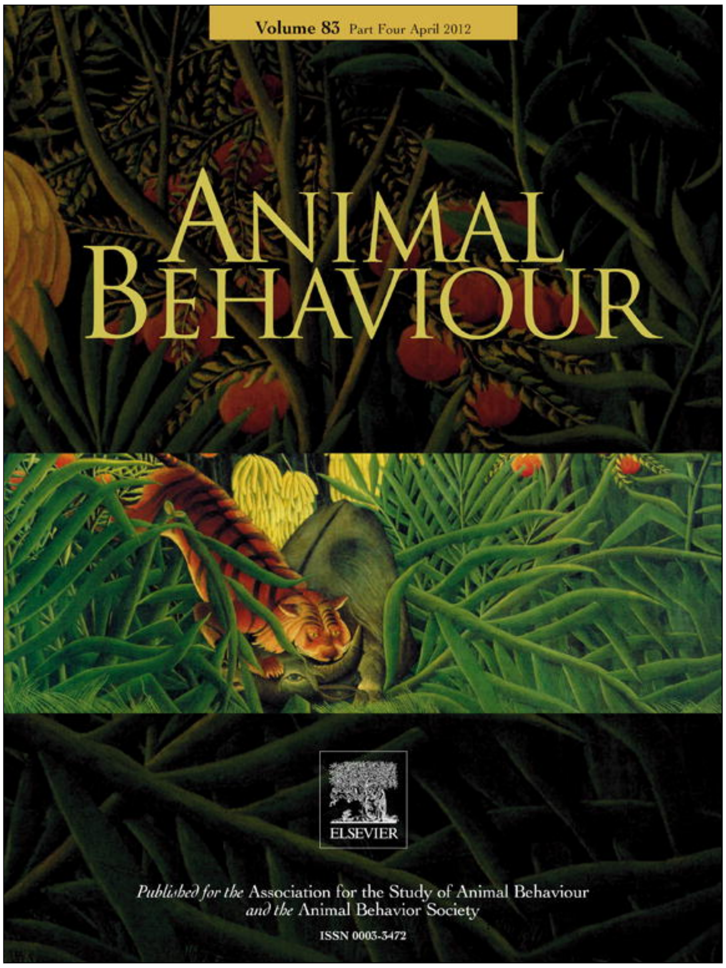
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Review

# The adoption of landmarks for territorial boundaries

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Although behaviours associated with territory maintenance are extensively studied, little is known about the establishment of territorial boundaries, a key process influencing individual fitness and population demography. In this regard, conspicuous features of the landscape and constructions such as scent marks (landmarks) can have an effect on whether and where boundaries are established. Landmarked boundaries have also been associated with altered social interactions, particularly contests that take place on boundaries. Some of these landmarks physically constrain a resident's perception or movement and may thus make the use of space beyond the landmark too costly. Other landmarks are purely conspicuous and appear to have no constraining effect, yet still have strong influences on boundary location by affecting social interactions. Factors that may influence whether a landmark is adopted for a boundary include the properties of the resident, properties of the landmark and the rate of encounter between neighbours. The purpose of this review is to consolidate and explicitly describe hypotheses relating to landmarked boundaries and highlight areas most in need of research. Ultimately, understanding the decision to adopt landmarked boundaries and the implications of these decisions for territorial populations is critical for understanding the link between landscapes, individual decisions and population ecology.


Territoriality, or site-specific intolerance of others, has evolved numerous times in a diversity of taxonomic groups (Alexander 1961; Brown 1964; van den Assem 1967; Dyson-Hudson & Smith 1978; Davies 1980; Hart 1987; Ostfeld 1990; Stamps & Krishnan 1998). Functionally, territoriality provides individuals with the benefits of having exclusive or priority access to resources within a given space (e.g. food, mates, shelter). Thus, territoriality will evolve when these benefits outweigh the costs of maintaining dominance in the area through aggression and display (Brown 1964). The existence of territoriality within a population has important spatial, social and demographic consequences that lead to variation in mortality and reproductive success (Patterson 1980; Elliott 1990; Calsbeek & Sinervo 2002). These fitness consequences of territoriality have important implications for the evolution of other phenomena such as aggression, communication and reproductive strategies (e.g. Tinbergen 1957; Beletsky & Orians 1987; McGregor 1993; Sinervo & Lively 1996; Morbey & Ydenberg 2001; Kokko et al. 2006).

