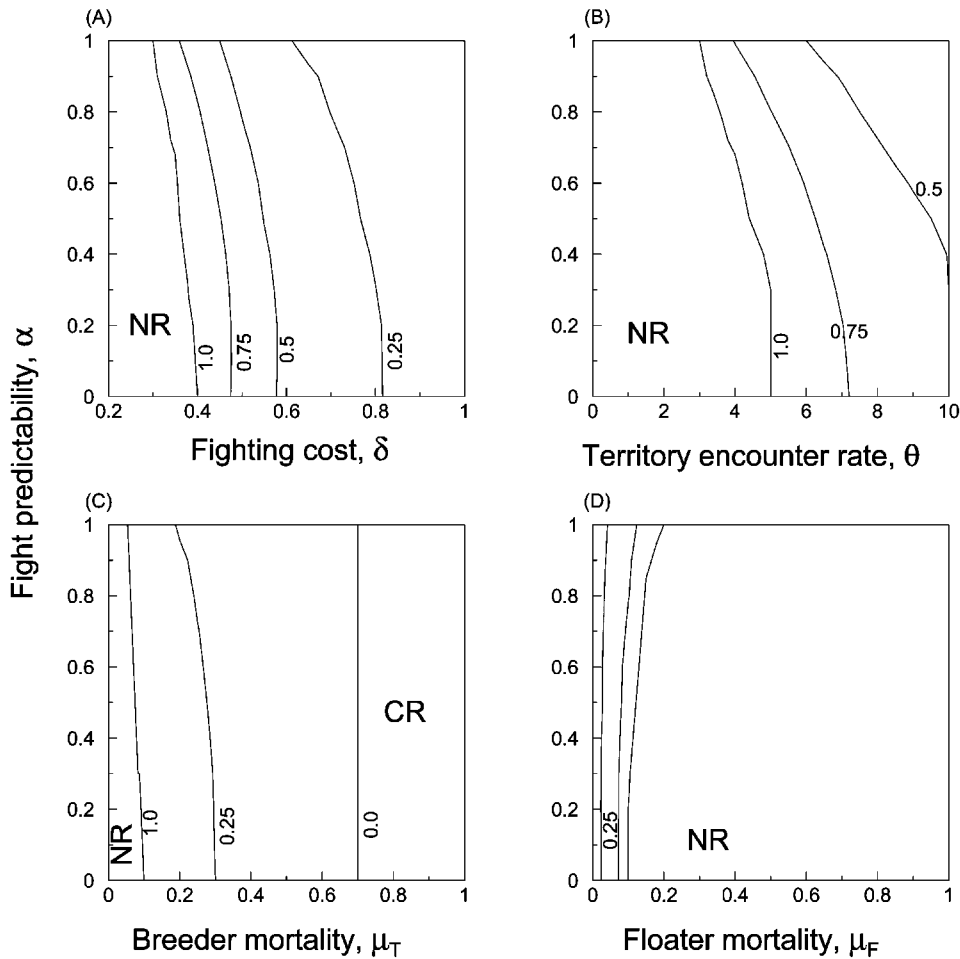
Figure 3: Evolutionary end points when evolution starts in the no-respect state ($x = y = 1$). Types of solutions are derived with varying values of fight predictability α, as indicated on the y-axis, and varying values of (A) fighting cost δ, (B) territory encounter rate θ, (C) breeder mortality μ_T, and (D) floater mortality μ_F, as indicated on each x-axis. Parameters, where not varied, are $\delta = 0.4$, $\theta = 5$, $\mu_F = \mu_T = 0.1$, and $\pi = 0.5$. The graph divides the parameter space into regions: "NR" indicates that the evolutionary end point is no respect, $x^* = y^* = 1$, and "CR" that it is complete respect, $x^* = 1$, $y^* = 0$. In any other region, the solution features partial respect, with the numbers indicating contour lines for the evolutionarily stable aggressiveness of intruders, y^*.

introduce a slightly stronger tendency to respect ownership. The tendency per se was already introduced by the feedback model with no RHP differences.

Discussion

The prior-residence effect was first reported by Davies (1978), who observed territorial contests in speckled wood butterflies *Pararge aegeria*. Since then, it has been found in a multitude of species (see table A1 for examples), and we are aware of only two species in which the paradoxical solution (i.e., intruders attack and residents retreat systematically) has been observed: a social

spider *Oecobius civitas* (Burgess 1976; but see Mesterton-Gibbons and Adams 1998) and the captive goldeye fish *Hiodon alosoides* (Fernet and Smith 1976). Clearly, this means that game theoretical models of animal contests cannot be taken seriously unless they are able to predict the extreme rarity of paradoxical solutions. Previous solutions have relied on assumptions such as cognitive capabilities allowing RHP assessment (Parker and Rubenstein 1981). Our reanalysis of old hawk-dove games, using self-consistent modeling of population processes, explains why paradoxical solutions are unlikely to develop in nature, regardless of how developed the cognitive machinery is. Frequency dependence operates differently

for intruders and for owners, and this has both theoretical and empirical consequences.

Regarding theoretical advances of applications of game theory in animal behavior, it is increasingly being realized that payoffs cannot be considered fixed parameters: when behavior evolves, not only does the expected behavior of a conspecific individual change, but the numbers of conspecific competitors, mates, etc., typically change, too (Le Galliard et al. 2005; López-Sepulcre and Kokko 2005; Houston and McNamara 2006). In other words, the ecological setting in which a population finds itself depends on the strategies used in the population. Here we have applied self-consistency to the very first problem—aggression and resource defense—where game-theoretic logic was introduced to the study of animal behavior.

Eshel and Sansone (1995) argue that fights lead to owners and intruders swapping roles in a way that maintains the arbitrary nature of these roles and that paradoxical solutions can thus prevail. This echoes the argument of our table A2, where both intruders and owners compare the same values of winning, V, and getting injured in a fight, C; hence, they experience the same payoffs. This logic does not hold, however, when population feedback is taken into account: it changes the payoffs of the game as aggressiveness levels change, mediated via population density and the number of vacancies present.

