Why do animals have territories?
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2 What do territory owners defend against?

Martin Hinsch · Jan Komdeur

Theoretical research on evolutionary aspects of territoriality has a long history. Existing studies, however, differ widely in modelling approach and research question. A generalized view on the evolution of territoriality is accordingly still missing. In this review we show that territorial conflicts can be classified into qualitatively distinct types according to what mode of access to a territory which competitor attempts to gain. We argue that many of the inconsistencies between existing studies can be traced back to the fact that, while using the same terminology, different instances of these types of conflicts have been investigated. We discuss the connections of each type of conflict to existing research within the wider area of animal conflicts. We conclude that a clear conceptual separation of different types of territorial conflicts is helpful but that a more general theory of territoriality has to account for interdependencies between them and that a more mechanistic approach to modelling territoriality is needed.

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Introduction

Territorial behaviour is common in animals. Theoretical musings about the "function" of territories have a long history (Stamps, 1994; Strassmann & Queller, 2014), but the first formalized studies only appeared in the 1960ies (see reviews Owen-Smith, 1977; Stamps, 1994). Since then a considerable number of theoretical studies have been published that cover various aspects of territoriality, such as the optimal size of a defended area (Ebersole, 1980; Schoener, 1983), the negotiation over territory borders between neighbours (Maynard Smith, 1982; Pereira et al., 2003; Vehrencamp et al., 2014), fights over territories between owners and floaters (Eshel & Sansone, 1995; Kokko et al., 2006; Morris & Maceachern, 2013), defence of territories against intruders (Davies & Houston, 1981; Hinsch & Komdeur, 2010) or the emergence of territories by means of local interactions (Stamps & Krishnan, 1999; Adler & Gordon, 2003; Giuggioli & Kenkre, 2014). While all of these studies are in a general sense concerned with how owners maintain their territories against competition by conspecifics they differ widely in modelling approach and research question. So far it is not clear whether, and if so, how these different approaches could be integrated into a general framework. A general theory of territoriality, that could explain why and under which circumstances territorial behaviour is adaptive is accordingly still lacking.

In this review paper we strive to facilitate the emergence of such a framework by attempting to resolve some of the apparent inconsistencies between the many different approaches that have been published so far. We will first define what we see as territoriality and argue that our definition implies that a game-theoretical approach is required when attempting to understand territorial behaviour. We then show that territory defence can be seen as consisting of several distinct, largely independent types of conflicts between territory owners and their competitors and that the differences between existing studies can for the largest part be attributed to which of these kinds of conflicts they consider. In the last part of the paper we outline how the different types of territorial conflict connect to a wider theory of resource defence and make suggestions for future research directions.

What is territoriality?

The terminology related to territoriality is notoriously ill-defined (see reviews Owen-Smith, 1977; Maher & Lott, 1995). For the purposes of this pa-
per we follow what appears to be the majority opinion in assuming that a territory is an area in which the territory owner has sole or prioritized access to one or several types of resources it contains such as mates, food or shelter (Maher & Lott, 1995). Territories are established and maintained by territorial behaviour (Potts & Lewis, 2014). For the sake of brevity we will in the following call individuals that own territories as well as populations that contain these individuals territorial. To distinguish territories from home ranges we further assume that in a territorial population there is competition for space or spatially distributed resources (Mitchell & Powell, 2012). In order to maintain the privilege of exclusive access territorial behaviour therefore has to include some form of territory defence (Brown, 1964; Börger et al., 2008). Territoriality finally denotes the complex of territorial behaviours and resulting population-level patterns that occur in territorial populations.

It is important to note that these are purely phenomenological definitions that are agnostic with respect to mechanism. In particular it can be very difficult to determine (empirically as well as theoretically) for a given behaviour whether it results in the formation of territories (and thus whether it is territorial) and conversely, given a situation with territories, which behaviour is responsible for creating and maintaining them (Maher & Lott, 1995; Riotte-Lambert et al., 2015; Potts & Lewis, 2016).