An important feature of a territory is the boundary within which the resident is intolerant of other individuals. Boundaries spatially define the territory and determine the effect that the territory and its resident have on a population. Therefore, much of the research into territoriality has focused on the spatial location of boundaries in response to environmental and social pressures (Adams 2001). However, we know little about how the location of the boundary depends on the interactions between individuals (Maynard Smith 1982; Stamps 1994; Adams 2001; Pereira et al. 2003). These interactions appear to be influenced by conspicuous features of the landscape, or landmarks. Additionally, some animals construct landmarks to delineate territorial boundaries. Exploring the relationship between landmarks and territorial boundaries is therefore important for understanding the decisions involved in boundary formation and maintenance and for how the landscape influences the division of space between individuals (St Louis et al. 2004; Smith 2011). Understanding these processes is then crucial for explaining variation between and within territorial populations and, ultimately, the evolution of territoriality.

In this review, we outline the manner in which landmarks affect territoriality through their influence on the location of boundaries and the interactions that take place there. We consider landmarks that do not constitute complete physical barriers to movement, but rather act as barriers owing to the consequences of crossing them. To avoid confounding landmarks with other types of territorial resource, we do not explicitly consider landmarks that provide or diminish reproductive and survival benefits (e.g. food, reproductive opportunities, improved visibility, shelter). We focus instead on landmarks that have no cost or value beyond their use as

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a boundary. The review begins with a synthesis of current research on the adoption of landmarked boundaries. This includes both direct and indirect evidence for an effect of landmarks on territorial boundaries and their individual- and population-level consequences. We then define two types of landmark, based on whether or not they impose a physical constraint on an individual's perception or movement. Even when boundaries impose no physical constraint, animals may sacrifice potentially larger territories in order to have a conspicuously marked boundary. We discuss how this behaviour could have evolved in terms of spatial associations or conventions to avoid agonistic costs. We then highlight the potential factors that could influence whether or not a given landmark is adopted for a boundary. We conclude with a brief summary and highlight key areas requiring greater research focus.

## ADOPTION OF LANDMARKED BOUNDARIES

Anecdotal reports, correlations and territorial maps suggest that boundaries can be significantly more common along natural or artificial features and features constructed by territorial residents than other areas (Table 1; McCartan & Simmons 1956; Kalleberg 1958; Barlow 1961; Ficken 1962; Miller 1964; Baylis 1974; Itzkowitz 1974; Finck 1990; Tupper & Boutilier 1995). Red grouse, *Lagopus lagopus scoticus*, for example, consistently establish boundaries along features such as hillocks, ridges, walls, steep banks and streams (Watson & Miller 1971). Similarly, St Louis et al. (2004) objectively determined the territorial borders of ovenbirds, *Seiurus aurocapilla*, and black-throated blue warblers, *Dendroica caerulescens*, as well as changes in vegetation, rocks, topography, water and trails. Results showed that the areas that were associated with a sharp decline in space use (i.e. territory boundaries) occurred in the same areas as sharp changes in the presence of bare rocks and slopes in topography, which are features unlikely to be used as internal territorial resources. This suggests that some landmarks are valuable for use as a boundary even if they are of no value in other circumstances. Experiments that manipulate the presence of landmarks have since demonstrated that a relationship between landmarks and territorial boundaries is not a coincidence, but can be the result of individuals modifying their behaviour (Table 2). For example, Eason et al. (1999) placed dowels in an established neighbourhood of cicada killer wasps, *Sphecius speciosus*, and showed that the wasps adjusted the arrangement of their territories to utilize the dowels for their boundaries within 24 h. Although explicit studies on landmarked boundaries are limited, there are a number of hypotheses relating to the effects of landmarked boundaries on individuals and populations, the types of landmark used and the conditions under which a landmark is adopted for a boundary. Below is a consolidation and explicit description of these hypotheses, with notes on the areas most in need of research.

## EFFECT OF LANDMARKED BOUNDARIES ON INDIVIDUAL BEHAVIOUR AND POPULATIONS

### *Individual behaviour*

The adoption of landmarks for boundaries has been associated with altered social interactions between individuals, of which reductions in the frequency and intensity of contests are relatively common (Table 1: 3, 9, 10, 14; Table 2: 1, 5, 6, 7, 8, 9, 11). For example, cicada killer wasp contests can be less frequent and of shorter duration along boundaries marked by dowels compared to nonlandmarked boundaries on the same territory (Eason et al. 1999). In such situations, landmarks have value as a boundary because they increase the tactical defensibility of the territory: the efficiency at which it can be defended (Eason et al. 1999). In addition to being less costly, contests may be more (Table 1: 10) or less (Table 1: 9; Table 2: 11) likely to occur at landmarked than nonlandmarked sections of the boundary and the rate of interactions unrelated to boundary defence may also be reduced (Table 1: 13).