The consequences differ for floaters and owners. The best option for a floater can change from "challenge" to "do not challenge" when floaters become more aggressive: more fights in the population mean that fellow floaters die more often, thus shortening the wait to find an available territorial vacancy. The less risky option of non-aggressive waiting therefore becomes better, creating negative frequency dependence on the floater strategy and stabilizing a mixed strategy for floaters. (The argument would become stronger still had we allowed owners to die after the fight even if they won it; increased aggressiveness would then imply more vacancies created this way.) Owners, on the other hand, do not experience negative frequency dependence: they should never switch from "defend" to "do not defend" when daring owners become more prevalent in the population. More fighting means that the number of floaters decreases, which makes it more, rather than less, beneficial for owners to be aggressive: the value of a territory that is rarely challenged is higher and should be defended more.

Population feedback can therefore generate owner-intruder asymmetries in behavior without a need to assume that owners are a priori more likely to win. This improves the realism of game theory models, as does the fact that we often predict partial respect, where breeders usually enjoy ownership rights but these are sometimes contested and takeovers may take place. Complete respect begs the question of why intruders should intrude at all if they always retreat (Grafen 1987), a problem not present in solutions featuring partial respect.

To empiricists, our most important message is that evidence for asymmetries between owners and intruders does not rule out that an underlying uncorrelated asymmetry has a strong influence on ownership evolution. The prevailing interpretation is that the prior-residence effect is not a sign of a pure convention, as proposed by Maynard Smith and Parker (1976). Rather, it is viewed a consequence of residence being correlated to asymmetries in competitive ability or value of the resource (e.g., Stokkebo and Hardy 2000). It has been suggested (Kemp and Wiklund 2001) that the role of conventions must be minor, because careful examination almost always reveals some asymmetry between owners and intruders in either RHP or the value of the territory. Together with the possibility of RHP assessment (Parker and Rubenstein 1981), asymmetries then appear sufficient to explain the owner-intruder asymmetry in strategies. For example, Kemp and Wiklund (2004) reexamined prior-residence effects in the speckled wood butterfly (the same species used by Davies [1978]) in a carefully controlled experimental setting. Through a clever series of experimentation, they found evidence supporting the idea that more intrinsically aggressive males accumulate as residents, which could then explain the prior-residence effect, too.

Our figure 3 suggests that RHP differences can play some role: solutions can incorporate differences in fighting ability and the accumulation of strong owners, and this strengthens ownership respect to some extent. Yet this does not mean that the signal of the underlying convention is absent, since predictions regarding ownership respect remain qualitatively similar if RHP differences diminish and vanish (fig. 3). Certainly, the results of controlled experiments such as those by Kemp and Wiklund (2004) are not compatible with partial- or complete-respect solutions in our model without RHP differences. However, we also predict that no respect can prevail as a stable solution, and, perhaps surprisingly, the results of Kemp and Wiklund can be completely reconciled with our approach if they are described as a no-respect solution with RHP differences. This solution is found in figure 3 under a wide set of parameter values. Under such a scenario, we would predict no difference in the willingness to initiate fights (which can be termed the "motivation" to fight, sensu Härdling et al. 2004), while the observed fight outcomes can be biased toward owners winning if strong individuals have accumulated in the owner population. Kemp and Wiklund (2004) reported that contests always ensued immediately; thus, their results regarding motivation are consistent with this interpretation.

This difference between fight initiation and fight out-

come highlights a large gap between empirical and theoretical approaches. Theoretical studies typically model the evolution of fighting strategies (motivational aspects, i.e., whether to attack or retreat), while most empirical studies record the outcome of those fights (i.e., who is observed to win). Although the outcome of a fight will be determined partly by the strategy (motivation) of both opponents (and some studies show a correlation between them; Grossman 1980; Mayr and Berger 1992; Chellappa et al. 1999; Maan et al. 2001), observing only fight outcomes is not sufficient to distinguish between strategies. For example, intruders are sometimes predicted to fight even when their chances to win are low (Grafen 1987). If one were to measure contest outcome in such a system, residents would win most of the time, suggesting a prior-residence effect, even if the intruder's strategy showed no respect for ownership at all.

While it is simple to define strategies of "intention" or motivation in theoretical models, it is far from easy to detect them in nature. If conflicts are solved by the convention "resident wins," most of those interactions are likely to be missed, since floaters end up not challenging resource owners at all (Grafen 1987). In fact, once a fight is observed, one can interpret that it occurred because both resident and floater have played daringly, and the task of the empiricist is then to try to assess the fraction of encounters that led to such a challenge. Most empirical studies, however, focus only on realized fights. For example, in a study investigating fighting tactics in mouthbrooding cichlid fish *Oreochromis mossambicus*, Turner (1994) excluded from the analyses all cases where fights did not occur because of intruders retreating—which added up to 95% of the total cases. Clearly, the respect of ownership becomes much more impressive if such cases are included. Other studies have applied similar selection criteria (e.g., Harvey and Corbet 1986; Bridge et al. 2000). A focus only on realized fights leads to a dilution of the importance of respect for prior ownership, which gives another reason why the role of conventions may remain underappreciated. Naturally, empiricists need to be aware of possible misassessments of the opposite kind, too: not all intrusions that end up in the intruder fleeing were meant to be territorial challenges in the first place (Grafen 1987).

We appreciate, of course, the complications that arise when trying to detect the historical evolutionary pathway. RHP differences or value asymmetries exist in many systems, often together with an appropriate assessment mechanism (Parker and Rubenstein 1981), and detecting "which came first" may require phylogenetically controlled comparative approaches. Most studies where residency is tested against RHP conclude that competitive ability (RHP) is a stronger determinant of fight outcome than residency. Evidence supporting strong prior-residence effects is most often found in three scenarios (see table A1 for a more detailed list of studies): first, when individuals are more or less matched in size (e.g., Hammerstein and Riechert 1988; Rosenberg and Enquist 1991; Stuart-Smith and Boutin 1994; Beaugrand et al. 1996; Petersen and Hardy 1996; López and Martín 2001); second, when individuals with a higher RHP tend to accumulate as residents (e.g., Lindström 1992; Alcock and Bailey 1997; Pratt et al. 2003; Pryke and Andersson 2003); and third, when residence confers a higher RHP—as is the case with resident butterflies being warmer (Stutt and Willmer 1998) or in organisms that defend burrows being in a better position to fight (e.g., Magnhagen and Kvarnemo 1989; Ranta and Lindström 1993; Jennions and Backwell 1996). This is in keeping with our model, where RHP differences simply strengthen a convention that already exists. In appendix B, we outline an empirical method to quantify the effects of asymmetries in the presence of an underlying convention.