A game-theoretical perspective

Owning a territory entails costs in terms of fitness since owners lose time and energy as well as potentially health or even their life while advertising their ownership status and searching for and fighting off intruders (Powers & Conley, 1994; Mares et al., 2012). Only if these costs are lower than the benefit of exclusive access to the territory’s resources can it be adaptive for the owner to be territorial (Brown, 1964). Early studies showed that - everything else being equal - the costs of maintaining a territory increase with the number of intruders that have to be chased away (Schoener, 1983) and their willingness to escalate the conflict with the owner (Maynard Smith, 1982). Many, in particular older studies that investigate aspects of the evolution of territoriality assume frequency as well as behaviour of intruders to be fixed or determined in a straightforward way by territory size or quality (e.g. Dill, 1978; Schoener, 1987). In these studies the question whether territorial behaviour is adaptive is consequently treated as a straightforward optimization problem (Adams & Tschinkel, 2001). Just as the owner, however, in-
truders usually have a choice between several alternative actions - such as whether to intrude or not - that is subject to selection (Hinsch & Komdeur, 2010). That means in particular that other individuals will only intrude on a territory and risk a fight with the territory owner if it pays for them in terms of net fitness benefits to do so, which in turn depends amongst others on the owner’s willingness to defend its territory (Maynard Smith & Parker, 1976; Hinsch & Komdeur, 2010).

Territory defence can therefore not be the result of a unilateral optimization process. Instead it should be seen as the optimal behaviour of only one side in a series of bilateral conflicts between owner and (potential) intruders (Pereira et al., 2003; Hinsch & Komdeur, 2010). Consequently, in order to correctly predict for a given situation whether territorial behaviour is adaptive or not, a game-theoretical approach is required that analyses the simultaneous evolution of defence as well as intrusion behaviour (Maynard Smith & Price, 1973; Maynard Smith, 1982; Morrell & Kokko, 2005).

Different kinds of conflicts

Given our definition of territoriality and the requirement for a game theoretical approach we can see territorial conflicts as a special case within the wider framework of animal conflicts over resources. Various factors have been shown to affect how best to behave in a conflict over resources.

First, properties of the object of the conflict play a central role, i.e. what each party can expect to gain or lose depending on the outcome (Maynard Smith & Parker, 1976; Grafen, 1987; Broom et al., 2015) or physical properties of the contested resource, such as - in the case of food - size, handling time or predictability of occurrence (e.g. Stevens & Stephens, 2002; Broom & Ruxton, 2003). Specific aspects of the context the conflict happens in can, however, also be important, such as the likelihood of a repeated conflict (Switzer et al., 2001), or the amount of knowledge an individual has about the opponents’ strategy (McNamara, 2006; Hinsch & Komdeur, subm.).

We know that even small differences in these factors can result in very different optimal strategies (Broom & Ruxton, 2003; Hinsch et al., 2012; McNamara, 2013). If we want to understand the selection pressures acting on the strategies of individuals participating in a given conflict for resources such as any territorial conflict, we therefore need to know what exactly the stakes of the conflict are and in which context it happens in.

A closer look at empirical and theoretical studies on territoriality shows that while the terminology that has been used to refer to territorial conflicts
Figure 2.1: Territorial conflicts can be classified according to what an intruder attempts to gain (rows) and where it comes from (columns). Different types of models have been used to study each of these conflict types.
What do territory owners defend against?

shows little variation, the properties of the conflicts that have been investigated differ substantially. It is generally agreed that the object of territorial conflicts is access to the territory (Brown, 1964; Maher & Lott, 1995). The kind of access that a competitor attempts to gain, however, can vary with correspondingly varying consequences for the owner (figure 1). More specifically, we can distinguish three different types of competition that potentially lead to territorial conflicts:

- Competitors can attempt to take over an entire territory from the previous owner (Kokko et al., 2006; Gintis, 2007).
- Neighbours can attempt to gain space by permanently changing territory layout (Stamps & Krishnan, 1999; Pereira et al., 2003).
- Intruders can try to gain additional resources by intruding on a territory (Gill & Wolf, 1975; Davies & Houston, 1981; Hinsch & Komdeur, 2010).