### *Populations*

The use of landmarks for boundaries can be expected to have an effect on territorial populations, since adopting landmarks for boundaries can influence the size, shape and defensibility of

**Table 1**
Species in which there is non-experimental evidence for landmarked boundaries, with IDs that are cited in the text

| ID | Species | Data available | | Landmark types | | Source |
|---|---|---|---|---|---|---|
| | | C | M | C | N | |
| **Mammals** | | | | | | |
| 1 | Golden jackals, *Canis aureus* | X | X | | X | Macdonald 1979 |
| 2 | Wolf, *Canis lupus* and *Canis simensis* | X | X | | X | Sillero-Zubiri & Macdonald 1998; Zub et al. 2003 |
| 3 | European badger, *Meles meles* | X | X | | X | Kruuk 1978 |
| 4 | Oribi, *Ourebia ourebi* | X | | | X | Brashares & Arcese 1999 |
| 5 | Tiger, *Panthera tigris* | X | X | | X | Smith et al. 1989 |
| 6 | Vicuna, *Vicugna vicugna* | | X | X | | Koford 1957 |
| **Birds** | | | | | | |
| 7 | Black-throated blue warbler, *Dendroica caerulescens* | X | X | X | X | St Louis et al. 2004 |
| 8 | Red grouse, *Lagopus lagopus scoticus* | | X | | | Watson & Miller 1971 |
| 9 | Pukeko, *Porphyrio porphyrio melanotus* | | X | | | Craig 1979 |
| 10 | Savannah sparrow, *Passerculus sandwichensis* | | X | X | X | Potter 1972; Welsh 1975; Reid & Weatherhead 1988 |
| 11 | Willow warbler, *Phylloscopus trochilus* | | X | | | May 1949 |
| 12 | Ovenbird, *Seiurus aurocapilla* | X | X | X | X | Ortega & Capen 1999; St Louis et al. 2004; Bayne et al. 2005 |
| 13 | Rufous-collared sparrow, *Zonotrichia capensis* | X | | | | Laiolo 2011 |
| **Reptiles** | | | | | | |
| 14 | Rainbow lizard, *Agama agama* | | X | X | X | Harris 1964 |
| **Fish** | | | | | | |
| 15 | Bream, *Abramis brama* | | X | X | | Fabricius 1951 |
| 16 | Black surfperch, *Embiotoca jacksoni* | | X | | | Hixon 1981 |
| 17 | Redlip blennies, *Ophioblennius atlanticus* | | X | X | | Nursall 1977 |
| 18 | White Cloud Mountain minnow, *Tanichthys albonubes* | | X | X | | Fabricius 1951 |
| 19 | Mozambique tilapia, *Tilapia mossambica* | | X | | X | Barlow 1974 |

The data available can be either (C) quantitative correlations between landmarks and boundaries or (M) maps that note both territorial boundaries and landmark positions. The types of landmark observed, if identifiable, could have been (C) constraining or (N) nonconstraining.

**Table 2**
Species in which there is experimental evidence for landmarked boundaries, with IDs that are cited in the text

| ID | Species | Landmark types | | Source |
|---|---|---|---|---|
| | | C | N | |
| **Mammals** | | | | |
| 1 | Mouse, *Mus musculus* | X | X | Mackintosh 1973 |
| **Birds** | | | | |
| 2 | Ovenbird, *Seiurus aurocapilla* | | | Machtans 2006 |
| 3 | Forest-dependent birds | | | St Clair 2003 |
| **Reptiles** | | | | |
| 4 | Bronze anole, *Anolis aeneus* | X | | Eason & Stamps 1992 |
| **Fish** | | | | |
| 5 | Mudskipper, *Boleophthalmus boddarti* | X | | Clayton & Vaughan 1986; Clayton 1987 |
| 6 | Pupfish, *Cyprinodon* sp. | X | X | Kodric-Brown 1978 |
| 7 | Three-spined stickleback, *Gasterosteus aculeatus* | X | | van den Assem 1967 |
| 8 | Rose bitterling, *Rhodeus ocellatus* | | X | Smith 2011 |
| 9 | Blockhead cichlid, *Steatocranus casuarius* | | X | LaManna & Eason 2003 |
| **Arthropods** | | | | |
| 10 | Mantis shrimp, *Gonodactylus oerstedii* | | X | Hazlett 1978 |
| 11 | Cicada killer wasp, *Sphecius speciosus* | | X | Eason et al. 1999 |

The types of landmark observed, if identifiable, could have been (C) constraining or (N) nonconstraining.

