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Evolution of defense against depletion of local food resources in a mechanistic foraging model

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Models of resource defense are usually based on the assumption that individuals fight over the possession of discrete food items. In many territorial species, however, conflicts occur over access to an area in space that contains resources rather than the resources themselves. We investigate under which conditions defense against depletion of local resources instead of single resource items can evolve from a nonaggressive ancestral population using a spatially explicit mechanistic model with resource dynamics and individual movement. We find that, in general, details of the model assumptions have a great influence on the costs and benefits of different behavior in the model. For patchy resources, defense evolves if fighting costs are very high or if individuals cannot unilaterally opt out of conflicts. If resources are distributed uniformly, defense appears only if individuals can make their behavior dependent on distance to their opponent. Introducing role asymmetries during conflicts in general increases the frequency of contests but reduces the probability that they escalate. If losers of a fight control how far they run, aggressiveness disappears or is greatly reduced for patchy resources but increases significantly for uniform resource distribution. Our results show how defense of space and territoriality could evolve even if resources are neither discrete nor clumped. The fact that seemingly minor differences in how individuals make decisions during encounters lead to huge differences in model outcome highlights the need for more mechanistic models of animal conflicts. *Key words:* exploitation competition, mechanistic model, resource defense, territoriality. *[Behav Ecol]*

INTRODUCTION

When competition for food leads to a conflict of interest between conspecifics, aggression can be a profitable means for individuals to ensure access to valuable resources (Brown 1964). Under which conditions individuals are willing to fight for or defend resource items has been investigated extensively, mostly based on game theoretical models derived from the Hawk–Dove game (Maynard Smith and Parker 1976). The early simple versions of the game have been refined to take into account for example sequential decisions, population dynamics, or ecological consistency and applied to various real-world scenarios such as kleptoparasitism or fights for territories (e.g. Kokko et al. 2006; Broom and Rychtár 2007; Gintis 2007). These models show that if conspecifics compete for discrete resources such as single food items, peaceful sharing is rare and individuals should be willing to defend and fight for food resources in at least some contexts within their life cycle (Mesterton-Gibbons 1992; Eshel and Sansone 1995; Kokko et al. 2006).

Next to direct competition for single food items, however, in many species indirect or exploitation competition occurs, where a focal individual's foraging success is reduced by the depletion of the local food supply caused by nearby conspecifics (Brown 1964; Waser 1981; Houston et al. 1985). Similar to direct competition, exploitation competition can also lead to resource defense. For example, individuals in many species whose food either does not occur in discrete items or where the items are too small or abundant to defend individually nevertheless engage in defense of feeding territories (e.g. fish competing for algae (Hamilton and Dill 2003; Alwany et al. 2005); birds competing for flowers containing nectar (Gill and Wolf 1975); or for insects (Davies and Houston 1981)).

While it has been shown that costly aggressive interactions between individuals with overlapping foraging ranges can lead to the emergence of separate (and defended) territories (Stamps and Krishnan 1999; Adler and Gordon 2003; Morrell and Kokko 2005), it is not clear under which circumstances this type of aggression should evolve in the first place. In contrast to the extensive literature on conflicts over resource items, there is only little theory on when and why exploitation competition leads to the evolution of aggressive behavior. According to Brown's (1964) notion of economic defendability, individuals should defend local resources against depletion if the increase in foraging success an individual could gain by excluding competitors from an area would offset the costs of the fighting this would require. This idea has been formalized in a number of models that predict the size of the area (containing food) a focal individual should be willing to defend against intruders depending on ecological and behavioral parameters such as fighting costs, frequency of intrusion, and resource properties (e.g. Schoener 1983, 1987; reviewed by Adams 2001; López-Sepulcre and Kokko 2005). Due to a number of simplifying assumptions, these models are, however, rather limited in scope. In particular, only the optimal behavior of the owner is investigated (Adams 2001). This does not account for strategic choices on the side of the intruders that can substantially alter costs and chance of success of defense (Hinsch and Komdeur 2010).

An intermediate position between models on contests for resource items and fights against depletion is taken by studies

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on aggression in feeding groups. In these models, individuals fight a resident individual foraging in a resource patch in order to be able to join it (e.g. Dubois et al. 2003; Dubois and Giraldeau 2007). Although nominally competition happens through depletion of resources in the food patch, due to absence of spatial extent, resource dynamics or changes in foraging rate patches are effectively treated as single (though shareable) resource items.

