

FORUM ARTICLE

Territorial tuatara? – a hypothesis still to be tested

Wayne L. Linklater

Centre for Biodiversity and Restoration Ecology, School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand (Email: wayne.linklater@vuw.ac.nz)

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Abstract: The term territorial is used in a variety of ways and is rarely defined unambiguously, or tested empirically. Nevertheless, attributing it correctly has far-reaching implications for our understanding and management of populations. Territoriality is commonly attributed retrospectively, as a convenient description of spatial pattern without an a priori and operational definition and tests for territorial behaviour. It is distinguished from female-defence or male-dominance mating systems by the defence of resources, including space. Thus, territories are defined operationally by site-specific dominance and their boundaries are determined by spatial changes in an individual's success in agonistic interactions with competitors. A number of recent articles describe the reptile, tuatara (*Sphenodon punctatus*: Rhynchocephalia) as territorial and use Gans et al. (1984) and Gillingham et al. (1995) in support. Neither Gans et al. (1984), nor Gillingham et al. (1995), provided operational definitions of territoriality, or tested for territorial behaviour, however. Gillingham et al. (1995) also confused the concepts of home range and territory by using the former to define the latter. The recent literature on tuatara includes the same errors. Home ranges continue to be used to define territories without measures of spatially dependent, female-independent dominance, and even though body size relates positively to success in male–male competition and access to females, neither of these factors influences 'territory' size. Instead, territory-like artefacts such as range dispersion and fidelity have been used as evidence of territoriality, although they can also be products of female-defence and male-dominance mating systems. Measures of the frequency, intensity and outcomes of male–male conflict where proximity of females and a priori territory boundaries vary, or ideally are varied experimentally, are necessary to tease apart the influence of females, resources and male dominance in the tuatara mating system.

Keywords: breeding system, mating strategy, Rhynchocephalia, *Sphenodon punctatus*

Introduction

Beyond the confines of science the term territorial is used to describe many types of behaviour. I have heard it used as a synonym for aggressiveness, asociality and inter-individual spacing behaviour, and to describe patterns in the structure of populations on the landscape. Science, however, seeks operational and exclusive definitions for terms to avoid confusion and to facilitate empirical testing and the unambiguous application of concepts. Untested hypotheses about territoriality, and their 'tendency to solidify into "quasifacts" and thus assume a stature that their original authors never intended' are long-standing problems (Stamps 1994).

Defining and testing territoriality in many species is difficult, especially in species that are relatively inactive and seldom interact with conspecifics. Nevertheless, the challenge does not reduce the importance of definitions and testable hypotheses as targets of empiricism because correctly attributing territoriality has far-reaching implications for the understanding and management of populations (e.g. Eadie et al. 1998; Durant 2000; Desrochers 2003). For example, reproductive skew, individual and gene dispersal, carrying capacity, and disease epidemiology are influenced by the social and spatial distribution of individuals. Territoriality imposes a unique, and sometimes extreme, influence on the dynamics of populations. It is unfortunately common for species to be

described as territorial without an operational definition of territoriality, or empirical tests for territorial behaviour (e.g. in equids; Linklater 2000). Instead, territoriality is commonly attributed retrospectively, as a convenient description of empirical pattern, although such patterns might not result from territorial behaviour.

Understanding the mating system of tuatara (*Sphenodon punctatus*: Rhynchocephalia) is necessary to make sense of the genetic and demographic structure of its populations and guide their management. Much good, detailed work has been achieved on the species and has had profound benefits for its conservation (Moore et al. 2008a, b; Hay et al. 2010; Mitchell et al. 2010). Recently, however, and for the first time, Gans et al. (1984) and Gillingham et al. (1995) were cited as evidence for territoriality in tuatara (Moore 2008) and the term features in the titles of subsequent articles (Moore et al. 2009a, b). I evaluate whether Gans et al. (1984) and Gillingham et al. (1995) can be used as evidence for territoriality in tuatara, whether more recent publications support the term's use, and suggest how territoriality might best be defined and tested.

Emlen and Oring (1977) classified polygynous mating systems into female- or resource- (territory) defence and male-dominance types. There are many definitions of territoriality and not all of them are rigorous or useful. Importantly, the best definitions of territoriality are those that are based on behavioural processes rather than outcomes because some

territory-like outcomes, such as exclusive range-use, site fidelity and site-specific breeding success, can also result from behaviours other than territoriality. Put another way: operational definitions of territoriality are better than conceptual definitions (Ostfeld 1987; Maher & Lott 1995).