territories (Table 1: 8, 18; Table 2: 1, 6). For example, the presence of landmarks has been shown to reduce territory size (Table 1: 18; Table 2: 1, 6, 7, 9, 10; Kalleberg 1958; Baylis 1974) and affect territory shape (Table 2: 4; Grant 1968). Consequently, these properties can influence how many individuals a habitat is able to support (Fretwell & Lucas 1969; Patterson 1980; Stamps & Krishnan 1990; Adams 2001). Specifically, the adoption of landmarked boundaries has been associated with increases in the number of individuals settling in an area (Table 1: 15, 18, 19; Table 2: 1, 5, 6, 7, 9; Miller 1964; Baylis 1974). This may be because territories do not need to be as big as they would otherwise, owing to the decreased costs of sharing space (Baylis 1974; Clayton 1987; LaManna & Eason 2003). For instance, competing pairs of blockhead cichlids, *Steatocranus casuarius*, were able to maintain exclusive territories when there was a row of unimposing, yet conspicuous, rocks at the midpoint between their nests, but rarely (<7% of cases) when the rocks were absent, despite the available area being identical (LaManna & Eason 2003). On the other hand, the adoption of landmarked boundaries may have little influence on population abundance or even reduce it (Table 1: 10, 12). This could occur if adopting landmarked boundaries results in larger territories owing to the reduction in defence costs or wide spacing between landmarks (Reid & Weatherhead 1988). Additionally, the arrangement of landmarks may make areas of the habitat unsuitable (Bayne et al. 2005). Despite the apparent association between landmarked boundaries and population abundance, factors that influence whether this relationship is positive, negative or neutral have not been adequately explored.

In addition to affecting population abundance, landmarked boundaries may increase the long-term stability of an arrangement of territories and thus a territorial population (Reid & Weatherhead 1988; Eason et al. 1999; LaManna & Eason 2003; Mesterton-Gibbons & Adams 2003). Landmarked boundaries have been observed to persist longer than nonlandmarked boundaries, although strong evidence is still lacking (Table 1: 3, 9; Table 2: 5, 6, 9). For instance, competing pairs of blockhead cichlids could maintain a stable boundary for at least 3 h when boundaries occurred over a row of rocks but not when the rocks were absent (LaManna & Eason 2003). Similarly, communal swamphen, *Porphyrio porphyrio melanotus*, boundaries were better defined and more resilient to intrusion when they were over drains and fences than when they were in open paddocks (Craig 1979). In addition to being more persistent over time for individual owners, landmarked boundaries can persist through multiple owners (Table 1: 10; Table 2: 6). For example, when the same rock was presented to different populations of pupfish, *Cyprinodon* sp., the location and configuration of boundaries over topographical features were remarkably consistent between independent settlement events (Kodric-Brown 1978). These results imply that the adoption of landmarked boundaries may result in less variation in population abundance over time because the size and occupancy of territories remains constant. In contrast, Nursall (1977) found that redlip blennies, *Ophioblennius atlanticus*, constantly redefined their boundaries over different topological features. Clearly, long-term comparisons of populations that differ in their use of landmarked boundaries are needed to determine the effect that landmarked boundaries have on the stability of a territorial neighbourhood.

## TYPES OF LANDMARK

The effects outlined above can be caused by two main classes of landmark that are characterized by whether or not the landmark imposes a physical constraint on an individual's perception or movement. Within these two classes, landmarks can be constructed by the animals themselves (e.g. walls, scent marks, middens, scratched substrate) or be a feature that exists without effort from the territorial resident (e.g. topography, rocks, rivers, fences, walls, roads, sticks). We include features that are constructed by animals (Table 1: 1, 2, 3, 4, 5, 19; Table 2: 1, 5; Baylis 1974) as landmarks because they are likely to serve a similar function to natural landmarks when used as boundaries. For example, European badgers, *Meles meles*, build paths along their boundaries, which are rarely crossed by neighbouring groups (Kruuk 1978). A shared function between natural and constructed features is supported by an association between constructed landmarks and areas that do not contain natural landmarks (Table 1: 2, 3, 19; Baylis 1974) as well as by concentrations of constructions at boundary zones (Table 1: 2, 3, 4, 5).

In the context of this review, the type of landmark can be confidently inferred in many cases (Table 1: 1, 2, 3, 4, 5; Table 2: 1, 4, 5, 8, 9, 10, 11), but there are some situations in which the presence of a constraint is uncertain (Table 1: 8, 9, 11, 13, 16; Table 2: 2, 3). For instance, it is unclear whether some topographical features are physically constraining to birds or fish that are able to move in three dimensions. Below, we discuss constraining and nonconstraining landmarks in more detail.