Here, we investigate under which conditions aggressive contest behavior can evolve if individuals only compete indirectly through local depletion of resources. The study has several aims. First, we test whether exploitation competition can lead to the evolution of resource defense from a peaceful ancestral state. Second, we explore which conditions favor the evolution of resource defense in this case. Third, we investigate to which degree the existing theory on animal contests for food items is applicable to the different competition type.

Following previous work, we assume that competitive interactions between individuals happen in dyadic conflicts that, depending on the individuals' behavior, can either end peacefully or escalate to a fight. Assumptions concerning the onset and consequences of conflicts, however, cannot easily be transferred from earlier models of direct competition. To explore to which degree the results are affected by this, we compare 3 submodels with different decision structures as outlined in the following.

If individuals compete for food items, opposing interests between conspecifics immediately arise when an individual that is searching for food encounters a competitor that is currently handling a food item and cease as soon as the food item is consumed. Within that short time span, the fitness consequences of aggressive versus peaceful behavior only depend on the opponent's choice of action and size or quality of the food item (but see Broom and Ruxton 2003). In most models, these conflicts are, therefore, appropriately approximated as discrete interactions with fixed payoffs.

Exploitation competition, in contrast, occurs between 2 individuals if their mutual presence reduces their respective (future) foraging rates due to local food depletion. In this case, a conflict of interest, therefore, gradually increases in strength with decreasing distance between competitors. It persists until either the individuals move apart voluntarily or a fight erupts and the loser is chased away.

This has 2 important consequences. First, there is neither a specific time or event that marks the beginning of a conflict of interest nor is the period of mutual impairment necessarily characterized by any differences in the participants' activities. Consequently, there are no obvious discrete points of decision at which individuals choose whether to be aggressive or not. We assume, therefore, that individuals asynchronously perform short bouts of behavior (movement, foraging, fighting) separated by an orientation phase during which they can detect and potentially attack competitors. Since different individuals will be performing different activities at the same time, the initiation of a conflict will necessarily almost always be a unilateral decision by the attacker that interrupts the attackee. In a one-shot game, this can be interpreted as implying sequential decisions with the attackee reacting to being attacked (but see Dubois et al. 2003). We explore the consequences of decision sequence by comparing a sequential and a simultaneous version of our model.

The second consequence of the gradual nature of competition in our scenario is that there is no fixed payoff for winning a fight. The winner gains an advantage by chasing away the loser and thus increasing its own foraging rate due to a reduction in number of close-by competitors (Davies and Houston 1981). This effect increases with decreasing distance between opponents. Therefore, we compare a "classical" Hawk–Dove game with mixed strategies with a situation where individuals decide whether to attack based on distance to the opponent. While winning a fight for a single resource item implies gaining control of that item, this is not the case for fights over access to local resources. How much the winner of a fight gains from chasing away a competitor, therefore, also depends on how far the loser runs after the fight. The length of this flight distance and whether it can be controlled by the winner or the loser will depend on details of the species and the actual mechanics of interactions during a fight. As these details are beyond the scope of our study, we investigate 2 simple cases. In the first model, variant losers are chased until the winner cannot detect them anymore. In the second variant, we assume that losers are in control and that flight distance is a part of their strategy.

Since the presence of asymmetries has been shown to potentially significantly affect which strategies evolve in conflicts (Maynard Smith and Parker 1976; Eshel 2005), we will compare versions of our model with and without asymmetries. Finally, we investigate the effects of population density, resource clumpedness, and fighting costs, which previously have been shown to be important factors in the evolution of aggressiveness (Maher and Lott 2000; Morrell and Kokko 2005).

BASIC MODEL

As explained in the Introduction, payoffs of winning a fight are in reality determined by distance to the opponent, local resource density, and dynamics as well as the number of close-by competitors. These factors are in turn not independent but interact by means of the individuals' foraging and fighting behavior (Hixon 1980; Waser 1981; Possingham 1989). The fitness consequences of attacking a competitor, therefore, depend nontrivially on interactions between the population strategy and properties of the local ecology (see Houston and McNamara 2006). Although it might be possible to find a higher level approximation, the easiest way to account for the spatial heterogeneity of resources and the emergent nature of payoffs as well as the aforementioned fine-grained temporal structure of individual decisions in a model is by using a mechanistic approach. We, therefore, use a detailed individual-based model where position and movement of individuals as well as current local amount and rate of replacement of resources are explicitly represented.

For the sake of clarity, we will throughout the model description use fictive physical units to quantify distances (distance unit, DU), durations (time unit, TU), movement speed (*DU/TU*), and energy (energy unit, EU).