It also remains to be tested whether conventions really do arise through frequency dependence in the payoff structure, as assumed by our model. This poses obvious challenges: to study population-level feedback, one requires, ideally, much more extensive information about the nature of density-dependent population regulation than is usually available (e.g., Kokko and Rankin 2006). However, differences in payoffs have been shown to correspond to changes in individual behavior (Hammerstein and Riechert 1988), which suggests that such an approach could prove extremely fruitful.

Further biological complexities certainly have the potential to influence the fitness prospects of a floater: learning can play a role in the development of ownership (Stamps and Krishnan 1999, 2001; Morrell and Kokko 2003) as well as the possibility that intruders negotiate some space for themselves by squeezing in between existing territories (Stamps and Krishnan 2001; Pereira et al. 2003; López-Sepulcre and Kokko 2005). Regarding such additions, our modeling simply shows that a potentially fundamental biological process strongly predisposes species to exhibit a prior-residence effect, even if no additional respect-strengthening mechanisms (such as RHP assessment; Parker and Rubenstein 1981) exist in a particular case. Together with the overwhelming ubiquity of the prior-residence effect regardless of the nature of the resource, type of weaponry, and other biological details of the diverse taxa in which such effects are reported (see table A1), this suggests to us that the prior-residence effect reflects a more fundamental biological process than a mere assertion that some asymmetry or other is usually present in animal populations.

Acknowledgments

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Appendix A from H. Kokko et al., "From Hawks and Doves to Self-Consistent Games of Territorial Behavior"

(Am. Nat., vol. 167, no. 6, p. 901)

Empirical Studies, Classic Hawk-Dove-Bourgeois Matrix, and Model Notation

Table A1

Studies assessing the effect of both ownership and resource-holding power (RHP) in the outcome of animal contests

Species	Study type[a]	Ownership	RHP	Source
Sea urchins:				
Rock boring urchin *Echinometra lucunter*	FE	+	+	Shulman 1990
Purple urchin *Echinometra viridis*	FE	+	+	Shulman 1990
Spiders and allies:				
Freshwater mite *Unionicola formosa*	SE	0	+	Edwards and Dimock 1991
Mediterranean wolf spider *Lycosa tarantula*	FE	+	0	Moya-Laraño et al. 2002
New Zealand jumping spider *Marpissa marina*	SE	+[b]	0	Jackson and Cooper 1991
Crab spider *Misumenoides formosipes*	SE	+	+	Dodson and Schwaab 2001; Hoefler 2002
Colonial spider *Metepeira incrassate*	FE	+[c]	+	Hodge and Uetz 1995
Colonial spider *Metepeira atascadero*	FE	+[c]	+	Hodge and Uetz 1995
Orb stretch spider *Metellina mengei*	FE	+	+	Bridge et al. 2000
Autumn spider *Metellina segmentata*	FE	+[d]	+	Hack et al. 1997
Funnel-web spider *Agelenopsis aperta*	FE	+[c]	+	Hammerstein and Riechert 1988
Crustaceans:				
Hermit crab *Pagurus filholi*	SE	+[c]	+	Yoshino and Goshima 2002
Porcelain fiddler crab *Uca annulipes*	FE	+[b]	+	Jennions and Backwell 1996
Atlantic sand fiddler crab *Uca pugilator*	FO	+[e]	+	Hyat and Salmon 1978; Pratt et al. 2003
Atlantic marsh fiddler crab *Uca pugnax*	FO	+	+	Hyat and Salmon 1978
Orange fiddler crab *Uca vocans*	FO	0	+	Jaroensutasinee and Tantichodok 2003
Sand-bubbler crab *Scopimera globosa*	FE	+[c]	+	Takahashi et al. 2001
Malaysian prawn *Macrobranchium rosenbergii*	SE	0[e]	+	Preebles 1979
Glass prawn *Palaemon elegans*	SE	+	+	Evans and Shehadi-Moachdieh 1988
Swamp crayfish *Procambarus clarkia*	SE	+	+	Figler et al. 1999
P. clarkia	SE	0	+	Figler et al. 1997
Signal crayfish *Pacifastacus leniusculus*	SE	+[b]	+	Ranta and Lindström 1993; Edsman and Jonsson 1996; Nakata and Goshima 2003
P. leniusculus	SE	+	0	Peeke et al. 1995
P. leniusculus juveniles	SE	0	+	Ranta and Lindström 1992
Japanese crayfish *Cambaroides japonicus*	SE	+[c]	+	Nakata and Goshima 2003
American lobster *Homarus americanus*	SO	+	+	Karnofsky and Price 1989
Insects:				
Large red damselfly *Pyrrhosoma nymphula*	FO	+	0	Gribbin and Thompson 1991
P. nymphula larvae	SE	+	0	Harvey and Corbet 1986
Neotropical damselfly *Hetaerina miniata*	FO, FE	+	0	Lefevre and Muehter 2004
Amberwing dragonfly *Perithemis tenera*	FO	+	0	Switzer 2004
Field cricket *Gryllus bimaculatus*	SE	+	+	Simmons 1986
Ant lion *Macroleon quinquemaculatus*	SE	+	+	Griffiths 1992

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Table A1 (*Continued*)

