Why do animals have territories?
Hinsch, Martin

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2017

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
3 Evolution of defense against depletion of local food resources in a mechanistic foraging model

Martin Hinsch · Jan Komdeur · Ido Pen

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 non-aggressive 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 can not avoid 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.

Behavioral Ecology 24 (1), 245-252
3 Evolution of defense against depletion

3.1 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 & 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; Gintis, 2007; Broom & Rychtář, 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 & 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 & Dill, 2003; Alwany et al., 2005; birds competing for flowers containing nectar: Gill & Wolf, 1975; or for insects: Davies & 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 & Krishnan, 1999; Adler & Gordon, 2003; Morrell & 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.
3.1 Introduction

depending on ecological and behavioral parameters such as fighting costs, frequency of intrusion and resource properties (e.g. Schoener, 1983, 1987; López-Sepulcre & Kokko, 2005; reviewed by Adams, 2001). 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 & Komdeur, 2010).

An intermediate position between models on contests for resource items and fights against depletion is taken by studies 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 & Giraldeau, 2003, 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 favour 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, can not easily be transferred from earlier models of direct competition. To explore to which degree the results are affected by this we compare three 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 & Ruxton, 2003). In most models these conflicts are therefore appropriately approximated as discrete interactions with fixed payoffs.

Exploitation competition, in contrast, occurs between two 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 two 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 attacker. In a one-shot game this can be interpreted as implying sequential decisions with the attacker reacting to being attacked (but see Dubois & Giraldeau, 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 & Houston, 1981). This increase is higher the closer the distance between opponents. We therefore 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. Since these details are beyond the scope of our study we investigate two simple cases. In the first model variant losers are chased until the winner can not 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 & Parker,
3.2 Basic Model

As explained above 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 non-trivially on interactions between the population strategy and properties of the local ecology (see Houston & 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 ($\frac{DU}{TU}$) 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/...
3 Evolution of defense against depletion

dryad.2p75f) or from the authors on request.

**Evolution and ecology**

We assume haploid non-sexually 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 3.1) 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 5,000 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 fig. S1 in the supplementary material).

Next to uniformly distributed resources we investigated two different scenarios of spatially correlated resource distribution (see fig. 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.
### 3.2 Basic Model

![Activity Graph]

**Figure 3.1:** 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).

#### Individual Behavior

Each individual is at any time performing one out of a set of possible different activities (see fig. 3.1). Activities have a specific fixed duration after which the individual immediately starts the next activity. Since 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 below).

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 below) 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 fig. 3.1).

While dispersal behavior certainly will 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 \( P(l) = C l^{-\mu} \) with \( l \in [m, \infty] \), we let the distribution's parameters \( \mu \) and \( m \) evolve so that the actual movement behavior will adapt to the resource settings (see table 3.1). 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 fig. 3.1 and pseudo-code in the supplementary material). 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 & Price, 1973). Both participants simultaneously choose whether to remain peaceful or to escalate, resulting in three 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
3.2 Basic Model

(i.e. both opt for aggressive behaviour) 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 two 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 3.1). 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 3.1). An asymmetry in this context can be thought of as any difference between individuals that can be perceived by both participants such as e.g. differences in coloration, size or ownership status. As first shown by Maynard Smith & 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 two roles - A or B - assigned at random. Individuals then base their behavior on the respective role. This is accomplished by having two 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). We therefore make the conservative assumption that the ancestral state is entirely non-aggressive.

**Parameters**

We varied asymmetry scenario, loser behavior, population density, clumpedness of resources and fighting costs (see table 3.2). In the high population density scenarios computation time became a constraint. In these scenarios we therefore kept number of individuals at 1,000 (instead of 4,000) and instead reduced world size to a quarter (i.e. to 100x100 DU) together with number of patches (where applicable) and number of resources. Re-
3 Evolution of defense against depletion

Table 3.1: Evolving traits and their initial values

<table>
<thead>
<tr>
<th>model</th>
<th>trait</th>
<th>initial value</th>
<th>role-dependence</th>
</tr>
</thead>
<tbody>
<tr>
<td>basic model</td>
<td>aggressiveness</td>
<td>0</td>
<td>no, yes</td>
</tr>
<tr>
<td>distance model</td>
<td>critical distance</td>
<td>0 DU</td>
<td>no, yes</td>
</tr>
<tr>
<td>sequential model</td>
<td>critical distance</td>
<td>0 DU</td>
<td>only attacker</td>
</tr>
<tr>
<td></td>
<td>aggressiveness</td>
<td>0</td>
<td>only attackee</td>
</tr>
</tbody>
</table>

Table 3.2: Model parameters

<table>
<thead>
<tr>
<th>parameter</th>
<th>values</th>
</tr>
</thead>
<tbody>
<tr>
<td>fighting costs ([EU])</td>
<td>0; 0.1; 1; 10</td>
</tr>
<tr>
<td>population density ([1/(200DU)^2])</td>
<td>250; 1,000; 4,000</td>
</tr>
<tr>
<td>resource distribution</td>
<td>uniform; clumped; patchy</td>
</tr>
<tr>
<td>loser behavior</td>
<td>f = visibility; f evolving</td>
</tr>
<tr>
<td>roles</td>
<td>no; random</td>
</tr>
</tbody>
</table>

Results from preliminary simulations suggested that running 10 replicates over 10,000 time steps are sufficient to reliably infer the evolutionary equilibrium state.