If no real-world system serves as a template, there is no obvious, easy way to choose the parameters of a detailed simulation model. We decided to set energy content of a resource item, movement speed, and resource visibility to unity. Given the technical limits to number of resource items and population size that we could simulate, this let us infer "reasonable" values for world size as well as energy consumption during movement. Similarly, the maximum range within which competitors can be detected was selected to keep the frequency of encounters between individuals technically manageable. Preliminary simulations showed that the durations of the individuals' activities strongly affect effective fighting costs. We adjusted these durations so that effects of the model parameters would not be masked by high effective fighting costs.

The simulation program has been implemented in C++ under GNU/Linux. Its source code is available online (Dryad repository: http://dx.doi.org/10.5061/dryad.2p75f) or from the authors on request.

Table 1
Evolving traits and their initial values

Model	Trait	Initial value	Role-dependence
All	*μ*	3	—
	min	1 DU	—
	f	1	—
Basic model	*aggressiveness*	0	No, yes
Distance model	*critical distance*	0 DU	No, yes
Sequential model	*critical distance*	0 DU	Only attacker
	aggressiveness	0	Only attackee

Evolution and ecology

We assume haploid nonsexually reproducing individuals. Following the phenotypic gambit, individuals' genes in our model are direct representations of their phenotypic traits (Grafen 1984). During reproduction, each evolving trait (see Table 1) has a probability of 0.01 to mutate. Mutation step sizes are normally distributed with a mean of 0 and a standard deviation of 0.1.

In our simulation, all individuals are born at the same time. After interacting for 5000 TU, their energy store is calculated as the sum of the energy content of all resources collected minus movement and fighting costs. Then, an offspring population is created with the probability of a parent to reproduce being proportional to its energy store. The offspring population subsequently replaces the parent population.

Individuals live in a square world with a size of 200 DU. To avoid edge effects, periodic boundary conditions are assumed (i.e. opposite edges are connected leading to a toroidal shape).

Resources

Resources are discrete items with a fixed energy content of 1 EU. At the beginning of the simulation, the landscape is seeded with 50 000 resource items. Consumed resource items are added back to the landscape at a random location subject to the resources' spatial distribution. In this way, we can study the effects of exploitation competition between individuals (through local depletion) while preventing global depletion and thus excluding additional effects from general resource availability. Preliminary simulations showed that the effective foraging range of individuals (as determined by movement speed and visibility of resources) was low enough to warrant local depletion of resources (see also Supplementary Figure S1).

Next to uniformly distributed resources, we investigated 2 different scenarios of spatially correlated resource distribution (see Supplementary Figure S1). To produce *clumped* resources, a heightmap with a given Hurst exponent is generated using the midpoint displacement method (Fournier et al. 1982). The probability of a resource item to end up at a given point in space is then proportional to that point's elevation.

A *patchy* resource distribution is generated by only placing resources in 40 randomly located circular patches of radius 5 DU.

Individual behavior

Each individual is at any time performing one out of a set of possible different activities (see Figure 1). Activities have a specific fixed duration after which the individual immediately starts the next activity. As there is no global time step, start and end of the individuals' activities are entirely asynchronous. Some activities can, however, be interrupted by contests with competitors (see Conflicts and fighting).

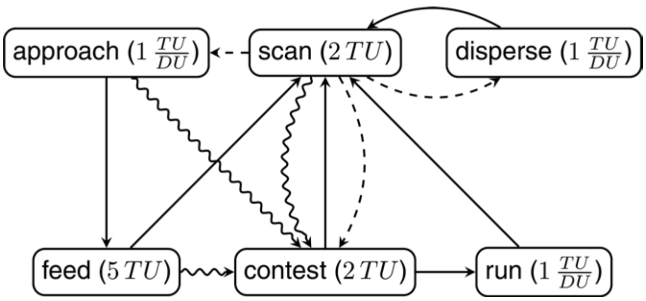

Figure 1
All activities available to individuals with durations and possible transitions between them. Dashed lines indicate alternative choices. Only the transition to the "contest" state that can follow a challenge by a competitor can interrupt the current activity before it is finished (snaked lines).

The activities available to individuals are *disperse, scan, approach, feed, contest,* or *run*. Dispersing individuals perform a long range movement between different locations. After arrival, they scan their surroundings for resources and competitors (see Supplementary Material for algorithm in pseudo-code). If an individual finds no resource (within a radius of 1 DU) during its scan, it disperses again. If food is found, it stays and starts a conflict with each competitor within detection range (5 DU). If a conflict escalates, both participants start a contest (the challengee aborts its current activity for this). After a contest, the winner starts to scan again, whereas the loser runs. Running losers go back to scanning after having arrived at their destination. A scanning individual that has found a resource and has not become involved in any contests with competitors starts to approach the resource by moving to its location at normal speed (see Movement) and starts to feed on it after arrival.