### *Constraining landmarks*

Many cases of the adoption of landmarked boundaries can be explained if the landmark impedes the perception or movement of an animal (Table 1, Table 2; landmark type = C). This concept is supported by studies that show landmarks being used for boundaries in the absence of competitors (e.g. van den Assem 1967). Constraints to perception are best represented by reduced vision (Table 1: 8, 10, 15, 18; Table 2: 1, 4, 7; Kalleberg 1958), although constraints to other sensory modalities are not impossible. Animals may not defend areas beyond a landmark that limits vision because it is more costly to detect and respond to intruders, predators, prey and mates beyond the landmark (Watson & Miller 1971; Reid & Weatherhead 1988; Eason & Stamps 1992; Breau & Grant 2002). Thus, in terms of visual constraints, defending the space beyond the landmark may be less beneficial than terminating the territory at the landmark, making it adaptive to adopt the landmark for a boundary. However, intentionally imposing visual constraints can also be adaptive; such is the case for mudskippers, *Boleophthalmus boddarti*, that build mud walls around their territories. In this species, close proximity coupled with visual stimuli of conspecifics results in aggressive behaviour. Therefore, when population density is high, individuals build walls around their territories that reduce visual stimulation and thereby allow the associated social costs to be reduced (Clayton 1987). Some landmarks can also constrain the movement of animals by acting as a physical barrier that establishes energetic and time costs to traverse (Table 1: 6, 8, 9, 10, 12, 15; Table 2: 6, 7). There may also be costs associated with increased predation risk when crossing some areas, such as rivers (Table 2: 3; Lima & Dill 1990). Hence, animals may adaptively decide not to defend past landmarks where the costs of gaining access to desirable areas outweigh the benefits.

*Nonconstraining landmarks*

Many landmarks used as territorial boundaries are unlikely to impede animals physically and seem only to be utilized because of their conspicuousness (Table 1, Table 2; landmark type = N). In other words, landmarks can be no more than a 'line in the sand', yet still affect an individual's behaviour. For instance, mantis shrimp, *Gonodactylus oerstedii*, kept in an enclosure with a line of gravel surrounding their burrow only attacked an intruder once the gravel line was crossed, regardless of the line's distance from the burrow (Hazlett 1978). Such patterns imply that there must be strategic benefits for adopting purely conspicuous landmarks as a boundary, since doing so can come at the cost of sacrificing the potential to defend a larger territory (assuming larger territories are more beneficial).

One likely functional explanation for the adoption of nonconstraining landmarks as boundaries is a reduction in defence costs (Eason et al. 1999; LaManna & Eason 2003; Mesterton-Gibbons & Adams 2003; Smith 2011). Empirical studies have shown that animals can invest less in defence over landmarked boundaries that are visually conspicuous than nonlandmarked boundaries (Table 2: 7, 8, 9, 11). For example, interactions between blockhead cichlids were of lower intensity, shorter duration and were less frequent when a row of rocks was adopted for the boundary than when the boundary was nonlandmarked (LaManna & Eason 2003). Furthermore, the reduction in the frequency of high-intensity contests in the presence of landmarks appeared to be associated with an increase in the frequency of low-intensity contests. Thus, high-intensity contests may have been replaced by low-intensity contests (although the overall frequency of contests was still lower when landmarks were present). Theoretically, boundaries marked by olfactorily conspicuous scent marks or visually conspicuous marks such as scratches are also associated with lower defence costs (Gosling & Roberts 2001; Lewis & Moorcroft 2001; Moorcroft & Lewis 2006; Hamelin & Lewis 2010). Reduced investment in territory defence may have a suite of other benefits to a resident, such as an increased ability to invest in exploitation of the territory (Schoener 1987; Ydenberg & Krebs 1987), decreased stress (Young & Monfort 2009) and more time to become familiar with their own space (Stamps 1995). Furthermore, according to the rubber disc hypothesis of territoriality, individuals may be able to use the savings made on defence of one boundary to expand in other directions (Huxley 1934). Although a decrease in defence costs associated with landmarked boundaries is well supported, the reason it occurs remains unclear (Eason et al. 1999; Smith 2011).

## LANDMARKED BOUNDARIES AND DEFENCE COSTS

At least two, nonmutually exclusive, hypotheses could explain how and why the adoption of landmarked boundaries is associated with a reduction in costs. First, landmarks may provide animals with a clear and easily defended boundary, provided the landmark can be used as a component in a spatial referencing system (the clear-boundaries hypothesis; Eason et al. 1999). Second, landmarks may be used as a convention that allows a cost-effective way for boundaries to be established, assuming that boundary formation is normally a costly process (the landmarks-as-convention hypothesis; Mesterton-Gibbons & Adams 2003). These hypotheses, although not mutually exclusive, differ in the way that residents benefit (Mesterton-Gibbons & Adams 2003). For the clear-boundaries hypothesis, individuals benefit unilaterally, in that any individual that adopts a landmarked boundary will experience some benefit. In contrast, the landmarks-as-convention hypothesis stipulates that settlers must mutually adopt the same landmark for their boundary in order for either to benefit.