As we will discuss in the following, for owner and intruder the stakes (in terms of effect on fitness) of the resulting conflict differ considerably between these cases and also depending on whether the intruder is itself a territory owner or a floater (see figure 1).

Furthermore, important aspects such as asymmetry of information between opponents (McNamara, 2006), likelihood of a repeated conflict (Switzer et al., 2001) and controllability of access (Stevens & Stephens, 2002) all vary dependent on which of these types of access to the territory individuals compete for. Each of these types of conflicts therefore has its own specific properties with specific evolutionary consequences for the individuals’ behaviour.

The state of the literature

In the existing literature many aspects of these different types of conflicts have been investigated with most studies focusing on one specific type of conflict in isolation.

Common terminology, however, does not distinguish between different types of conflicts (Maher & Lott, 1995). Across different studies the term territory defence is used to denote very different things while at the same time authors often fail to explicitly specify what they intend the term to mean. It is therefore often unclear which type of conflict is the subject of a specific study.
In addition in many models it is even difficult to determine with certainty what animals are assumed to compete for. In economic defendability models for example (e.g. Dill, 1978; Ebersole, 1980; Schoener, 1987; see Adams & Tschinkel, 2001), owners defend their territories against numerous intruders. The descriptions of some of these models as well as the way they have been applied to empirical data suggest that the intruders are assumed to be floaters looking to steal food on the territory (Gill & Wolf, 1975, 1979; Davies, 1980). Since conflicts are not explicitly modelled, however, the effect of losing on the owner and thus the stakes of the conflict are not defined within the model.

When discussing previous studies we will therefore have to distinguish between the type of territory access individuals are assumed to compete for by the authors and the type of competition that is supported by the model mechanics.

Entire territories

In many territorial populations the benefits accrued by owning a territory are not distributed equally, either because territories differ in quality or because only a part of the population is able to occupy a territory in the first place (Lenda et al., 2012). Territory owners therefore face competition from other owners with territories of lower quality (Alonzo, 2004) or from non-territorial individuals (new arrivals or floaters; Lenda et al., 2012; Morris & Maceachern, 2013). These occasionally attack and subsequently replace them as occupants of the territory (Davies, 1978), often without significant changes to the size and shape of the territory itself (e.g. Koda et al., 2012).

There is a considerable amount of theoretical work on the conflict over entire territories. Nearly all of it traces its roots back to the seminal papers by John Maynard Smith and co-workers (that at the same time laid the foundations for the development of evolutionary game theory) and in particular to the Hawk-Dove-game introduced therein (Maynard Smith & Price, 1973; Maynard Smith & Parker, 1976). In the most basic version of this model two individuals compete for an indivisible resource of fixed value and decide simultaneously whether to fight (Hawk) or concede (Dove). If fighting is costly enough then only a mix of both strategies (either on population or individual level) can be evolutionarily stable (Eshel, 2005). More importantly, though, in a slightly extended form of the game conventional conflict resolution can evolve where individuals make their behaviour dependent on arbitrary asymmetries. Ownership status - if it is visible to the contestants - can serve as such an asymmetry. The evolutionarily stable Bourgeois
strategy - fight as owner, retreat as intruder - then leads to stable territory ownership and only low levels of aggression (Maynard Smith & Parker, 1976). While this result was able to elegantly explain the existence of territory ownership and the low frequency of contests in natural populations it came with a caveat - the stability of the opposite strategy, intruders fighting and owners retreating, is mathematically just as sound and plausible. Much of the development of the field since then has been motivated by the attempt to reconcile the prevalence of ownership in the natural world with the ambiguity of the predictions of these models (Sherratt & Mesterton-Gibbons, 2015).