In my opinion the best definition, and one that is appropriate for use with an easily observable animal like the tuatara, is site-specific dominance (Kaufmann 1983). That is, a male's dominance is associated with a site such that a dominance (territory) boundary can be measured by spatial changes in the success of an individual in agonistic encounters. Dominant males are those winning the majority of same-sex interactions involving aggressive behaviours. One would expect dominance reversals to occur for tuatara that are not on their territories. Importantly, this definition requires site defence to occur independently of female presence and allows one to differentiate empirically between polygynous species that defend harems or sequences of females in their range, from those that defend space. Although territoriality can result in monopolised females, it is the space (or its resources) that is primarily defended. Male access to females is a secondary consequence of successful territory defence. Kaufmann's (1983) operational definition accords well with earlier conceptual definitions of a territory as 'any defended area' (Noble 1939).

Gans et al. (1984) described the behaviour of two adult males *ex situ* in arena. They described male combat behaviour in proximity to the female, i.e. mate guarding or defence, and male-male competition for a mate, but not territorial behaviour. Gans et al. (1984) use the term 'territoriality' once, and inappropriately, since their experiment did not differentiate defence of space from defence of a female. Gillingham et al. (1995) conducted an experiment in which a model tuatara on a mobile platform was moved by remote radio control to within 2–3 m of a male tuatara. Although the proximity of a foreign, previously unknown, male-like model might elicit male defence behaviour, this is not evidence for territoriality unless compared with the same male's response to the same model when it and the model are outside the male's supposed territory. It is possible that males were defending females, not space, or just responding to a novel male near them (i.e. responding to a threat or defending inter-individual distance). The difference in response to male and female models described by Gillingham et al. (1995) is also not a test of territoriality, only an illustration that males discriminate sexually; an unsurprising result.

When reporting methods and field observations Gillingham et al. (1995) stated: 'Defended home range (=territory) size for male tuatara was estimated by the minimum polygon method' (p. 6) and 'The size of the home range for 16 male tuatara was estimated in February 1987. Because the entire boundaries of these home ranges were defended, they shall henceforth be referred to as territories' (p. 10). Thus, they confused the concepts and measurement of home range and territory, especially since they did not demonstrate that boundaries were defended. It is unfortunate that Gillingham and Miller (1991) did not elaborate empirically when they wrote that 'territorial boundaries were defined by noting daily aggressive encounters between individuals'. A home range is not a territory, either in the historical (Noble 1939; Burt 1943) or modern (Kaufmann 1983) use of the term.

The closest Gillingham et al. (1995) came to testing for territoriality in males is the following account: 'In all cases we observed ($n = 7$) where the female's territory overlapped the

territorial boundary between two males, and her retreat took her into another male's territory, the courting male following the female was approached by the second male and a territorial skirmish ensued' (p. 10). However, this interaction might have been motivated by the presence of a female, not transgression by a male across a territorial boundary. More importantly, they did not report who won the male-male conflict. If territoriality is an appropriate definition for male behaviour, then the males on their territories are more likely to have won the encounters. Did they? And, in another part of the article: 'The resident doing the biting subsequently returned to his territory' (p. 11). Did that male win an encounter off his territory? If so that would contradict most, except the least rigorous, definitions of territoriality. When Gillingham et al. (1995) wrote that 'Male tuatara are polygynous and appear to defend females as a resource within their territories' (p. 15) it becomes clear that they confused female-defence with site-defence and home ranges with territories in ways that 'muddy' evidence. Gans et al. (1984), Gillingham et al. (1995) and Gillingham & Miller (1991) do not define, test, or provide evidence for male territoriality and should not be used as references in support of it.

The lack of definition and empirical support for territoriality continues when Gillingham et al. (1995) considered female tuatara. They stated: 'Both bush and paddock females defended only a 1–2-m radius around their burrows' (p. 12) but this is their only reference to female site-specific dominance or defence and it contradicts Newman's (1987) observations of sequential burrow use. The evidence is not sufficient to conclude: 'Also, like many lizards, both male and female tuatara exhibit a strong and well-structured territorial defense' (p. 15). Clearly, tuatara are sedentary, have home ranges, males defend females and females defend nests, have a dominance hierarchy, and defend personal space and occupied burrows (which were seldom shared; Newman 1987), but use of the term territorial as a description of their mating system is unconvincing. The problem stems from a failure to provide rigorous *a priori* definitions of home range and territoriality that differ and are defined by behaviour, not synonymous outcomes. Gans et al. (1984) and Gillingham et al. (1995) do not demonstrate territoriality in tuatara.