Species	Study type[a]	Ownership	RHP	Source
Caddis fly *Agrypnia pagetana*	SE	+	+	Englund and Otto 1991
Caddis fly *Arctopsyche ladogensis*	SE, FE	+[e]	+	Englund and Olsson 1990
Fruit fly *Drosophila melanogaster*	SO	+	+	Hoffmann 1987
Fruit fly *Drosophila simulans*	SO	+	+	Hoffmann 1987
Caribbean fruit fly *Anastrepha suspense*	SE	+[c]	+	Burk 1984
Scorpionfly *Harpobittacus nigriceps*	FO	+[c]	+	Thornhill 1984
Desert ant *Cataglyphis niger*	SE	+	0	Wenseleers et al. 2002
Beewolf *Philantus basilaris*	FO	0[e]	+	O'Neill 1983
Tarantula hawk wasp *Hemipepsis ustulata*	FE	+	0	Alcock and Bailey 1997
Parasitoid wasp *Goniozus nephantidis*	SE	+[d]	+	Petersen and Hardy 1996
Solitary wasp *Mellinus arvensis*	FO	+	+	Ghazoul 2001
Banksia bee *Hylaeus alcyoneus*	FE	+[e]	+	Alcock 1995
Common hook-tip moth *Drepana arcuata*	SE	+	+	Yack et al. 2001
Weidemeyer's admiral butterfly *Limenitis weidemeyerii*	FO	+[c]	+	Rosenberg and Enquist 1991
Common eggfly butterfly *Hypolimnas bolina*	FO	+	0	Kemp 2000, 2002
Evening brown butterfly *Melanitis leda*	FO	0	+	Kemp 2003
Speckled wood butterfly *Pararge aegeria*	FE	0[b,e]	+	Kemp and Wiklund 2004
Japanese nitidulid beetle *Librodor japonicus*	SE	+	+	Okada and Miyatake 2004
African ball-rolling scarab *Khepher platynotus*	FO	+	+	Sato and Hiramatsu 1993
Fish:				
Goldeye fish *Hiodon alosoides*	SE	−	−	Fernet and Smith 1976
Swordtail fish *Xiphophorus* sp.	SE	+	+	Heuts and Nijman 1998
Green swordtail fish *Xiphophorus helleri*	SE	+[c]	+	Beaugrand et al. 1996
Northern cavefish *Amblyopsis spelaea*	SE	0	+	Bechler 1983
Ozark cavefish *Amblyopsis rosae*	SE	+	0	Bechler 1983
Spring cavefish *Chologaster agassizi*	SE	0	+	Bechler 1983
Southern cavefish *Typhlichtys subterraneus*	SE	+	+	Bechler 1983
Atlantic salmon *Salmo salar*	SE	+	+	Cutts et al. 1999
Coho salmon *Onchorhynchus kisutch*	SE	+	+	Rhodes and Quinn 1998
Arctic grayling *Thymallus arcticus*	SE	+	+	Kratt and Smith 1979
Freshwater angelfish *Pterophyllum scalare*	SE	+	0	Chellappa et al. 1999
Green terror cichlid *Aequidens rivulatus*	SE	+	+	Maan et al. 2001
Snail cichlid *Lamprologus ocellatus*	SE	0	+	Brandtmann et al. 1999
Convict cichlid *Cichlasoma nigrofasciatum*	SE	0	+	Wazlavek and Figler 1989
C. nigrofasciatum pairs	SE	+[c]	+	Itzkowitz et al. 1998; Draud and Lynch 2002
Firemouth cichlid *Cichlasoma meeki*	SE	+	+	Neil 1983
Mozambique mouthbrooder *Oreochromis mossambicus*	SE	+[d]	+	Turner 1994
Sand goby *Pomatoschistus minutes*	FE	0[e]	+	Lindström 1992
P. minutes	SE	+[b]	+	Magnhagen and Kvarnemo 1989
Bay goby *Lepidogobius lepidus*	SO	+	+	Grossman 1980
Freshwater goby *Padogobius martensi*	SE	0	+	Parmigiani et al. 1987
White seabream *Diplodus sargus*	SE	+	+	Caballero and Castro 1999
Estuarine triplefin *Forsterygion nigripenne*	SE	0	+	Mayr and Berger 1992
Olive rockfish *Acanthoclinus fuscus*	SE	0	+	Mayr and Berger 1992
Blue gourami *Trichogaster trichopterus*	SE	0	+	Frey and Miller 1972
Three-spine stickleback *Gasterosteus aculeatus*	FE	+[c]	+	Candolin and Voigt 2003
Variegated pupfish *Cyprinodon variegates*	FO, FE	0[e]	+	Leiser and Itzkowitz 2004
Amphibians:				
Eschscholtz salamander *Ensatina eschscholtzii*	SE	+	Weak	Wiltenmuth 1996

Table A1 (*Continued*)

Species	Study type[a]	Ownership	RHP	Source
Red-backed salamander *Plethodon cinereus*	SE	+	0	Smith and Pough 1994
Mountain dusky salamander *Desmognathus ochrophaeus*	SE	+	0	Smith and Pough 1994
Dart-poison frog *Dendrobates pumilio*	SE	+	0	Baugh and Forester 1994
Carpenter frog *Rana virgatipes*	FO	+[e]	+	Given 1988
Green frog *Rana clamitans*	FO	+	+	Wells 1978
Reptiles:				
Iberian wall lizard *Podarcis hispanica*	SE	+[c]	+	López and Martín 2001
Arboreal lizard *Abronia vasconcelosii*	SE	0	0	Formanowitcz et al. 1990
Sand lizard *Lacerta agilis*	FO	0	+	Olsson 1992
Birds:				
Magellanic penguin *Spheniscus magellanicus*	FO	+	+	Renison et al. 2002, 2003
Pigeon guillemot *Cepphus columba*	FO	+	0	Nelson 1984
Western gull *Larus occidentalis*	FO	+	+	Pierotti and Annett 1994
Great tit *Parus major*	FE	+[d]	0	Krebs 1982
Pied flycatcher *Ficedula hypoleuca*	FE	+[d]	0	Dale and Slagsvold 1995
F. hypoleuca	FO			
Red-winged blackbird *Agelaius phoeniceus*	FE	+	0	Shutler and Weatherhead 1991
European robin *Erithacus rubecula*	FE	+[d]	+	Tobias 1997
Red-shouldered widowbird *Euplectes axillaries*	SE, FE	0[e]	+	Pryke and Andersson 2003
Mammals:				
Common shrew *Sorex araneus*	SE	+	+	Barnard and Brown 1982
American red squirrel *Tamiasciurus hudsonicus*	FE	+[c]	+	Stuart-Smith and Boutin 1994
Harbor seal *Phoca vitulina*	FO	+	+	Neumann 1999
Northern elephant seal *Mirounga angustirostris*	FO	+	+	Haley 1994

Note: A plus sign indicates positive correlation, 0 indicates no effect, and a minus sign indicates inverse correlation (i.e., paradoxical).