Discussing all studies in this area would go far beyond the scope of this article. We would therefore like to refer to the excellent review by Sherratt & Mesterton-Gibbons (2015) for further details and will in the following only give a brief overview within the context of our general question.

Extensions to the basic model can be roughly grouped into three categories. First, many authors have investigated the effects of adding details to the basic interaction between contestants, such as variation in size or resource holding potential (RHP) (Maynard Smith & Parker, 1976; Hammerstein, 1981; Härdling et al., 2004), limited information (Leimar & Enquist, 1984; Crowley, 2000), multiple asymmetries (Eshel & Sansone, 2001) or repeated interactions (Houston & McNamara, 1991).

A second important development has been the incorporation of population-level feedbacks into models on the conflict over entire territories. It has been noted early on that the basic Hawk-Dove(-Bourgeois)-game is inconsistent if seen on the population level (Grafen, 1987). The constant payoffs of the basic game do not take into account that the fitness effects of status as an owner or a floater depend on population-level variables such as the number of free territories or turnover due to death of individuals (Houston & McNamara, 2006). This was confirmed by subsequent studies that included a.o. the effects of territory retention (Mesterton-Gibbons, 1992; Eshel & Sansone, 1995; Mesterton-Gibbons & Sherratt, 2014), settlement sequence (Dunham et al., 1995; Broom et al., 1997; Härdling et al., 2004), mortality (Mesterton-Gibbons, 1992; Gintis, 2007) or population dynamics (Kokko et al., 2006).

Finally, although the vast majority of studies directly extend the basic Hawk-Dove(-Bourgeois)-game, different interaction mechanics have been explored by some authors, notably the War of Attrition (e.g. Maynard Smith & Parker, 1976; Leimar & Enquist, 1984; Gintis, 2007; Broom et al., 2015).
Space

The value of a territory in many cases increases with size, in particular if territories are compressed due to high population density. Owners therefore often would profit from extending the borders of their territories at the detriment of their neighbours (Schoener, 1987; Paterson, 2002). Similarly, if an individual attempts to gain a territory either by budding off that of its parents (Komdeur & Edelaar, 2001) or by establishing a new one in the gaps between existing ones (Beletsky, 1992) it has to claim space from other territories. In all these cases two or more individuals directly compete for space, resulting in a conflict over where one territory ends and the other one starts.

Models used in theoretical studies of the conflict between neighbours over space can generally be divided into two broad categories. In the first, simpler type of model no assumptions concerning the process that leads to the separation of space or the establishment of a boundary are made. Individuals in the models presented by Parker & Knowlton (1980) decide solely on either how much space they intend to claim or how much effort they invest into defence. Resulting occupancy and territory sizes (and thus fitness) are then simply calculated based on order of settlement or ratios of aggressiveness, respectively. One of these models (“defensive effort”) has been extended by López-Sepulcre & Kokko (2005) to be more ecologically consistent (Houston & McNamara, 2006) by including feedback effects between territory size, defence costs, number of floaters and population dynamics. Interactions between individuals, however, are similarly not modelled explicitly.

In contrast to that in the second type of model territory size and/or boundary position are the result of interactions between individuals. These interactions have been understood in two distinct ways. Maynard Smith (1982) and subsequent authors assume that individuals compete for the - continuous - amount of space each owner retains. The resulting conflict therefore resembles a process of negotiation. Stamps & Krishnan (1999) and Morrell & Kokko (2003, 2005) on the other hand assume that more or less discrete pieces of space (“sites”) are being fought over with each fight being similar to a more traditional one-off Hawk-Dove game.

The earliest example for an interaction-based model of competition for space is the analysis of the negotiation process between two territory owners by Maynard Smith (1982). Here individuals are assumed to compete over the location of the territory border on a line between their nest sites. This model has been extended to take into account how hunting behaviour of a sit-and-wait predator determines the value of space to its owner (Pereira et al., 2003) or to explore the effects of landmarks (Mesterton-Gibbons &
What do territory owners defend against?