Movement

For the sake of simplicity, we assume that all types of movement (i.e. dispersal, approaching, running) are performed at the same speed (1 DU/TU) and carry the same (distance-dependent) energy costs of 0.1 EU/DU (see Figure 1).

Although dispersal behavior will certainly have a strong impact on local population density, and thus strength of competition between individuals, it is not in the center of our interest. To avoid bias in our results, we, therefore, attempt to let dispersing individuals move optimal for a given resource distribution. This in itself is not a trivial problem by any means; however, it has been shown that movement into a random direction with distance following a Lévy distribution (a so-called Lévy walk) optimizes search efficiency of foraging animals under many circumstances (Viswanathan et al. 1999). Given a probability distribution of movement lengths $P(l) = Cl^{-\mu}$ with $l \in [m, \infty[$, we let the distribution's parameters μ and *m* evolve so that the actual movement behavior will adapt to the resource settings (see Table 1). Dispersal distances are limited to world size (200 DU).

Feeding

As soon as an individual starts feeding on a resource item, the item disappears. If the individual finishes feeding without being interrupted, it receives the energy value of the resource.

Conflicts and fighting

A scanning individual starts a conflict with each competitor within a detection range of 5 DU that is currently not running, in a contest or dispersing (and therefore has to be scanning, approaching, or feeding, see Figure 1 and Supplementary Material for algorithm in pseudo-code). If there is more than one competitor present, conflicts are resolved in random order.

A conflict consists of a simple game with simultaneous moves similar to the original Hawk–Dove game (Maynard Smith and Price 1973). Both participants simultaneously choose whether to remain peaceful or to escalate, resulting in 3 possible different outcomes—both peaceful; both aggressive; one peaceful, one aggressive. If both individuals decide to be peaceful, nothing happens and both continue with their respective activities. We define a contest as an interaction in which at least one individual is aggressive. Contests abort the previous activities of both participants. An escalated fight (i.e. both opt for aggressive behavior) in addition results in fighting costs for both individuals.

Peaceful individuals interacting with aggressive ones automatically lose the contest, whereas the winner in an escalated fight is determined at random. After the contest, the winner starts to scan again, whereas the loser runs away. A running individual moves in the opposite direction of its opponent until the distance between the 2 individuals is equal to its (the loser's) flight distance *f*. A description of the algorithm in pseudo-code can be found in the Supplementary Material.

Strategies

In the basic model, the conflict strategy of an individual consists of a simple probability to escalate during an interaction (trait *aggressiveness*, see Table 1). In addition, we also investigated the effects of the existence of an asymmetry during conflicts on the evolution of defense by making aggressiveness role-dependent in some scenarios (see Table 1). An asymmetry in this context can be thought of as any difference between individuals that can be perceived by both participants such as differences in coloration, size, or ownership status. As first shown by Maynard Smith and Parker (1976), the existence of any such asymmetry—even if it has no direct effect on fighting ability or resource value—can lead to the evolution of role-dependent strategies that can greatly reduce the occurrence of escalated fights. In a scenario with asymmetry, both participants in a contest get one of the 2 roles—*A* or *B*—assigned at random. Individuals then base their behavior on the respective role. This is accomplished by having 2 independent versions of the trait aggressiveness (instead of one), each corresponding to one of the two roles.

Evolutionary stability of a strategy does not necessarily imply that it can easily evolve (Geritz et al. 1998). Therefore, we make the conservative assumption that the ancestral state is entirely nonaggressive.

Parameters

We varied asymmetry scenario, loser behavior, population density, clumpedness of resources, and fighting costs (see Table 2). In the high population density scenarios, computation time became a constraint. Therefore, in these scenarios, we kept number of individuals at 1000 (instead of 4000) and instead reduced world size to a quarter (i.e. to 100 × 100 DU) together with number of patches (where applicable) and number of resources. Results from preliminary simulations suggested that running 10 replicates over 10 000 time steps each is sufficient to reliably infer the evolutionary equilibrium state.