*Clear-boundaries hypothesis*

There are at least three, nonexclusive ways in which having clear boundaries could reduce the frequency and intensity of agonistic interactions (Kodric-Brown 1978; Eason et al. 1999; LaManna & Eason 2003). First, the resident may restrict its activity (i.e. movement and defence) to within the landmarked boundary, thereby reducing its intrusions into areas defended by other individuals (Eason et al. 1999). Second, potential intruders into the resident's territory (either neighbours or nonterritorial individuals) will recognize the landmark as a boundary and avoid accidentally or intentionally crossing it because intrusion is reliably associated with an aggressive response from the resident. A reduction in intruder pressure may additionally diminish the resident's need to patrol boundaries or devote time to vigilance in addition to decreasing agonistic interactions (Eason et al. 1999). Third, landmarks may increase the stability of the boundary and reduce the need for contests that function to re-establish it, although this stability could come at the cost of reduced flexibility in territory size when conditions change (Eason et al. 1999).

In order for a nonconstraining landmark to be utilized as a clear boundary, animals need to associate the landmark and/or the area beyond it with the interactions that take place there. In other words, territorial animals may be required to make spatial associations in order to determine which areas to avoid, exploit or treat as a boundary (Stamps & Krishnan 1999; Sih & Mateo 2001) and landmarks could be used to make or facilitate spatial awareness of these areas, including boundaries (Eason et al. 1999; Gosling & Roberts 2001; St Louis et al. 2004; Smith 2011). Support for using landmarks as spatial references for boundaries comes from studies that demonstrate the use of landmarks as spatial references for navigation and foraging (e.g. Tinbergen 1968; Warburton 1990; Benhamou 1997; Collett & Collett 2002; Odling-Smee & Braithwaite 2003; Kelly et al. 2009; Bruck & Mateo 2010). Additionally, familiarity with the arrangement of landmarks in a novel area appears to affect contest behaviour and territory settlement (de Boer & Heuts 1973; Heuts & de Boer 1973; Figler et al. 1975, 1976). Finally, individuals involved in contests near landmarks may be unwilling to return there, lest another contest takes place (Stamps & Krishnan 1999; Gosling & Roberts 2001; Zub et al. 2003). For instance, a map of pupfish territories suggests that neighbours mutually avoid some conspicuous features, even patches of algae that are otherwise used for food (Kodric-Brown 1978).

*Landmarks-as-convention hypothesis*

The landmarks-as-convention hypothesis suggests that animals use landmarks as arbitrary boundary locations instead of using costly interactions to determine a location that better represents the asymmetry in individual abilities (Mesterton-Gibbons & Adams 2003). If the cost of boundary settlement is sufficiently high and competitors are uncertain about each other's abilities, then a resident may benefit from adopting a landmarked boundary even when the outcome is a territory that is smaller than it would have been if the convention were ignored. In other words, it can be better to accept an arbitrary convention than risk a potentially rewarding, but also potentially costly interaction. Consequently, the model formulated to test this hypothesis suggests that individuals are more likely to accept a landmarked boundary if it provides them with a large territory, boundary establishment through contests is costly or the uncertainty regarding their opponent's abilities is high. Furthermore, in order for the use of landmarks-as-convention to evolve, a species must already be influenced by landmarks in some way (Mesterton-Gibbons & Adams 2003). For instance, the landmark would have to constrain an individual physically, exploit a pre-existing sensory bias or have the potential to be used as a spatial reference in navigation or territorial defence.

*Identification of the clear-boundaries and convention hypotheses*

The clear-boundaries and landmarks-as-convention hypotheses are not mutually exclusive and make many of the same predictions (Mesterton-Gibbons & Adams 2003). However, each hypothesis is associated with explicit testable assumptions and predictions, which allow one or the other to be ruled out (or considered unlikely). The landmarks-as-convention hypothesis can be ruled out when different individuals choose different landmarks for their boundaries, since the hypothesis requires that both individuals will converge on a single boundary location. The landmarks-as-convention hypothesis also predicts that the tendency to accept a landmarked boundary increases with the skew and declines with the variance of the distribution of fighting abilities in a population (Mesterton-Gibbons & Adams 2003). On the other hand, the clear-boundaries hypothesis requires that animals make spatial associations between contests and landmarks, even when the landmark is not being used as a boundary. This assumption can be tested by determining whether individuals exposed to contests in the presence of a landmark show changes in behaviour when subsequently exposed to the same landmark. Additionally, associations made near landmarks should be more precise than those made elsewhere. In other words, an individual exposed to a negative stimulus near a landmark is expected to avoid a smaller area (directly around the landmark) than if it were exposed to the stimulus in the absence of a nearby landmark owing to uncertainty regarding the location of the negative experience. Finally, removal of a landmark that is being used as a boundary should result in residents becoming less efficient at using space and more likely to be involved in costly interactions because the spatial association has been removed.