[a] FE = field experiments; SE = staged experiments; FO = field observations; SO = staged observations.

[b] Ownership enhances competitive ability (RHP).

[c] Owners win only when size differences between contenders is small.

[d] Ownership may be correlated to resource value.

[e] Individuals with higher RHP tend to accumulate as owners in natural conditions.

Table A2
Payoff matrix of the classic hawk-dove-bourgeois game (Maynard Smith 1982) extended to include bourgeois and antibourgeois strategies

	Hawk	Dove	Bourgeois	Antibourgeois
Hawk	$(V - C)/2$	V	$(3/4)V - (1/4)C$	$(3/4)V - (1/4)C$
Dove	0	$V/2$	$V/4$	$V/4$
Bourgeois	$(V - C)/4$	$(3/4)V$	$V/2$	$(V/2) - (C/4)$
Antibourgeois	$(V - C)/4$	$(3/4)V$	$(V/2) - (C/4)$	$V/2$

Note: In this nonecological game (i.e., no self-consistency), the focal player, whose possible strategies are given by the rows, is half the time in the role of the intruder and half the time in the role of an owner. Fight outcomes are randomly determined, winning the resource brings the payoff V, and fighting costs the loser C fitness units. For example, if the focal player plays hawk and the opponent plays bourgeois, half of all encounters lead to a fight (i.e., those where the opponent is the owner), with payoff $(V - C)/2$. In the other half of interactions, the focal player is the owner, which leads to payoff V; thus the expectation is $(3/4)V - (1/4)C$. If the opponent plays antibourgeois, the payoffs are exactly the same: the only difference is that the fight now happens if the opponent is an intruder rather than an owner. If the strategies bourgeois and antibourgeois compete, it is better for each player to converge on the same strategy, i.e., the same convention, since $V/2 > V/2 - C/4$. There is nothing in the game predicting that bourgeois should prevail over antibourgeois.

Table A3

Model notation

Notation	Definition
Fixed parameters:	
θ	Number of territories a floater can inspect in a time unit
μ_T	Background mortality of breeders ($\mu_T < 1$)
μ_F	Background mortality of floaters
δ	Probability of lethal injury resulting from losing a fight
α	Predictability of fight outcomes (in the model with resource-holding power [RHP] differences)
π	Proportion of strong newborns (in the model with RHP differences)
Feedback parameters (depends on population strategy):	
n	Number of intruders per territory in a time unit
v	Rate at which vacancies form
m_T	Total mortality rate of territory owners
m_F	Total mortality rate of floaters
Variables:	
u	Rate at which floaters usurp territory owners (per floater)
d	Rate at which territory owners are displaced (per owner)
w_T	Fitness (reproductive value) of a territory owner
w_F	Fitness (reproductive value) of a floater
x	Aggressiveness of an owner, i.e., the probability that an owner defends his territory by playing daring; evolutionarily stable aggressiveness is denoted x^*
y	Aggressiveness of an intruder, i.e., the probability that a nonowner intrudes aggressively by playing daring; evolutionarily stable aggressiveness is denoted y^*

Note: In addition, notations will be specific for individuals of given fighting ability (subscript S = strong, W = weak) in the model with RHP differences.

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Appendix B from H. Kokko et al., "From Hawks and Doves to Self-Consistent Games of Territorial Behavior"

(Am. Nat., vol. 167, no. 6, p. 901)

Mathematical Derivations and Empirical Methods

Calculation of Evolutionary Equilibria and Their Conditions

Consider a population in which fighting probabilities x and y are in use. We need an expression for the fitness of a mutant who uses a different strategy (x' or y'). First, we solve for the conditions under which increased aggressiveness is selected for in owners. The owner's aggressiveness increases its death rate (according to eq. [2]): as an owner, the mutant will die at a rate $m'_T = \mu_T + (x'yn\theta\delta/2)$.

Aggressiveness, on the other hand, can help reduce the rate with which the owner is displaced from its territory to become a floater. We denote this rate by d. When there is an intrusion, the owner is displaced to become a floater if it does not defend itself and the intruder is aggressive, or if it defends and loses the fight but nevertheless stays alive. Finally, displacement may occur if neither intruder nor owner plays daring, and occupation is then determined randomly, as in encounters between two doves in hawk-dove games. A mutant owner who uses x', therefore, becomes displaced at a rate

$$d' = n\theta\left[(1 - x')\left(y + \frac{1 - y}{2}\right) + x'y\frac{1 - \delta}{2}\right] = \frac{n\theta}{2}(1 - x' + y - x'y\delta). \tag{B1}$$

It is important to note that the number of intruders, n, is calculated using the equilibrium condition (eq. [4]) derived for the population strategy, not the rare mutant's strategy.

An owner gains fitness at a rate w_F (the reproductive value of newborns, which become floaters) through reproduction. If the owner is displaced at a rate d' and dies at a rate m'_T, its reproductive value is determined by the equation

$$\frac{dw'_T}{dt} = w_F - m'_T w'_T + d'(w_F - w'_T), \tag{B2}$$

which gives, when setting $(dw'_T/dt) = 0$,

$$w'_T = \frac{d' + 1}{d' + m'_T}w_F. \tag{B3}$$

Although this equation assumes that mutants produce offspring whose reproductive value does not differ from that of the rest of the population, it leads correctly to the ESS solution of state-dependent behavior (for details of this argument, see Houston and McNamara 1999).