Expanding on earlier purely proximate models (Lewis & Murray, 1993; Stamps & Krishnan, 1999; Sih & Mateo, 2001) a more mechanistic line of research has focused on how the evolution of movement behaviour can lead to a partitioning of space: Using spatially explicit models several studies show independently that if encounters between territory owners are costly, individuals evolve to avoid conspecifics which leads to the emergence of territories (Lewis & Moorcroft, 2001; Adler & Gordon, 2003; Morrell & Kokko, 2005; Hamelin & Lewis, 2010). It is important to note, however, that aggressive behaviour is an assumption, not an outcome of these models.

Although the potential significance of the competition between established territory owners and founders of new territories for space was recognized early on (Verner, 1977), only few theoretical studies have investigated this problem. Parker & Knowlton (1980), Getty (1981) and Stamps & Krishnan (1990) explore the best strategy for individuals that sequentially settle a new habitat patch, while López-Sepulcre & Kokko (2005) take into account the effect of individuals squeezing in between existing territories in their model. In all cases, however, territory size is assumed to be at the sole discretion of the founder, without any direct interaction between individuals.

Resources

On the most basic level individuals in a territorial population compete for the use of limited resources (Davies, 1980; Hinsch et al., 2012). Depending on various factors such as resource dynamics and distribution, non-territorial floaters as well as territory owners will therefore be interested in obtaining resources from the territory of another individual (Matsumoto & Kohda, 2004; Hinsch & Komdeur, 2010). Via depletion this “theft” can seriously affect the owner of the intruded territory, leading to a potential conflict between owner and intruder (Gill & Wolf, 1975, 1979; Davies & Houston, 1981).

The economics of the owner's side of this conflict have been explored by a line of - mostly older - theoretical studies that determine the net payoff of territory ownership in terms of costs of defence and the benefits of exclusive access to resources (e.g. Carpenter & MacMillen, 1976b; Hixon et al., 1983; Schoener, 1987; reviewed a.o. in Adams, 2001). This type of model has in several cases successfully been used to give post-hoc explanations for the observed behaviour of territorial individuals (Gill & Wolf, 1975; Carpenter & MacMillen, 1976b). It is, however, of very limited use for the study of the evolution of territoriality: First, intruder behaviour does not evolve at all.
Second, owners are assumed to always attack (and successfully expel) any intruder they encounter. Territorial behaviour is therefore part of the assumptions of the model instead of its consequences.

A step towards a more comprehensive approach has been taken by Davies & Houston (1981, 1983) and Houston et al. (1985). They model the owner’s decision whether to tolerate the presence of an additional individual on the territory depending on resource dynamics and intruder pressure. While the first intruder’s impact on the owner’s foraging success is represented in the model, the effect of any further intruders is only taken into account as additional fixed defence costs. An interesting variation on this approach explores the effects of some simple optimizations of the intruders’ behaviour on the owner’s willingness to defend its territory (Switzer et al., 2001). In a slightly different context Tao et al. (2016) use a similar type of model to investigate temporal dynamics of home range sizes. Finally, some work has been done on the related issue of food sharing between foragers or hoarders (Stevens & Stephens, 2002; Dally et al., 2006; Hadjichrysanthou & Broom, 2012).

In contrast to the competition for resources between owners and intruders, that between territorial neighbours has received barely any attention in the theoretical literature. To our knowledge the only study to date to explicitly focus on this problem has been presented by Hinsch & Komdeur (2010). They use a game-theoretical model to investigate under which conditions territory owners should be expected to steal from their neighbours.

**Connections with existing theory**

Now that we have established a clear logical distinction between the different types of territorial conflicts we can attempt to find a way to embed them into the wider area of resource defence theory. We can indeed find some clear structural parallels between each of the conflict types and existing theory outside of territoriality.

