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How residency duration affects the outcome of a territorial contest: Complementary game-theoretic models

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HIGHLIGHTS

- First discovers often become owners, but sometimes it is unclear who got there first.
- When rival claims to property arise, contest duration increases with residency time.
- Game-theoretic models based on increasing belief or motivation explain these effects.

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ABSTRACT

While the first individuals to discover and maintain territories are generally respected as owners, under some conditions there may be ambiguity as to who got there first. Here we attempt to understand the evolutionary consequences of this ambiguity by developing a pair of game-theoretic models in which we explicitly consider rival residency-based claims to ownership. Following earlier qualitative explanations for residency effects, we assume that either the value of the territory (Model A) or an interloper's self-belief that it is the owner (Model B) increases with duration of residency. Model A clearly demonstrates that if the value of a territory increases to a resident over time, so should its motivation to fight in terms of the effort it invests in fighting. Indeed, only a small increase in territory value with residency duration can be sufficient for longer established residents to win disputes, even without any arbitrary convention or other form of priority effect. Likewise, Model B shows that the observed increase in fighting persistence with residency duration can be readily explained as a consequence of increasing confidence on behalf of the interloper that it is the rightful owner. Collectively, the models help to explain some general findings long observed by empiricists, and shed light on the nature of conflicts that can arise when individuals do not have complete information about rival claims to ownership.

1. Introduction

It has long been appreciated that respect for ownership can play a role in settling disputes over contested resources, although the extent to which this deference arises as a convention or as a consequence of asymmetry in resource holding potential and/or value remains unclear (see Kokko, 2013; Kemp, 2013; Sherratt and Mesterton-Gibbons, 2015 for reviews). Ironically, however, it appears that this respect can also result in escalated contests if both contestants consider themselves the resident (Waage, 1988). If a territory is large or complex, for instance, then a territory holder may be present when another individual arrives, but the two individuals do not detect one another until both have been present for some time. Waage (1983, 1988) observed precisely this set of events in territorial *Calopteryx maculata* damselflies and showed experimentally that the protracted contests that arose under these conditions were best understood as a consequence of "habitat-mediated confusion" over ownership. Likewise, a resident may move away temporarily from its territory to forage or repel intruders, only to be replaced by an interloper. Particularly long disputes between interlopers and the returning resident have been widely observed under natural conditions (e.g., Wickman and Wiklund, 1983; Waage, 1988; Gribbin and Thompson, 1991; Rutowski, 1992; Kemp, 2003) and they have also been frequently

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reported in manipulative experiments following the removal and subsequent re-introduction of the former resident (e.g., Davies, 1978; Krebs, 1982; Alcock and Bailey, 1997; Kemp, 2000; Kemp and Wiklund, 2004; Takeuchi, 2006; Peixoto and Benson, 2012). Intriguingly, while the temporary interlopers in the above experiments are frequently successful at repelling any non-resident intruders, the original residents often win the escalated contests that arise on their return (Wickman and Wiklund, 1983; Krebs, 1982; Alcock and Bailey, 1997; Kemp, 2000; Kemp and Wiklund, 2004; Takeuchi, 2006). This is a key observation, because it rules out the possibility that animals with rival time-based claims to the same territory use entirely arbitrary conventions based on current occupancy, and instead suggests that the sense of ownership and/or motivation to retain the property develops over time. Indeed, there is clear evidence that the period of time an interloper is in residence affects both the duration of the subsequent contest with the former owner and the likelihood that it will win. For example, Krebs (1982) removed resident pairs of great tits (*Parus major*) from their territories and released them back after replacement pairs had occupied the areas for a controlled period of time. The duration of the contests between the former resident great tits and their interlopers was an increasing function of replacement time, as was the probability that the interlopers would retain the territory. Alcock and Bailey (1997) conducted an analogous experiment with territorial tarantula hawk wasps *Hemipepsis usulata* and found that interlopers that had been on the territory for longer tended to fight longer and harder against the original owner, before ultimately losing.