Differentiating gives us the condition

$$\left(\frac{dw'_T}{dx'}\right)_{x'=x} > 0 \Leftrightarrow 2[1 - \mu_T(1 + \delta y)] > \theta\delta ny(1 + y). \tag{B4}$$

This equation states the conditions under which territory owners are selected to become more aggressive than their current level, x.

Next, we solve for selection on floater behavior. As with breeders, aggressiveness increases mortality: a mutant

floater of aggressiveness y' will die at a rate $m'_F = \mu_F + (xy'\theta\delta/2)$. However, aggressiveness also brings about the benefit of improving the rate u with which a floater usurps successfully and becomes a breeder. Taking into account all possible fight outcomes, the rate at which a mutant usurps equals

$$u' = \theta\left\{y'\left[\frac{x}{2} + (1 - x)\right] + \frac{(1 - y')(1 - x)}{2}\right\} = \frac{\theta}{2}(1 - x + y').$$ (B5)

In addition, floaters acquire territories without aggression if they find vacant territories (rate v; eq. [5]). The reproductive value of a mutant floater is solved from

$$\frac{dw'_F}{dt} = -m'_F w'_F + (v + u')(w_T - w'_F) = 0.$$ (B6)

Note that the rate of finding vacancies, v, depends on the population strategy y rather than the mutant's own strategy y', because the mortality of owners is determined by the outcomes of fights in the population in general. The solution of equation (B6) at equilibrium is

$$w'_F = \frac{v + u'}{v + u' + m'_F} w_T.$$ (B7)

For floaters, increased aggressiveness is selected for if

$$\left(\frac{dw'_F}{dy'}\right)_{y'=y} > 0 \Leftrightarrow 2(\mu_F - v\delta x) > \delta\theta x(1 - x).$$ (B8)

The results of the main text can be proved as follows:

1. No ESS exists where owners play a mixed strategy ($0 < x^* < 1$). For such an ESS to exist, condition (B4) should switch from being fulfilled to being not fulfilled when x increases. In other words, the quantity $2[1 - \mu_T(1 + \delta y)] - \theta\delta ny(1 + y)$ should be a decreasing function of x. In this expression, the only variable that depends on x is n: it is a decreasing function of x (eq. [4]). Since $\delta \geq 0$, $\theta > 0$, and $y \geq 0$, the above expression increases when n decreases. Consequently, it is impossible to have negative frequency dependence in x that leads to a mixed strategy in owners.

2. The only possible ESS of the form $\{0, y^*\}$ is the pure paradoxical strategy $\{0, 1\}$. When $x = 0$, equation (B8) simplifies to $2\mu_F > 0$. This is always true, and floaters should always challenge aggressively if territory owners do not resist.

The conditions for the possible stable solutions are as follows:

3. The commonsense complete-respect solution, where owners defend their territories and intruders respect ownership, is an ESS if the background mortality of territory owners is large and fighting is risky. This situation is described by $x = 1$, $y = 0$. Owners should in this case stay with being aggressive, since equation (B4) becomes $1 - \mu_T > 0$, which is always true, given that $\mu_T < 1$ is required for the population to exist. But intruders should remain careful only if (from eqq. [4], [5], after setting $x = 1$ and $y = 0$ and simplifying)

$$\mu_T > \frac{1}{1 + \delta}.$$ (B9)

4. The paradoxical solution, where owners retreat and intruders replace them without fights, can be an ESS. Equation (B8) is always true for $x = 0$ and $y = 1$ (see above), so floater behavior conforms to paradoxical behavior. In addition, it must hold that breeders are selected to refrain from aggressiveness if floaters always challenge owners. Changing the sign in inequality (B4) and evaluating n (eq. [4]) with $x = 0$, $y = 1$ yield the conditions for breeders to refrain from defending,

$$\frac{\delta\theta}{\mu_F}(1 - \mu_T) + \mu_T(1 + \delta) > 1. \tag{B10}$$

Note that from equation (B9) it follows immediately that equation (B10) is fulfilled: any commonsense ESS is accompanied by a paradoxical ESS.

5. Similarly to result 3, the no-respect solution, where individuals always fight when meeting each other ($x = y = 1$), can be an ESS. The conditions that have to be simultaneously satisfied are obtained by setting $x = y = 1$ in both equation (B4) and equation (B9). The result can be summarized as

$$\frac{\mu_T\delta}{\mu_F} < \frac{1 - \mu_T}{\mu_F + \delta\theta} < \frac{1 - \mu_T(1 + \delta)}{\delta\theta}. \tag{B11}$$

6. The mixed partial-respect ESS with $x^* = 1$, $0 < y^* < 1$ can be stable. This is solved by setting $x = 1$ and solving for the value of y^* that yields an equality in equation (B8). Thus, y^* has to yield a value of v that satisfies $v = \mu_F/\delta$. This is

$$y^* = \frac{\mu_F}{\delta^2\theta\mu_T}[1 - (1 + \delta)\mu_T]. \tag{B12}$$

Stability requires that owners are not selected to decrease their aggressiveness at $\{1, y^*\}$. Substituting equation (B12) into equation (B4) leads to the condition $\delta^2\theta\mu_T/\mu_F y^*(1 - y^*) > 0$ for increased owner aggressiveness at $\{1, y^*\}$, which is true whenever $0 < y^* < 1$. For floaters, stability requires that equation (B8) changes from being fulfilled to being not fulfilled at y^* when y increases. This is true because the left-hand side of equation (B8) is a decreasing function of v, which in turn is a decreasing function of n, which is a decreasing function of y. Thus, the mixed equilibrium of partial respect for ownership is stable if y^* falls between 0 and 1.