In models of the conflict over entire territories, ownership is well-defined and decided by a single interaction between owner and intruder. Territories are therefore treated as fully controllable, non-shareable resources. Conflicts over this type of resource - including for example food items (Broom & Rychtář, 2007), larval provisioning (Bentley et al., 2009), shelter or mates (Härdling et al., 2004) - is subject of a large body of theory mostly also based on the Hawk-Dove game or its descendants (Sherratt & Mesterton-Gibbons, 2015).
In conflicts over space on the other hand the resource is still assumed to be controllable, but in this case it can be shared. The amount allocated to each participant of the conflict therefore has to be determined by some form of negotiation. Similar conflicts have been investigated in other contexts such as parental care (Johnstone & Hinde, 2006) or reproductive skew (Shen & Kern Reeve, 2010; Binmore, 2010).

The conflict over resources on territories between owners and floaters or neighbours finally has some similarities with that over cached resources (Vander Wall, 2003), mates (Kokko & Morrell, 2005) or big food sources such as carcasses (Stevens & Stephens, 2002; Dubois & Giraldeau, 2007). As in these cases the resources within a territory are in principle shareable and at the same time not physically controllable by the current owner. Therefore the decisions that lead to a conflict become asymmetric: An intruder first decides whether to attempt to use the resource. If the owner does not react the resource is shared and only if the owner decides to challenge the intruder does a conflict take place (Hinsch & Komdeur, 2010). As an additional complication, however, due to resource replenishment the costs of tolerating theft can be considerably lower than the benefits gained by the thief in the case of territoriality (Davies & Houston, 1981; Waser, 1981).

Caveats

So far we emphasized the mutual independence of these conflicts - a notion that is reinforced by the fact that most existing studies focus on one type of conflict in isolation. While this is helpful for the sake of conceptual clarity it is important to note that the separation of territorial conflicts into independent mechanisms could be less clear-cut in the real world.

First, even if we assume that the conflict types per se can be cleanly separated, the behaviour individuals show in one of them will influence the fitness payoffs of behaviours in the others. The value of owning a territory and thus the payoff in a fight for entire territories for example depends amongst others on the costs of maintaining it against stealing intruders and encroaching neighbours (Pereira et al., 2003; Hinsch & Komdeur, 2010). The costs of establishing a new territory will depend on the willingness of present owners to defend their borders, which might again be dependent on turnover and social stability (Beletsky, 1992). On purely theoretical grounds it seems therefore advisable to take interdependencies between the different types of conflicts into account (López-Sepulcre & Kokko, 2005; Houston & McNamara, 2006).
In addition it is, however, not entirely clear to which degree the conceptual separation that we discussed above actually exists for a given system and if so, whether we are able to recognize it.

As observers we can detect cases in which a conflict has ended in a success for the intruder - i.e. territory borders changed, the intruder stole some resources or took over a territory. However, we can not know what the intentions of the intruder were before a conflict happens and what a conflict was about if the owner wins.

It is therefore difficult to tell if any or both of the individuals involved in a territorial conflict make a distinction similar to the one outlined above. An intruding floater for example might intend to poach on a territory while at the same time being open for a take over attempt should the owner turn out to be weak. Even if intruders are committed to a specific action, however, that does not necessarily imply that owners will be able to detect it. Although there is in many cases a certain amount of information exchange between intruders and owners (e.g. Schmidt et al., 2007; de Kort et al., 2009; Vehrencamp et al., 2014), we do therefore not know how well owners and intruder can predict each other's behaviour (Laidre et al., 2008). Limited information on both sides has not only the potential to drastically change the optimal behaviour for both parties (McNamara, 2006; Hinsch et al., 2012) but it might make it impossible to separate different types of conflicts.

The way forward

Given the separation into conflict types we outlined above, their connection to existing theory and taking into account the caveats we discussed, we can make some suggestions for a research program that will lead to a more complete evolutionary theory of territoriality.

