Why do animals have territories?
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7 General discussion

In the following I will come back to the main questions set out in the introduction and discuss the contributions this thesis has made to answering them.

7.1 What is territoriality?

As laid out in the introduction a single accepted definition of territoriality is missing. This thesis obviously does and can not change that. The results put forth do however provide some insight into why this is such a difficult question and how progress might be made in the future.

Chapter 2 introduces the definition of territoriality that is used - explicitly or implicitly - throughout the thesis: territoriality means individuals defend space against conspecifics that compete for it. However, as is shown in the same chapter, this definition - albeit more specific than many existing ones - is unexpectedly ambiguous. On closer examination it turns out that defence of space comprises three very different types of conflicts between territory owners and intruders all of which have been called territory defence in the existing literature.

The remaining chapters further demonstrate the limits of the working definition. In chapter 3 it is shown that under certain conditions “defence” of local depletable resources can evolve. This defence, however, consists entirely of distance-dependent attacks on conspecifics that are in visible range and has no relation to the location and thus any kind of territory. In the strict sense of the working definition this kind of behaviour would therefore not be seen as territorial. On the other hand it is clearly more “spatial” than a straightforward defence of resource items and therefore seems to be situated somewhere in between resource defence and territoriality.

In chapter 4 a similar scenario is investigated but on a slightly higher level of abstraction. While in this case individuals associate a certain preference level with locations in space and thus can be thought of as having a notion of territory there is no concept of winning or losing a conflict. Instead interactions between individuals lead to two different flavours of outcomes that
individuals can use to determine whether to reduce or increase their preference for the specific location that the interaction took place at. Therefore, while there is a clear sense of inhabited area, individuals compete for space and exclusive use of space evolves in this model, defence in the strict sense does not take place. Leaving aside the problems with some of the assumptions of the model such as fixed interactions costs, the question remains whether this behaviour should be termed territorial or not.

In a similar notion chapter 6 demonstrates that the concept of defence is not as straightforward as it might appear. It is shown that under specific conditions completely ineffective defence that is costly for owner and intruder but does not prevent exploitation of the owner’s territory can be sufficient to maintain respect for ownership. In this case defence becomes equivalent with punishment.

We can see that what is commonly called territoriality is a combination of complex behaviours and that on the other hand there is a range of phenomena that show some aspects of territoriality but would not be captured by a strict definition of the term. Promising advances have been made to define specific aspects of conflicts over resources that connect territoriality with the wider field of resource defence theory (Strassmann & Queller, 2014; Hare et al., 2016). In the end it might therefore be useful to abandon the idea that there is a monolithic and well-delineated phenomenon that could be captured by the term ‘territoriality’ and instead attempt to see the various types of territorial behaviour as special cases of resource defence.

7.2 How do territories emerge?

Substantial progress has been made in recent years on the theoretical understanding of the mechanics of territory creation and maintenance (Giuggioli & Kenkre, 2014; Potts & Lewis, 2014). Since the focus of this thesis is on the evolutionary aspects of territoriality, however, it only contributes to this topic peripherally.

In chapter 4 the predictions of an evolutionary mechanistic model of territorial behaviour are tested. While the original work it is reimplementing (Morrell & Kokko, 2005) is clearly motivated by an attempt to model territorial behaviour based on first principles the results presented in chapter 4 show that some crucial aspects of the underlying processes that happen in nature are missing in the model. In some of the scenarios defence of space evolves, however, the space individuals inhabit ends up consisting of disjointed patches instead of a contiguous area. A promising follow-up of this
7.3 Why is territorial behaviour adaptive and how does it evolve?

This thesis contributes in a number of different ways to an evolutionary understanding of territoriality.

Evolution

It has been shown before that territorial partitioning of space can evolve in a non-territorial population if interactions between individuals are costly (Adler & Gordon, 2003; Morrell & Kokko, 2005) without however specifying how these costs come about. In chapter 3 we see that even without any spatial cognition individuals can evolve to defend local resources against depletion by competitors. This provides us with a mechanism for interaction costs and thus the origin of territoriality from first principles without having to make any additional assumptions. As an aside - these results interestingly also demonstrate that - contrary to previous assumptions (Stamps, 1994; Maher & Lott, 2000) - a clumped resource distribution does not seem to be a requirement for the evolution of defence of space.