Krebs (1982) interpreted his results to have arisen as a consequence of an increase in value of the territory over time to an interloper, and a decrease in value over time to the former owner. Possible reasons for this gradual change in value of the territory include the residents' increasing familiarity with their physical surroundings, but also with their neighbors. Tobias (1997) likewise conducted removal experiments in European robins *Erithacus rubecula* and found that newcomers were more likely to resist eviction by the original owners, the longer they were allowed to hold the territory. Just as Krebs (1982) had proposed, Tobias (1997) argued that newcomers had to pay non-transferable settlement costs when negotiating boundaries with neighbors, so that the net value of a territory to a resident increased over time. Indeed a significant asymmetry in net value favoring the interloper is possible if, the longer a resident is absent from its territory, the more likely it will have to renegotiate its boundaries when it returns.

Of course, not all territories will increase in value to the resident as a consequence of its increasing familiarity with its surroundings and its neighbors. Indeed, Kemp and Wiklund (2001) felt that such effects were unlikely in butterfly species, where territories are small and individuals appear not to be able to specifically recognize their neighbors. Alcock and Bailey (1997) proposed that the residency-duration effect they observed in hawk wasps could also be mediated by a change in perceived value, but suggested that it might arise indirectly through the interloper being increasingly convinced that the former resident would not return. Walton and Nolan (1986) made a similar case for the importance of uncertainty over roles when describing the territorial behavior of prairie warblers (*Dendroica discolor*) after their spring migration. Naturally, increasing familiarity with one's surroundings and confusion over ownership are not mutually exclusive explanations for the time-in-residence effects. For instance, Takeuchi (2006) found that green hairstreak (*Chrysozephyrus smaragdinus*) butterflies that replaced an original owner fought longer against original occupants as their residence duration in the territory increased, and invoked both the above arguments to explain his results.

Given the role of time in residency in affecting both the duration and outcome of disputes involving "co-owners" with joint claims for ownership, it is somewhat surprising that no model of territorial conflict has been presented to help understand these fundamental phenomena. To elucidate the significance of these behaviors from an adaptive perspective, we develop two separate but complementary game-theoretic models. The first model addresses how an increase of resource value with time on territory affects the effort expended in a contest over ownership, when no role asymmetry is perceived by the contestants. This model is new. The second model addresses how increasing belief in ownership on the part of an interloper affects contest duration, when the roles of owner and intruder are perceived by two contestants, but imperfectly. This model is an adaptation of Hammerstein and Parker's (1982) asymmetric war of attrition. Separate mathematical models allow us to focus, as far as possible, on one of these two effects in isolation from the other. We will refer to the first model as Model A and to the second as Model B.

2. Model A: no role asymmetry perceived by the contestants

First we explore how an increase of resource value with time on territory affects effort expended in a contest over ownership, when no role asymmetry is perceived by the contestants.

Accordingly, consider two animals that have discovered an otherwise unoccupied territory, whose value at time s since discovery is $V(s)$. That is, $V(s)$ is the site value to an animal that has been in residence for time s, assuming that it retains the resource after contesting it. If one animal has been on site for time s_O and the other for time s_I, then in general $s_O \neq s_I$, and so the respective site values, $V(s_O)$ and $V(s_I)$, also differ. We assume that site value is zero initially and increases with time on territory towards a maximum value of 1. Specifically, we assume

$$V(0)=0, \quad V'(s)>0, \quad V(\infty)=1, \tag{1}$$

where a prime denotes differentiation with respect to argument. We note that some territories may have immediate value to residents on arrival (so that $V(0)>0$), and their ultimate value may even decline with increasing residency duration (so that $V'(s)<0$). However, the inequalities assumed in (1) are the simplest starting point to quantitatively evaluate earlier verbal hypotheses as to why interlopers should fight longer to retain a territory, the longer they have been in residence.

Each of the animals is initially unaware of the other's attachment to the site—there is habitat-mediated confusion (Waage, 1983, p. 25), with two co-discoverers both continually present. One of these individuals is the focal individual or Player 1, from whose perspective we analyze their interaction; this individual plays a potential mutant strategy, and the other individual—Player 2—plays the population strategy. Eventually, these two animals will meet. Let t be the time that has then elapsed since Player 1 discovered the territory, and let T be the corresponding time for Player 2. Although t is then known to Player 1, from Player 1's perspective, T is a random variable, which we assume to be continuously distributed over $(0,\infty)$ with probability density function g, and distribution function G defined by

$$G(s)=\int_0^s g(\xi)\,d\xi. \tag{2}$$

Without loss of generality, we assume that time is measured in units of the mean of this distribution, so that its mean becomes 1 and its variance is

$$\sigma^2=\int_0^\infty (s-1)^2 g(s)\,ds. \tag{3}$$