The mixed partial-respect equilibrium, when it exists, always coexists with the paradoxical equilibrium. Above, we showed that the mixed equilibrium is stable if $0 < y^* < 1$. The stability of the paradoxical equilibrium requires that the quantity $X = (\delta\theta/\mu_F)(1 - \mu_T) + \mu_T(1 + \delta)$ fulfills $X > 1$ (eq. [B10]). From equation (B12) with $0 < y^* < 1$, it follows that $\mu_T(1 + \delta) > 1 - (\delta^2\theta\mu_T/\mu_F)$; thus,

$$X > \frac{\delta\theta}{\mu_F}(1 - \mu_T) + 1 - \frac{\delta^2\theta\mu_T}{\mu_F} = 1 + \frac{\delta\theta}{\mu_F}[1 - \mu_T(1 + \delta)]. \tag{B13}$$

If $1 - \mu_T(1 + \delta) > 0$, it follows that $X > 1$. From equation (B12) with $0 < y^* < 1$, we know that $1 - \mu_T(1 + \delta) > 0$, because all other terms are positive. This completes the proof.

Calculation of the Dynamic Equilibrium

Fight outcomes will now depend on the types of individuals that meet each other. The death rates and displacement rates of strong territory owners are, respectively,

$$m_{ST} = \mu_T + xyn\theta\left[\frac{p_F\delta}{2} + \frac{(1 - p_F)\delta(1 - \alpha)}{2}\right] \tag{B14}$$

and

$$d_{ST} = n\theta\left((1 - x)\left(y + \frac{1 - y}{2}\right) + xy\left((1 - \delta)\left[\frac{p_F}{2} + (1 - p_F)\left(\frac{1 - \alpha}{2}\right)\right]\right)\right). \tag{B15}$$

Here p_F is the probability that a randomly chosen floater is strong. For weak territory owners, the equations are similar:

$$m_{WT} = \mu_T + xyn\theta\left[\frac{p_F\delta(1+\alpha)}{2} + \frac{(1-p_F)\delta}{2}\right],$$ (B16)

and

$$d_{WT} = n\theta\left((1-x)\left(y + \frac{1-y}{2}\right) + xy\left\{(1-\delta)\left[p_F\left(\frac{1+\alpha}{2}\right) + \frac{1-p_F}{2}\right]\right\}\right).$$ (B17)

Denoting, similarly, by p_T the probability that a randomly chosen territory owner is strong, we obtain the death rate and usurpation rate by strong floaters,

$$m_{SF} = \mu_F + xy\theta\left[\frac{p_T\delta}{2} + \frac{(1-p_T)\delta(1-\alpha)}{2}\right],$$ (B18)

and

$$u_{SF} = \theta\left(y\left\{x\left[\frac{p_T}{2} + (1-p_T)\left(\frac{1+\alpha}{2}\right)\right] + (1-x)\right\} + \frac{(1-y)(1-x)}{2}\right),$$ (B19)

respectively. For weak floaters, the corresponding expressions are

$$m_{WF} = \mu_F + xy\theta\left[\frac{p_T\delta(1+\alpha)}{2} + \frac{(1-p_T)\delta}{2}\right]$$ (B20)

and

$$u_{WF} = \theta\left(y\left\{x\left[p_T\left(\frac{1-\alpha}{2}\right) + \frac{1-p_T}{2}\right] + (1-x)\right\} + \frac{(1-y)(1-x)}{2}\right).$$ (B21)

Denoting by n_{SF} and n_{WF} the number of strong and weak floaters per territory, respectively, we have $n = n_{SF} + n_{WF}$, and the system follows the dynamics

$$\frac{dn_{SF}}{dt} = (-v - u_{SF} - m_{SF})n_{SF}(t) + d_{ST}p_T(t) + q,$$ (B22)

$$\frac{dn_{WF}}{dt} = (-v - u_{WF} - m_{WF})n_{WF}(t) + d_{WT}(1 - p_T(t)) + (1-q).$$ (B23)

The equilibrium for p_T must satisfy conditions where "inputs" of strong and weak individuals as territory owners balance "outputs." Denoting inputs as a and b for strong and weak individuals, respectively, and outputs as cn_S and dn_W, where n_S and n_W are the numbers of strong and weak individuals, respectively, the equilibrium proportion of strong individuals in the population of owners is $ad/(ad + bc)$. By substitutions $a = (v + u_{SF})n_{SF}$, $c = d_{ST} + m_{ST}$, etc., we obtain

$$p_T = \frac{(v + u_{SF})n_{SF}(d_{WT} + m_{WT})}{(v + u_{SF})n_{SF}(d_{WT} + m_{WT}) + (v + u_{WF})n_{WF}(d_{ST} + m_{ST})}.$$ (B24)

Setting equations (B22) and (B23) to 0 and using equation (B24) to calculate p_T leads to the equilibrium solution for n_{SF}, n_{WF} and p_T. This is calculated numerically, once we also take into account that v equals

$$v = \frac{\mu_T}{n_{SF} + n_{WF}}. \tag{B25}$$

Reproductive values and selection. Reproductive values are solved from

$$\begin{pmatrix} dw_{ST}/dt \\ dw_{WT}/dt \\ dw_{SF}/dt \\ dw_{WF}/dt \end{pmatrix} = \begin{pmatrix} -m_{ST} - d_{ST} & 0 & d_{ST} + \pi & 1 - \pi \\ 0 & -m_{WT} - d_{WT} & \pi & d_{WT} + 1 - \pi \\ v + u_{SF} & 0 & -m_{SF} - v - u_{SF} & 0 \\ 0 & v + u_{WF} & 0 & -m_{WF} - v - u_{WF} \end{pmatrix} \begin{pmatrix} w_{ST} \\ w_{WT} \\ w_{SF} \\ w_{WF} \end{pmatrix}.$$

When this matrix is $\mathbf{A}$, the eigenvalues of $\mathbf{A} + \mathbf{I}$ give the relative reproductive values at equilibrium (see Härdling et al. 2003 for justification). These are solved numerically. Given that individuals are assumed to know whether they are territory owners or floaters but not whether they or their opponents are good or poor fighters, the strength of selection will operate according to the proportions p_T, solved from equation (B24), and $p_F = n_{SF}/(n_{SF} + n_{WF})$:

$$\frac{dx}{dt} = p_T \sum_{j=1}^{4} w_j \frac{\partial}{\partial x} A_{1j} + (1 - p_T) \sum_{j=1}^{4} w_j \frac{\partial}{\partial x} A_{2j},$$

$$\frac{dy}{dt} = p_F \sum_{j=1}^{4} w_j \frac{\partial}{\partial y} A_{3j} + (1 - p_F) \sum_{j=1}^{4} w_j \frac{\partial}{\partial y} A_{4j}.$$