The results presented in chapter 3 lead us to some important and interesting questions for future research. While the model that was used includes considerably more physical detail than most models on animal conflict, the actual interactions between animals are still handled in a rather abstract way. Similarly the various types of strategy spaces concerning the individuals’ behaviour during these interactions that have been investigated are chosen in a somewhat ad hoc manner (see Houston & McNamara, 2006;
Fawcett et al., 2012). While a model by definition is a simplification of a part of reality it is in no way clear or even easy to determine whether and to which degree the simplifications taken here are valid and how the inclusion of more details with respect to physics, physiology and cognition would affect the model results.

The second major new question has been mentioned before in this discussion and concerns the connection with previous models of (the evolution of) territorial behaviour. Given that we now know how the defence of resources within a certain distance of an individual can evolve, how do we get to the defence of resources at a certain location? Put differently, how do we close the gap between chapter 3 and chapter 4? A rigorous approach would make it necessary to model the emergence of spatial memory and cognition without assuming any of it (see Fagan et al., 2013). In my opinion this poses some serious challenges in terms of modelling technique as well as with respect to the question which scenarios would be required to make this development happen.

In general chapter 3 demonstrates that there is a large unexplored space between traditional resource defence models and the most mechanistic models of territoriality.

Chapter 4 confirms earlier results (Adler & Gordon, 2003; Morrell & Kokko, 2005) that, given costly interactions, it is adaptive for individuals to avoid sharing space and to maintain non-overlapping home ranges. Taking into account the results from chapter 3 this might be taken to suggest that there is a clear evolutionary path from competition for spatially homogeneous resources via defence against depletion to real territoriality. A closer look reveals, however, that there are a number of caveats and unresolved issues that make this conclusion less straightforward than it appears.

First of all, the results presented in chapter 4 show that which of the various end states evolves depends heavily on the initial conditions (for a similar effect see Van Doorn et al., 2003b,a). Evolution of territoriality from an entirely non-territorial state would therefore have to pass through one out of only a few specific intermediary stages in order to end up at a territorial end point. Then, as discussed before, defended, exclusive space as it evolves in the model in chapter 4 is not identical to “true” territoriality in the sense that there is no actual defence (that includes the possibility of choosing not to attack) and that in many cases non-contiguous home ranges emerge. Finally, the way benefits resulting from foraging and costs incurred from range overlap are calculated (following the implementation by Morrell & Kokko, 2005) are difficult to justify in terms of lower level processes. Before a more rigorous modelling effort has been made, great caution therefore has to be
applied when making far reaching conclusions from these results. A promising way towards a more rigorous model might be to translate the more mechanistic (but still manageably simple) feeding and conflict model from chapter 6 into a spatially explicit situation.

In general, however, the results of chapters 3 and 4 taken together provide the first steps towards an understanding of a possible path of the evolution of territoriality from a non-territorial ancestral state. More research is needed to find the right modelling approach to implement a full model of this process.

**Adaptiveness**

While the discussion about the conditions under which territorial behaviour can be adaptive goes as far back as Brown (1964)’s idea of economic defendability most of the contributions are based on the assumption that territory defence is primarily aimed at floaters looking for resources or territories (e.g. Schoener, 1987, see chapter 2). In chapter 5 the adaptiveness of defence against poaching neighbours is investigated for the first time. Surprisingly it turns out that under a large range of conditions it should pay for neighbours to steal resources which - together with stochastic effects - should lead to the slow erosion of territory defence in evolutionary time. This presents a major conundrum since poaching of resources appears to be rare in nature (e.g. Gill & Wolf, 1979). While it is possible that stealing by neighbours has been largely overlooked in empirical studies, territoriality obviously exists, putting the model results at odds with observations.