Table 2
Model parameters

Fighting costs (EU)	0; 0.1; 1; 10
Population density [$1/(200\ \mathrm{DU})^2$]	250; 1000; 4000
Resource distribution	Uniform; clumped; patchy
Loser behavior	*f* = *visibility*; *f* evolving
Roles	No; random

Results

Our scenarios differ with respect to number and meaning of traits evolving (see Table 1). It is, therefore, inconvenient to compare their outcomes based on trait values alone. Since we are primarily interested in the resulting behavior during conflicts, we instead focus on the probability that a conflict ends with a specific kind of outcome, as inferred from the population mean trait values. Specifically, we distinguish 2 outcomes—*contest*, that is, at least one of the participants behaves aggressively and *fight*, that is, both participants behave aggressively. The occurrence of contests reflects the general willingness to defend resources, whereas deviations of the frequencies of escalated fights from the expected square of the frequencies of contests allow us to detect the evolution of role-dependent (e.g. Bourgeois-like) conflict resolution strategies. The results for uniform and clumped resource distribution were nearly identical; therefore, only results for uniform and patchy resources are shown.

In the basic model, contests do only occur in scenarios with patchy resources, otherwise aggressiveness stays close to 0 (i.e. individuals are always peaceful). If there is no asymmetry between contestants, individuals furthermore are less aggressive for high fighting costs and high population densities even if resources are patchily distributed (see Figure 2).

Introducing an asymmetry leads to the evolution of aggressive behavior for all fighting costs. However, under high fighting costs, role-dependent strategies with one aggressive and one peaceful role emerge so that contests rarely escalate (Figure 3).

Letting losers choose flight distance reverses the effect of resource distribution (Figure 3, bottom row): For patchily distributed resources, losers remain clear within detection range after a fight (Supplementary Figure S2), which leads to the disappearance of aggressiveness. For uniform resource distribution and low and medium population density, high flight distances evolve that in turn enable resource defense.

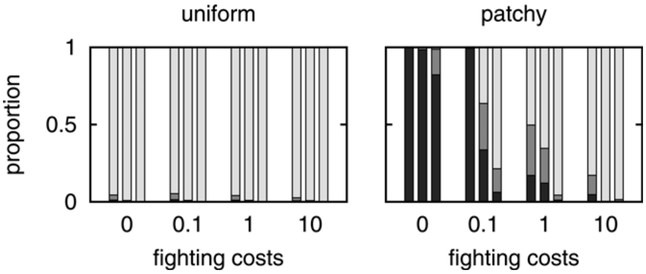

Figure 2
Evolved proportions of conflict outcomes (white: peaceful; light gray: contest; dark gray: escalated fights) in model 1 without role asymmetries and with fixed flight distance. Positions within a group of bars correspond to population density. Aggression only evolves for patchy resources (right) and decreases with fighting costs and population density.

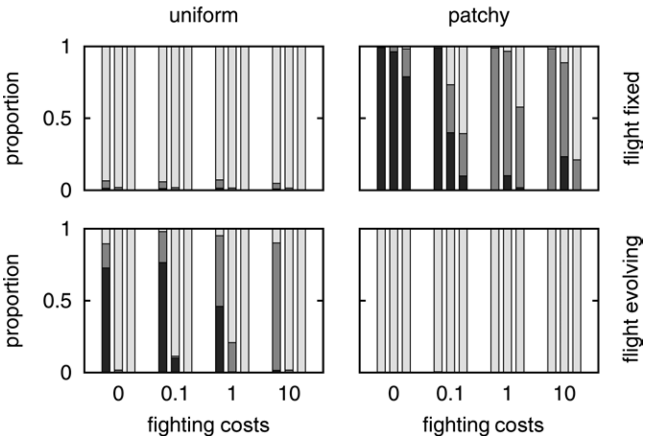

Figure 3
Evolved proportions of conflict outcomes (white: peaceful; light gray: contest; dark gray: escalated fights) in model 1 with asymmetric interactions for different resource distribution (left: uniform; right: patchy) and loser behavior (above: fixed flight distance; below: evolving flight distance). Positions within a group of bars correspond to population density. For high fighting costs, escalated fights are rare, therefore conventional conflict resolution evolves. Letting losers choose how far to run after a contest reverses the effect of resource distribution.

MODEL 2—CRITICAL DISTANCE

In the second model, individuals determine their behavior during a conflict based on their distance to the opponent. The trait aggressiveness is, therefore, replaced by critical distance, which can also be role-dependent. Individuals only escalate conflicts if their opponent is closer than their own critical distance.

For scenarios without asymmetry population mean critical distance gives a rough measure of the likelihood of escalated fights versus peaceful resolution. If there is asymmetry, minimum and maximum of the (population means of the) 2 critical distances corresponding to the 2 roles are roughly equivalent to *p(fight)* and *p(contest)*: Only encounters at distances below maximum distance lead to contests, which escalate to fights if the distance is below minimum distance.