## CONDITIONS INFLUENCING THE USE OF LANDMARKS AS BOUNDARIES

Species and individuals vary in their use of landmarks for territorial boundaries (Table 1: 3, 8, 9, 10, 12, 16; Table 2: 3; Harris & Reed 2002; Mesterton-Gibbons & Adams 2003). For example, in a manipulative experiment involving 41 bird species, only ovenbirds adopted narrow linear clearings for territorial boundaries (Machtans 2006). Thus, there must be variation in the costs and benefits associated with accepting a landmarked boundary, yet the factors that explain this variation have not been adequately explored (Smith 2011). Current evidence suggests that the propensity to adopt or construct landmarked boundaries can be influenced by the properties of available landmarks, the properties of the individuals involved and the risks of encounter between individuals, each of which we discuss below.

*Properties of available landmarks*

The properties associated with the landmarks present in a habitat are likely to affect their utility as a boundary and thus whether or not an individual will choose to adopt one as such (Mackintosh 1973; Kodric-Brown 1978). This includes variation in their placement, conspicuousness, dimensions and the type of constraint that they pose. Individuals may also choose to construct a landmarked boundary when it is more cost-effective than adopting a natural landmark that is unsuitable in these properties (Barlow 1974; Baylis 1974; Kruuk 1978). This can be tested by observing an individual's response to the addition or removal of natural features with suitable properties. Despite the potential importance of variation in landmark properties, studies investigating this are rare (Table 2: 1, 5, 6; Mesterton-Gibbons & Adams 2003) in comparison to those that simply test for an effect of landmark presence.

In terms of boundary placement, the location of a landmark is likely to influence whether it is used for a boundary since the location of boundaries determine the territory's value. A model that shows settlers only using landmarks for boundaries if the benefits of adopting the landmark outweigh the costs of a territory that is too small supports this concept (Mesterton-Gibbons & Adams 2003). Observationally, when the movement of plant fronds used as a boundary by an individual minnow, *Tanichthys albonubes*, resulted in a territory that was too small, the individual abandoned its territory and usurped the territory of another (Fabricius 1951; see also Barlow 1961 for a similar observation). In contrast, mice, *Mus musculus*, did not opt to defend a nonlandmarked over a landmarked boundary, which was gradually shifted in one direction, once their territories got too small. Instead, the individuals with the smaller territories became submissive to their opponents (Mackintosh 1973). However, this could have been caused by shifts in dominance relationships associated with the experimental methods. In any case, there are few reliable data on the effect of landmark placement on whether the landmark will be adopted for a boundary. The preference for a landmark in a given location may also be affected by the number of alternative landmarks to choose from. For instance, a landmark that is being used as a boundary may not be used if another landmark is added in a preferable location.

Variation in the conspicuousness of the landmark is likely to determine when a nonconstraining landmark will be adopted for a boundary, since features that are more conspicuous may provide a clearer boundary. In addition to conspicuousness, the dimensions of a landmark are likely to be important since larger landmarks are likely to be more obvious and provide greater utility when being utilized as a conspicuous feature (Eason et al. 1999). For instance, a long, linear feature may provide a more effective clear boundary than a smaller feature. In terms of constraining landmarks, the costs associated with the landmark are likely to increase with its dimensions, thus making them preferable as a boundary (Reid & Weatherhead 1988; Harris & Reed 2002; Lees & Peres 2009). Finally, the type of constraint that a landmark imposes on a territorial resident may be important in determining whether it is used as a boundary (Eason & Stamps 1992). For instance, a resident may be unwilling to defend areas beyond a landmark that constrains vision but would defend those areas if the landmark constrained movement (Clayton 1987).