First, the similarities between territorial conflicts and other areas of animal conflict need to be explored. It seems that it should be possible to identify some general properties of resources such as clumpedness, shareability, controllability or handling time that affect the evolution of conflict behaviour independent of the context. Some studies on the effects of “generic” resource properties have been done (Both & Visser, 2003; Broom & Ruxton, 2003; Hinsch et al., 2012). A systematic investigation of these similarities and differences between kinds of resources might pave the way for a general theory of resource competition that would apply to all situations where individuals find themselves in a conflict over access to resources.

Second, we need to understand the limitations of modelling each type of
What do territory owners defend against?

conflict in separation (see McNamara, 2013). In the first instance a straightforward combination of existing approaches, including two or more conflict types within one model, could be investigated. At the very least this would allow us to determine to which degree the more complex payoff structure of these combined models leads to differences in predictions as compared to previous results and thus whether interdependencies need to be taken into account.

Whether territorial animals distinguish between different types of conflicts in the first place is primarily an empirical question. Theory can contribute to solving this problem, however, by trying to understand under which conditions they should make this distinction and whether they would be able to do it. At this point this is still very much an open field, but there is a wealth of previous results on intention recognition (Moniz Pereira et al., 2011), the value of information in conflicts (McNamara, 2006), commitment (Cant & Shen, 2006), cognitive constraints (Fawcett et al., 2012) and costs of cognition (Burns et al., 2011) to draw upon.

Finally, for several reasons a more mechanistic theoretical approach might be useful. By modelling territoriality from first principles the problem of interactions between conflict types could be sidestepped. Furthermore modelling the evolution of territoriality from a non-territorial population without assuming the existence of any aspect of territorial behaviour probably requires a mechanistic approach (Hinsch et al., 2012). Lastly, we know that adding details and context to game theoretic models can significantly change their outcome (Van Doorn et al., 2003b; Houston & McNamara, 2006; McNamara & Weissing, 2010; McNamara, 2013). In addition it has recently been argued convincingly that a purely phenotypic view of the evolution of behaviour is misleading and that the actual mechanisms and constraints of cognition have to be taken into account (Blumstein, 1996; McNamara & Houston, 2009; Fawcett et al., 2012; Berg & Weissing, 2015).

Building a mechanistic model of territoriality is not without its challenges, in particular with respect to the individuals’ cognition. Higher order conflicts - such as over border location or territory ownership - presuppose considerable cognitive processes in the individuals. A conflict over territory borders for example implies the ability to remember ownership of the locations of their habitat. Furthermore this structure is not static but the emergent result of the individuals’ activities, namely the history of their movements and interactions (Stamps & Krishnan, 1997), a process that we have only recently begun to understand (Giuggioli et al., 2011; Giuggioli & Kenkre, 2014; Potts & Lewis, 2016). If border conflicts are being studied in isolation these mechanisms can be abstracted away from the single actions of individuals...
and cognition can be made implicit in the model structure (e.g. Maynard Smith, 1982; Pereira et al., 2003; Hamelin & Lewis, 2010). A mechanistic model however needs to accommodate them while at the same time allowing for higher order processes such as change of ownership of the entire territory to take place.

Promising first steps towards modelling territoriality from first principles have been made (Morrell & Kokko, 2005; Hinsch et al., 2012; Giuggioli & Kenkre, 2014; Tao et al., 2016). For a full picture, however, it will be necessary to integrate habitat and species properties (e.g. Iyengar, 2008; Rousseu et al., 2014), cognitive mechanisms (Fagan et al., 2013), interaction mechanisms (Számadó, 2008; Broom et al., 2015), population feedbacks (López-Sepulcre & Kokko, 2005) and resource properties (Waser, 1981; Broom & Ruxton, 2003).

Territoriality is a complex phenomenon that spans several levels of organization and relies on a number of different feedbacks with population and environment variables. It is conceivable that a full theoretical understanding of territorial behaviours will only ever be possible for specific cases. However, we argue that the realisation that previous studies have investigated a number of formally quite different phenomena under the same name is the first step towards finding connections with existing theory on resource competition and towards developing a more integrated view of the evolution of territoriality.

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