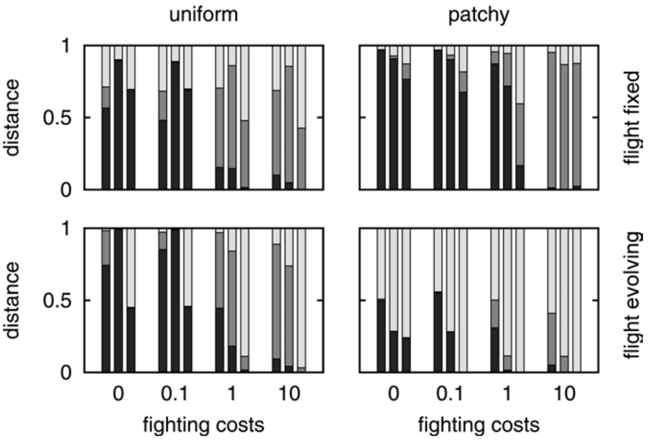

Figure 4
Evolved contest outcomes dependent on distance (white: peaceful; light gray: contest; dark gray: escalated fights) in model 2 with asymmetric interactions for different resource distributions (left: uniform; right: patchy) and loser behavior (above: fixed flight distance; below: evolving flight distance). Positions within a group of bars correspond to population density. Defense evolves for patchy as well as uniform resource distribution. As before, the effect of resource distribution on critical distance depends (albeit to a lesser degree) on whether loser behavior is fixed or not.

In all graphs, values are given relative to the fixed detection range (5 DU).

Results

The existence of a role asymmetry has similar effects in model 2 as in model 1. For the sake of conciseness, we will, therefore, only discuss the asymmetric case, which we consider the more realistic one (see Eshel 2005).

Although critical distance is generally lower for nonpatchy resources, the differences between patchy and uniform resource distribution are much less pronounced for distance-dependent behavior than in model 1 (Figure 4, top row). For both resource distributions, only opponents that are close to the edge of the detection range are not attacked. For high fighting costs, role-dependent strategies evolve with individuals in one role having a high critical distance and thus attacking and those in the other role having a low critical distance and thus retreating most of the time.

As in model 1, the effect of giving losers control over flight distance depends on resource distribution. For uniform resources, evolving flight distance slightly increases critical distances, whereas for patchy resources, the values are significantly reduced. In both cases, a strong effect of population size appears.

MODEL 3—CRITICAL DISTANCE, SEQUENTIAL DECISIONS

In the third submodel, we assumed decisions to take place in sequence: First, the challenger decides whether to attack. If it does not, no encounter takes place. As opposed to models 1 and 2, challengers can, therefore, unilaterally avoid conflicts. Only if the challenger does attack is the challengee required to decide whether it retaliates. Note that this implies the existence of a correlated asymmetry (Maynard Smith and Parker 1976) between challenger and challengee. We again let the challenger choose its behavior based on distance to the opponent, whereas the challengee's reaction is described by a simple probability.

Results

If individuals are given the option to avoid entering a conflict, they do so, in particular for patchy resources, except if fighting costs are very high or population density is low (see Figure 5, top row).

Letting flight distance evolve only has an effect if resources are patchily distributed (Figure 5, right column). In this case, flexible loser behavior causes conflicts to be initiated even for moderate fighting costs.

INTERPRETATION

Comparing the results between scenarios can give us some insight concerning the underlying mechanisms. In general, as long as loser behavior is fixed, patchy resources seem to lead to either higher aggressiveness or a higher critical distance. This can be explained by the fact that although fighting costs as such are similar for all resource distributions, losing a contest when resources are patchily distributed can mean being expelled from a resource patch (see Supplementary Figure S1).