Results

Our scenarios differ with respect to number and meaning of traits evolving (see table 3.1). 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 use as a response variable the probability that a conflict ends with a specific kind of outcome, as inferred from the population mean trait values. Specifically we distinguish two outcomes - contest, i.e. at least one of the participants behaves aggressively and fight, i.e. both participants behave aggressively. The occurrence of contests reflects the general willingness to defend resources while 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.
3.2 Basic Model

Figure 3.2: 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 3.3: 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.
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 fig. 3.2).

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 (fig. 3.3).

Letting losers choose flight distance reverses the effect of resource distribution (fig. 3.3, bottom row): For patchily distributed resources losers remain clear within detection range after a fight (fig. S2 in the supplemental material) 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.

### 3.3 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) two critical distances corresponding to the two roles are roughly equivalent to $p(\text{fight})$ and $p(\text{contest})$: Only encounters at distances below maximum distance lead to contest which escalate to fights if the distance is below minimum distance.

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).

While critical distance is generally lower for non-patchy resources the differences between patchy and uniform resource distribution are much less
Figure 3.4: 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.
pronounced for distance-dependent behavior than in model 1 (fig. 3.4, 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 while for patchy resources the values are significantly reduced. In both cases a strong effect of population size appears.

3.4 Model 3 - critical distance, sequential decisions

In the third sub-model 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 (sensu Maynard Smith & 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 fig. 3.5, top row).

Letting flight distance evolve only has an effect if resources are patchily distributed (fig. 3.5, right column). In this case flexible loser behavior causes conflicts to be initiated even for moderate fighting costs.

3.5 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
3.5 Interpretation

Figure 3.5: Evolved contest behaviour 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.
Evolution of defense against depletion

critical distance. This can be explained by the fact that while 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 fig. S1 in the supplementary material).

If conflicts can not be avoided by the participants (models 1, 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 since the low flight distance that evolves (see fig. S2 in the supplementary material) 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 fig. 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 two 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 since 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 fig. 3.5).

3.6 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 & 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 & Knowlton (1980).

One of the most important components in our model turned out to be the behavior of the loser after the contest, i.e. 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. Ours as well as previous studies on the defense of territories (Switzer et al., 2001; Morrell & Kokko, 2003; Hinsch & Komdeur, 2010), however, suggest that for certain
3 Evolution of defense against depletion

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 &
Lott, 2000). In contrast to that recent studies show that territorial behavior
can evolve for uniform resource distribution (Adler & Gordon, 2003; Morrell
& 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 individu-
als 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 interest-
ing 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
& 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 & Lott, 2000). Since some of
these resources show very different properties from food it would be inter-
esting 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 am-
biguity can be avoided by embedding the model in a “realistic” ecological
context and by increasing the level of detail, thus giving a mechanistic inter-
pretation to some of the model’s parameters (Bolker & Deutschman, 1997;
Lomnicki, 1999; Houston & McNamara, 2006). On the other hand this often
opens up several alternative ways to represent the same abstract mecha-
nism in a more detailed way. In our case we ended up with three different
models for the interactions of individuals with several variants each.

Our three sub-models only differ in how individuals decide whether to en-
Discussion

3.6 Discussion

These differences are relatively subtle yet lead to vastly different outcomes. The exact structure of a conflict - i.e. the sequence of decisions and the information available to participants at each point therefore is of crucial importance. While it is not a new insight that the choice of strategy space can determine which behavior evolves in a model (see e.g. Hurd & Enquist, 1998; Van Doorn et al., 2003b; Dubois & 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 & 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.

While 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 individuals aiming to chase away a competitor. Furthermore, since 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 & 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 con-
3 Evolution of defense against depletion

straints (McNamara & Houston, 2009).

Acknowledgements

The authors would like to thank Franz J. Weissing and two anonymous reviewers for insightful comments on an earlier version of the manuscript.
Supplementary data

Figure 3.6: Examples of uniform, clumped and patchy resource distribution (grey dots and density isoclines) with the corresponding distribution of individuals (black dots) after 10,000 generations (model 3, 1000 individuals, constant flight distance).
3 Evolution of defense against depletion

Figure 3.7: Evolved relative flight distance $f$ in model 1 to 3 plotted over population densities for different resource distributions (left - uniform, right - patchy). The dashed line indicates detection range. For patchy resources flight distance always stays far below visibility. For uniform resource distribution distances are considerably higher and decrease with population density.

**control flow - top level**

for 10,000 generations:
  landscape setup
  for 5,000 TU:
   individuals interact
   reproduction, mutation

**control flow - scanning**

wait 2 s
if resource visible (1 DU):
  for all visible (5 DU) neighbours n:
   if n not running, dispersing, contest:
     conflict with n
   if no conflicts or all conflicts peaceful:
     start approaching resource
else:
  start dispersing

**control flow - conflict**

a : focal, n : neighbour

if role-dependence:
  a, n get random role
a, n choose action
if a peaceful:
  if model 3 or n peaceful:
    nothing happens
else:
n interrupts current activity
both wait 2 TU
if both escalate:
    both pay fighting costs
determine winner
loser starts running
winner starts scanning