An Empirical Method to Quantify the Effects of Asymmetries

For literature cited in this appendix, see appendix A. Logistic regression is a useful tool for detecting effects of RHP differences on contests (Hardy and Field 1998; see also Petersen and Hardy 1996; Taylor and Jackson 2003). We suggest that future studies should use a range of individuals with different RHPs. These differences—where they can be measured accurately—can then be used as explanatory variables explaining differences in fight outcome (fig. B1*A*) and preferably motivation, too, where it can be measured (fig. B1*B*). The prior-residence effect can then be quantified as an effect of ownership that remains where RHP differences vanish (fig. B1*A*). Note that at this particular point of no asymmetry in RHP, there should be no difference between motivation and outcome (fig. B1*B*). This is because motivation should be the determining factor of fight outcomes when the ability to fight does not differ between contestants.

How can motivation be distinguished from fight outcomes in practice? Some species may prove amenable to innovative experimental manipulation that allows measurement of motivation (e.g., testing against unbeatable opponents; Kemp 2002). Otherwise, an obvious first step is to try to quantify the frequency with which the intruder is the fight initiator (fig. B1*B*), but this is not an all-inclusive measure because other aspects of behavior can co-vary with the willingness to fight. It is therefore essential to include behavioral descriptions of territorial interactions instead of or in addition to just their outcomes. Our work suggests that the prior-residence effect may be stronger when viewed in the light of motivation than in the context of fight outcome (fig. B1*B*: the intruder's maximal willingness to fight remains less than its maximal chance of winning). Indeed, empirical studies focusing on behavioral details of fighting, such as attack initiation, often find stronger support for prior-residence effects than those that report only fight outcomes. For example, in two species of crayfish, owners initiate most conflicts, even if they are smaller (Edsman and Jonsson 1996; Figler et al. 1999). Likewise, regardless of size, attack rates in freshwater angelfish *Pterophyllum scalare* are higher for owners than for intruders (Chellappa et al. 1999). Similar results, where owners are more aggressive than intruders regardless of their competitive ability, have been found in a variety of taxa (Englund and Olsson 1990; Baugh and Forester 1994; Wiltenmuth 1996; Caballero and Castro 1999; Maan et al. 2001; Wenseleers et al. 2002).
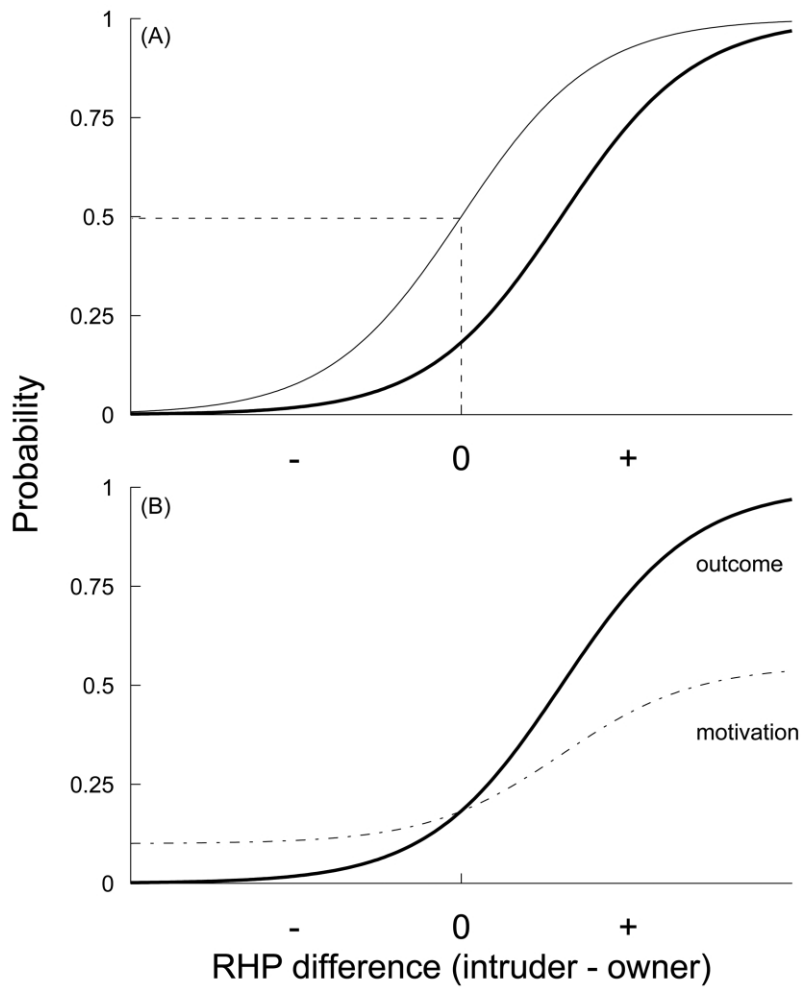
Figure B1: Hypothetical logistic regression outcomes to study prior-residence effects. An experiment is set up that assumes that the RHP difference between intruder and owner can be measured (positive values indicate that the intruder is stronger) and that both the outcome of fights (intruder wins: probability on *y*-axis in *A* and for "outcome" in *B*) and behavioral aspects related to motivation (intruder is more motivated: probability on *y*-axis in *B* for the motivation curve) are measurable. *A*, No prior-residence effect is found if an RHP difference of 0 predicts no asymmetry in outcomes (*thin line*), but the thick line shows evidence of the prior-residence effect: RHP = 0 has <50% intruders winning, and the difference with the null hypothesis of 50% is a measure of the prior-residence effect. *B*, In cases where prior-residence effects are found, the effect is predicted to be stronger if one measures the motivation to fight rather than fight outcomes. This is because intruders, even if they are strong, tend to remain in the less daring role and are only predicted to become more frequent initiators of attacks if they are much stronger than residents.