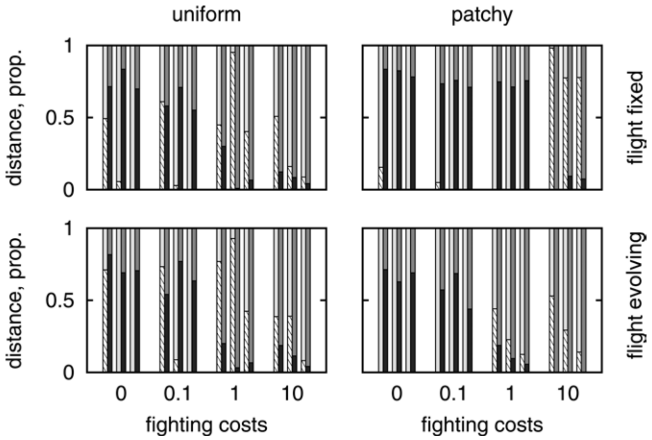

Figure 5
Evolved contest behavior in model 3 for different resource distribution (left: uniform; right: patchy) and loser behavior (above: fixed; below: evolving). Distances above the challengers critical distance (left bar: white area) lead to peaceful resolution. For closer distances (hatched area), challengee aggressiveness (right bar) determines whether a contest (light gray) or an escalated fight (dark gray) takes place. Positions within a group of bars correspond to population density. For low fighting costs, individuals rarely enter conflicts. For high fighting costs, challengers attack close-by competitors who back down in most cases. Patchiness and loser behavior have only little effect.

If conflicts cannot be avoided by the participants (models 1 and 2), there is, therefore, a strong incentive for attempting to win a potential contest and thus to be aggressive. Letting losers decide how far to run negates this effect because the low flight distance that evolves (see Supplementary Figure S2) strongly reduces the costs of losing a contest. Furthermore, if losers move only a small distance, the benefit of winning is low. In this case, losing a potential contest, therefore, becomes cheaper than risking a costly escalation for a low payoff and aggressiveness remains low. If decisions are sequential on the other hand (model 3), conflicts can be avoided altogether no matter which costs losing implies.

For uniform resource distribution, in contrast, individuals remain peaceful in model 1. This indicates that the additional costs resulting from aggressive behavior (foraging time lost by entering a contest and potential fighting costs) outweigh the benefits of driving away competitors and avoiding to lose contests. This holds even if the presence of an asymmetry would allow individuals to avoid escalated fights and thus would reduce the costs of contests to the time spent on them. The situation changes if flight distance evolves. Since resources occur everywhere (see Supplementary Figure S1), it pays to attempt to avoid conspecifics altogether by running a long distance, which again makes attacking competitors worthwhile at least for low population density.

The high level of aggressiveness evolving in the scenario where individuals use a critical distance to determine their behavior (model 2) during a conflict can be explained by a combination of 2 factors. First, individuals can choose only to be aggressive if competitors are close enough to affect them, which makes aggressive behavior cheaper in general. Second, an individual that increases its aggressiveness in model 1 reduces the likelihood of the outcomes losing and peace and increases the proportion of winning and escalate for all its encounters thus creating a tradeoff between different options. In contrast to that, an individual that increases its critical distance effectively only changes the outcome of all encounters with a distance larger than the population's critical distance but lower than its own and only changes them from peaceful to winning, which is usually beneficial.

If decisions happen in sequence on the other hand, the only options for a challengee are to escalate the contest to a fight or to run away because the challenger has already committed to being aggressive. Running can be the cheaper option for the challengee under a number of circumstances—if costs of running away are low due either to uniform resource distribution or to evolving flight distance or if fighting costs are high. In these cases, challengees opt for peaceful behavior, which in turn makes starting a contest affordable for the challenger (see Figure 5).

DISCUSSION

Our results show that defense of local resources can indeed evolve from a peaceful ancestral population, that the mechanisms involved, however, vary considerably and are only in specific cases comparable to the defense of single resource items. Combinations of resource distribution and constraints on the strategy space within which the individuals' decisions take place lead to strong variations not only in effective costs of conflicts but also of the relative costs of the different outcomes conflicts can have. Therefore, details of the model assumptions determine whether and why conflicts and contests for access to local resources evolve.

Evolution of defense

We see that competition for a local resource pool—as opposed to competition for resource items—can indeed lead to conflicts and fights, albeit for reasons that vary between scenarios. If resources occur in patches, individuals defend their position within the patch. If only aggressiveness evolves, this effectively results in a classical Hawk–Dove(-Bourgeois) game (Maynard Smith and Parker 1976) with the option to stay in the patch being the payoff of winning a contest. For uniform resource distribution and if behavior depends on distance, individuals defend local resources against depletion by competitors as described by Brown (1964) or Schoener (1983). If critical distance evolves and the decisions of contestants are made simultaneously, the size of defended areas escalates. This is similar to the "spiteful" territory sizes seen by Parker and Knowlton (1980).