Recent additions to the large and growing literature on tuatara have introduced the species as territorial (Moore et al. 2008a, 2009b; Miller et al. 2009), but do not define territoriality or advance on Gans et al. (1984) or Gillingham et al. (1995) by providing tests for it. Instead, the term 'territorial' appears to be applied retrospectively as a convenient description of a 'territory-like' pattern in the use of space. Like Gillingham et al. (1995), Moore et al. (2009b) use the terms home range and territory interchangeably, by defining male 'territories' as '95% minimum convex polygons because these areas were actively defended...', without measures of spatially dependent defence. Minimum convex polygon (MCP) dispersion, small size, and the fidelity of males to them are cited as evidence for territorial behaviour (Moore et al. 2009b). MCPs, however, were seldom adjacent such that they shared contestable boundaries. Indeed, most either overlapped or failed to share any boundaries with other males, i.e. there was space between adjacent 'territories' (fig. 2 in Moore et al. 2009b). The apparent territories of males were also small (c. 30 m², see also Gillingham & Miller (1991), table 1: 6.9 to 24.1 m²), such that their entire extent was probably within the sensory range of a male tuatara wherever it was within it, especially since visual communication is so important to the

species (Gillingham et al. 1995). The remarkably small size of apparent territories raises the possibility that inter-individual spacing behaviour might explain male range use better than territoriality. Range dispersion and fidelity might result from a positive relationship between the presence of neighbours and the ability to attract more females than can isolated males. A congregation of breeding males does not require that an individual's space be a territory – only core home-range loyalty, conspecific attraction and individual spacing behaviour among males. Range dispersion can result from the defence of females, especially where habitat is restricted (the male tuatara territories of Moore et al. (2009b) were located in a small forest fragment) such that inter-individual spacing behaviour gives the appearance of site-defence. Spatial constraints (i.e. restrictive habitat or topographical boundaries) can result in range dispersion and exclusive use of space without territorial behaviour (e.g. Rubenstein 1981).

Moore et al. (2009b) also found that although there was a positive relationship between body size and success in male–male competition and access to females, body size and access to females were not related to territory size. This latter finding should raise doubts about tuatara being territorial. The authors suggested that territoriality was still an appropriate term because males that were more successful at guarding females monopolised them in areas where females were most dense. I consider that both these positive relationships are more suggestive of mating systems structured by female defence or male dominance without recourse to territories. Importance has been attributed to potential mates as the driving force for territoriality in tuatara (Moore et al. 2009b), but territoriality is primarily distinguished from other social systems by the defence of space, not females. A simpler explanation is that the patterns in the spacing of males and females are not a consequence of territorial behaviour.

In summary, the recent literature on tuatara appears to have confused home ranges or inter-individual spacing with territories, and female-defence with site-defence. The term 'territorial' appears in articles about tuatara without critique although it may be inappropriate (and unimportant) to the core study – and so the potential myth grows (i.e. quasifact; Stamps 1994). What would be needed to test for territoriality in tuatara? If we follow Emlen and Oring's (1977) classification, sites should be occupied and defended independently of the proximity of females. In an important rejoinder, Ostfeld (1987) pointed out that Emlen and Oring's classification has lasting heuristic value, but for many species females and resources may both have an influence, although one is likely to predominate. Some species might primarily defend resources, but the territory might also be modified by the presence of females and vice versa. It is possible that tuatara fall neatly between site-defence and female-defence mating systems, or require the application of concepts from male-dominance mating systems. Whatever the situation, a measure of the frequency and intensity of male–male conflict that can be related to the participant's location and the proximity or residence of females is required in order to tease apart the influence of site versus mate. If the influences of resources and females appear to interact, then experiments in which one or the other is removed or added might be informative. If male–male agonistic interactions are rare, they might be stimulated by moving or introducing males at strategic locations, with and without proximal females. Neighbours might be moved, or novel animals introduced relative to hypothetical boundaries, to test for territories described a priori (Ostfeld 1987). Until such experiments are

done I recommend much less confidence be placed in the use of the term territoriality to describe the breeding strategies of tuatara. It remains a hypothesis to be tested.

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