Chapter 6 shows that respect for ownership can vastly increase in evolutionary time if potential intruders are able to adjust their behaviour to the owners’ aggressiveness in individual time. This presents a potential solution to the problem posed by the results of chapter 5 especially since neighbours necessarily will have the best possible information on an owner’s aggressiveness in a given population (Akçay et al., 2009). Furthermore it shows that the range of scenarios in which defence of resources in general and defence of territories (in all senses as presented in chapter 2) in particular can be evolutionarily stable might be substantially bigger than expected. It therefore strongly suggests that any model of territoriality and of resource defence in general needs to take into account the effects of deterrence. In a more general sense the results demonstrate that punishment and defence can be seen as two points on the same continuum, thereby creating a connection between the two fields of evolution of cooperation and resource defence theory.
The next step forward from these specific results towards a greater understanding of the scenarios in which territorial behaviour can be adaptive will have to build on both of these models while taking into account the results from chapter 4 and keeping in mind the classification of conflicts as presented in chapter 2.

7.4 Future directions

This thesis makes a number of contributions concerning specific aspects of the mechanics, evolution and adaptiveness of territoriality. It also provides us with some general ideas concerning promising future directions for research.

Across the different chapters the results give us an indication of the most crucial aspects of territorial behaviour and the environment that it evolves in that will become important in future modelling efforts:

Many models of territoriality either do not include space at all (e.g. Hixon, 1980; Switzer et al., 2001; Sherratt & Mesterton-Gibbons, 2015) or only in a very implicit way (Parker & Knowlton, 1980; López-Sepulcre & Kokko, 2005). The results presented in chapter 3 and in particular the shortcomings of a non-mechanistic modelling effort as demonstrated in chapter 4 show that the “mechanics” of a territory can depend crucially on the movement of individuals in space as well as their perception of it.

Resources have often been treated as static payoffs in models of territoriality (e.g. McNamara & Merad, 1991; Morrell & Kokko, 2005; Mesterton-Gibbons & Sherratt, 2014; but see Lewis & Moorcroft, 2001; Pereira et al., 2003). As chapters 3 and 5 demonstrate the temporal and spatial dynamics of resources can be of critical importance in some scenarios. This will notably be the case if individuals compete for mates instead of food resources.

In nearly all theoretical studies on territoriality the interactions between individuals during encounters are treated as a black box that simply produces an outcome in terms of e.g. win/lose. Results from other areas of resource defence theory indicate that (agonistic) encounters can be complicated, however, and that details such as sequence of action, knowledge of the participants or the physics of interactions are often crucial in determining the outcome (e.g. Van Doorn et al., 2003b; McNamara, 2006; van Lieshout & Elgar, 2011; Gilroy & Hantula, 2016). Chapters 3 and 6 similarly show that details of the interactions between individuals can have substantial consequences for the evolution of other aspects of behaviour in models of territoriality.
7.5 Concluding remarks

By definition simplification is a necessary part of building a model. Only by leaving out details is it possible to make a model and its results understandable and to isolate the relevant mechanisms that produce a given phenomenon. In many systems, however, such as in those presented in this thesis, the relationship between macroscopic behaviour and level of detail is highly non-linear. Adding or changing a specific low-level mechanism can therefore lead to completely different results. Modelling such a system therefore has to be an iterative process of modifying low-level details in order to determine the sensitivity of the model results to these details.

For that to happen in the course of regular scientific conduct, however, it is necessary to be aware of a model’s assumptions and to be explicit about them when publishing its results. As chapters 2 and 4 demonstrate this is not necessarily an easy task.

As the famous aphorism goes, all models are wrong but some are useful (Box, 1979). Models with the wrong assumptions are not any more wrong than others but the class of real-world systems they map to is too small to make them useful. Even the best model in the end is just a (rather elaborate) logical statement: ’if assumptions A hold, then behaviour B will be observed’ (Hinsch & Assmann, 2002). It can test for logical consistency and inspire new hypotheses and research questions. Only if it ultimately increases our understanding of empirically observed phenomena, however, is it useful.