One of the most important components in our model turned out to be the behavior of the loser after the contest, that is, whether it can control how far it runs away from the winner. This is not surprising insofar as flight distance directly determines the benefit of winning a contest. In previous studies on contests over resources this effect has not been found largely due to the fact that under the assumption that contested resources are immediately consumed by the winner loser behavior is indeed not relevant. This study as well as previous studies on the defense of territories (Switzer et al. 2001; Morrell and Kokko 2003; Hinsch and Komdeur 2010), however, suggest that for certain types of resources and situations, it is crucial to consider how much future control the winner of a contest can exert over the contested resource.

It has been argued that due to their better defendability especially clumped resources should be conducive to the evolution of territoriality (Maher and Lott 2000). In contrast to that, recent studies show that territorial behavior can evolve for uniform resource distribution (Adler and Gordon 2003; Morrell and Kokko 2005), however, only if it is assumed that individuals attack conspecifics on encounter. Our results give an explanation for the occurrence of aggression in these cases and thus indicate how territorial behavior might evolve even if resources are not defendable in the strict sense (see Brown 1964).

At this point, we can only show that individuals attack nearby conspecifics if this is their only way of protecting their resources. By letting individuals choose between defense of resource items and defense of local resource level, further insights could be gained into the conditions under which we would expect one or the other to evolve. In particular, it would be interesting to systematically investigate the effect of resource properties (beyond spatial distribution) such as graininess, predictability, size, or handling time that have been empirically shown to influence resource defense (see Maher and Lott 2000).

Finally, while we restrict ourselves to competition for food in our study in order to keep an already complex model manageable, it is well known that animals compete for other spatially distributed resources such as mates, resting sites, or shelter from predators (Maher and Lott 2000). Since some of these resources show very different properties from food, it would be interesting to extend our approach to include additional factors that might affect defense of space.

Which is the “correct” model?

Simple abstract models tend to be amenable to ambiguity, which allows for differing interpretations of the same model (Eshel 2005). Parts of this ambiguity can be avoided by embedding the model in a “realistic” ecological context and by increasing the level of detail, thus giving a mechanistic interpretation to some of the model’s parameters (Bolker et al. 1997; Łomnicki 1999; Houston and McNamara 2006). On the other hand, this often opens up several alternative ways to represent the same abstract mechanism in a more detailed way. In our case, we ended up with 3 different models for the interactions of individuals with several variants each.

Our 3 submodels only differ in how individuals decide whether to enter a contest and when to be aggressive during a contest. These differences are relatively subtle, yet lead to vastly different outcomes. The exact structure of a conflict, that is, the sequence of decisions and the information available to participants at each point, therefore, is of crucial importance. Although it is not a new insight that the choice of strategy space can determine which behavior evolves in a model (see e.g. Hurd and Enquist 1998; van Doorn et al. 2003a; Dubois and Giraldeau 2007), this effect is usually disregarded in studies on animal contests and deserves to be emphasized.

It is difficult to decide which of the versions of the model is “correct”. It has been argued before that the symmetrical structure of the classical Hawk–Dove game for example does not capture how real conflicts between animals take place and that in particular the decision to appropriate a resource should be separate from the decision how to behave during a potential conflict (Grafen 1987; Dubois and Giraldeau 2005). Our model supports the relevance of this claim insofar as it shows that the choice of conflict structure can make for considerably different outcomes.

Although there is obviously no clear owner–intruder asymmetry in a situation where individuals compete through exploitation (as long as there are no territories), it seems plausible to assume that starting a conflict is a unilateral decision by one individual aiming to chase away a competitor. Furthermore, because distance determines the effect of depletion by a competitor on a focal individual, it seems natural for that individual to base conflict behavior on the distance to the opponent. A more detailed analysis pitting strategies of varying complexity against each other (see van Doorn et al. 2003b) is, however, needed to confirm these intuitions.

Whether individuals could control their own flight distance turned out to be an important factor in our model. A model where contests themselves are not a black box—as in our and most other models of conflicts over resources—but are resolved into microscopic interaction steps (see e.g. Matsumura and Hayden 2006; Számadó 2008) would be however required to determine under which circumstances this is a realistic assumption. The spatially and temporally explicit nature of our modeling framework would easily allow for this increased level of detail.

Next to strategic effects, under which circumstances individuals can decide to attack others and which information they take into account could also be constrained by the physiology of the species (sensory and cognitive capabilities) and the properties of its habitat and the contested resources (visibility, does feeding impair vision, can feeding be interrupted, etc.). An even more mechanistic approach taking into account physiological and physical details might be required to gain a better understanding of these constraints (McNamara and Houston 2009).

SUPPLEMENTARY MATERIAL

Supplementary Material can be found at http://www.beheco.oxfordjournals.org/

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