*Properties of individuals and species*

Differences between individuals and species are likely to account for some variation in the use of landmarks owing to variation in fighting abilities, behavioural strategies and ecology. Theoretical evidence suggests that variation in fighting ability can be important, in that better fighters may be less willing to adopt landmarked boundaries because they are more certain that they can claim larger territories than landmarks would allow (Mesterton-Gibbons & Adams 2003). This also implies that the distribution of fighting abilities within a population is an important factor for predicting the adoption of landmarked boundaries (Mesterton-Gibbons & Adams 2003). Additionally, Smith (2011) found that variation in how strongly rose bitterlings, *Rhodeus ocellatus*, responded to landmarked boundaries was correlated with the individual's natural propensity to intrude. Thus, variation in behavioural strategies such as the time of arrival to a habitat, aggression and tendency to intrude could affect the likelihood of a landmark being adopted. Such strategies are also expected to vary between populations and species. Ecologically, landmarked boundaries may be more common in populations that have high costs associated with boundary maintenance or establishment (Smith et al. 1989; Eason et al. 1999; Lewis & Moorcroft 2001; Mesterton-Gibbons & Adams 2003; Hamelin & Lewis 2010). Furthermore, optimal territory size is strongly dependent on resource availability (Adams 2001), implying that landmarks will only be adopted for boundaries if an individual does not need to extend its territory beyond the landmark in order for the territory to be economical. The adoption of landmarked boundaries has been observed to vary across seasons and years (Watson & Miller 1971; Kruuk 1978; Reid & Weatherhead 1988), which may be associated with changes in resource availability. Additionally, factors associated with the natural history of a species may affect the costs and benefits associated with crossing landmarked boundaries; this is implied by correlations between the ecological niche filled by woodland birds and their willingness to cross constraining landmarks (Harris & Reed 2002; Lees & Peres 2009). Habitat specialists, for instance, appear more likely to restrict their movements within habitat gaps than generalists. However, this could be associated with the ability of the guilds to use the gap for foraging. Finally, the evolutionary history of a species may influence whether it uses a given landmark for a boundary (King et al. 1996; St Clair 2003). For example, some woodland birds tend to use rivers as boundaries, possibly because crossing rivers is associated with a predation risk. Roads, in comparison, are not used as boundaries despite being associated with equivalent risks. This may be because the birds had adapted to avoid rivers, but have not yet done so for roads owing to their recent introduction (St Clair 2003).

*Risk and consequences of encounter*

Under the clear-boundaries hypothesis, a landmark's effectiveness is determined by the conditioned association between the agonistic response of the resident to intrusions over the landmark. Thus, an individual will be less likely to cross a landmarked boundary as the chance and costs of encountering the resident increase (Smith et al. 1989; Stamps & Krishnan 2001). The risk of an intruder encountering a resident when ignoring a landmark may increase with factors such as population abundance, the number of territory owners, proximity between territories, limitations to visibility, shared use of resources and the mobility of resources (Lewis & Moorcroft 2001; Moorcroft & Lewis 2006; Hamelin & Lewis 2010).

The nature of the association between crossing a boundary and the resident's response may explain why constructed landmarks (such as scent marks, middens and scratched substrate) are used instead of natural landmarks in complex habitats or extensive territories (Table 1: 1, 2, 3, 4, 17, 19; Table 2: 1). In such conditions, the visibility of boundaries is limited, thereby prohibiting residents from responding to every intrusion. Therefore, residents may signal how likely they are to be found in an area by marking it on each visit (Smith et al. 1989). Like natural features in appropriate conditions, these constructions may allow intruders to recognize areas that are more costly to use (Smith et al. 1989; Gosling & Roberts 2001; Zub et al. 2003). For instance, models of scent-marking behaviour in wolves, *Canis lupus*, demonstrate that individuals that retreat from conspecific scent marks and produce their own scent marks along borders have a reduced risk of encountering their neighbours, providing a selective advantage when the costs of encounter are sufficiently high (Lewis & Moorcroft 2001; Hamelin & Lewis 2010). This hypothesis predicts that the effectiveness of a constructed landmarked boundary will increase with the density and decrease with the age of constructions (Smith et al. 1989).

## CONCLUSIONS AND FUTURE DIRECTIONS

The adoption of constraining or nonconstraining landmarks for territorial boundaries is, under certain conditions, associated with changes in the interactions between neighbours and the size, shape and defensibility of territories. Consequently, the use of landmarked boundaries has important implications for territorial populations and ultimately the links between landscapes, individual decisions and population dynamics. In particular, landmarks bear directly on processes involved in boundary establishment and maintenance. Because of this link, it may be necessary to consider the topography of the landscape, in addition to resource availability and intruder pressure, to gain a complete understanding of territorial behaviour. However, explicit studies into landmarked boundaries are rare and we lack data on factors causing variation in the adoption of landmarked boundaries and their population-level consequences.

Although some research has begun to focus on landmarked boundaries, more work is needed to identify factors that influence variation in whether landmarks are adopted as boundaries within and between species. This will involve bettering our understanding of the costs and benefits associated with nonconstraining landmarks used for boundaries, including explicit tests of the clear-boundaries and landmarks-as-convention hypotheses. In terms of understanding the population-level consequences of landmarked boundaries, future research should focus on the costs and benefits associated with landmarked boundaries over extended periods of time and the conditions in which population size increases or decreases in response to landmarked boundaries. Finally, to develop both individual- and population-based hypotheses, we require data on how individuals behave when they have multiple landmarks to choose from. There is clearly wide scope for further empirical and theoretical development and this review provides the initial framework for these advances by identifying testable hypotheses relating to the causes and consequences of adopting landmarked boundaries.

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