# Punishment and persistence pay: a new model of territory establishment and space use

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**Existing game theory on aggressive interactions associated with territory establishment typically assumes that pairs of contestants engage in 'winner takes all' fights for indivisible space. New work by Stamps and Krishnan explores an alternative scenario where space use emerges from a series of aggressive interactions where punishment and persistence, rather than winning *per se*, shape observed patterns. This new approach generates novel predictions for game theory, such as the possibility of gaining space not by winning, but by 'nagging'.**

In many systems, a good territory is a key requirement for survival and successful reproduction. Although many studies have examined territorial behavior after territories are established, relatively little is known about the processes and dynamics of territory settlement. The usual view is that animals acquire territories and establish boundaries by engaging in aggressive interactions. Existing theory on these interactions is built on a scenario where two contestants fight for an indivisible territory and the outcome of the fight determines who gets the space – that is, the winner gets the territory and the loser moves on. However, a recent model and literature review by Stamps and Krishnan[1,2] emphasizes that this might not fit all systems. In many cases, patterns of space use emerge not from a single 'winner takes all' contest, but instead from an ongoing series of aggressive interactions, many with no clear winner, that together determine how settlers will partition divisible space. In this alternative view, each fight is part of a learning process of site-based negative and positive experiences that eventually shape the use of space by each individual.

Previous theory on aggression, territory establishment and maintenance is based primarily on game theory. General game models (suitable for contests for any resource type – food, mates and territories) assume that two individuals engage in a 'winner takes all' fight for a given territory. The evolutionarily stable strategy (ESS) predicts fight intensity as well as when individuals should give up and cede the territory to the winner[3,4]. More specific game models focus on interactions during a series of pairwise 'winner takes all' contests[5,6]. The ESS involves site choice – should each individual settle for the next best available territory or fight to try to take over a better, occupied territory? The outcome is the sequence of site choices as territories are filled. By contrast, Stamps and Krishnan model a more fluid process where no single interaction determines the winning of an entire indivisible territory. Instead, individuals move through a large, suitable, divisible area and learn which sites are more or less attractive (based on food, refugia, fights with conspecifics etc.). Fights involve punishment (the inflicting of costs) that reduces the attractiveness of an area for both individuals. The outcome is a pattern of space use – home range sizes (the total area used by each individual), territory sizes (exclusive area used by each individual) and exclusivity (territory size/home range size). This new approach provides both new twists on understanding familiar phenomena, and novel predictions that are, in some cases, counterintuitive.

Stamps and Krishnan use a spatially explicit, individual-based modeling framework, drawing, in part, on their long-term observations of territory establishment in juvenile *Anolis aeneus* lizards. Individuals randomly settle on a computer-simulated landscape (two settlers on a $5 \times 5$ grid or 15 settlers on a $10 \times 20$ grid). For simplicity, the authors assume that grid spaces do not differ in habitat quality. Individuals then move through space one grid at a time. If they find a space unoccupied, their explorations are rewarded by increased knowledge about the resources (food, shelter, potential mates, etc.) in that space. Increased knowledge increases the attractiveness of that site – that is, the likelihood that an individual will return to that site. If, however, two individuals meet at a site, they have an aggressive interaction. Both individuals inflict punishment on the other. The interaction might involve a fight, a chase (or series of chases), or threats and displays. Regardless of the outcome, because both individuals suffer costs from having visited that site, they both are less likely to return in the future. The model keeps track of the net attractiveness of each site for each individual. After several days of moving and interacting, the contestants settle into relatively stable patterns of space use. Mean home range sizes, territory sizes and exclusivity depend on the functions that describe the degree of negative and positive feedback associated with visits that do or do not involve aggressive encounters.

Stamps and Krishan's models provide an example of the synthesis of behavioral ecology and psychology, integrating both learning theories and cost–benefit thinking to predict behavioral strategies and outcomes (e.g. Refs 7,8; Box 1). Their initial model assumed that competitors are identical – that is, all individuals inflict the same amount of punishment on others, and all gain the same amount of positive or negative feedback depending on whether they engage in an aggressive interaction[1]. A later model added individual variation in aggressiveness – that is, differences between individuals in punishment inflicted and received[2].

The models corroborated several standard observations and predictions of game models. First, individuals generally favor familiar sites. If introduced in an unfamiliar site, they tend to return to a familiar site; that is, they home. In pairwise interactions, Stamps and Krishnan's models generated: (1) a prior residence effect – occupants tend to hold space when challenged by newcomers; (2) a 'desperado effect' – individuals persist in visiting sites where they are continually punished if they have few other available options; and

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**Box 1. A learning-theory approach to territory establishment**

Stamps and Krishnan draw from the fields of comparative psychology and behavioral ecology to model the way in which positive and negative learning experiences influence space use[a,b]. Aggressive interactions (e.g. fights, chases or displays) inflict punishment, a form of instrumental conditioning, which decreases the likelihood of either participant returning to an area, because that area is now associated with negative consequences. That is, through Pavlovian conditioning, the specific area comes to elicit fear, and individuals learn to avoid or to leave the area to reduce this fear ('conditioned place aversion'). This 'loser effect' can be characterized by individuals avoiding the location where they lost, regardless of the presence of conspecifics. However, in many taxa, winning an agonistic interaction is highly rewarding[c,d], and winners become more aggressive and more likely to win future aggressive interactions. In addition, winners develop a conditioned place preference and are more likely to return to the area in which they previously fought and won[e,f]. Thus, for many species, the positive effects of winning should be a significant component to a learning-based model of territory establishment.

Other aspects of learning can be included in future models, such as the conditional effects of experiences with other species. For example, because encounters with predators might be more aversive than are fights with conspecifics, predator-free areas should be attractive, even if an individual engages repeatedly in aggressive interactions in those areas. Incorporation into the model of learned associations between locations and predator encounters (ranging from sightings of predators to actual predation attempts) might reveal surprising tradeoffs between avoidance of intra- and interspecific punishment. Second, residency in one year could affect the establishment of territories in subsequent years. Knowledge of an area or of conspecifics (especially in species with long-term individual recognition) is likely to influence aggressive tendencies and likelihood of regaining previous territories[g,h]. Finally, future models could incorporate not just learning, but also adaptive forgetting. In a changing environment, organisms should forget old information that is no longer useful for understanding current or predicting future events. If aggressive neighbors sometimes leave an area or die, individuals need to forget about past negative experiences to re-explore the newly opened sites.

**References**


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(3) particularly persistent aggression when two individuals become familiar with the same site (i.e. when both think they are resident at the same site). In larger groups, higher mean aggression levels (i.e. greater punishment) result in greater territory exclusivity, and more aggressive individuals tend to hold larger territories.

Although these results are not surprising, they are produced by a different mechanism than the usual game models. Rather than being the outcome of 'winner takes all' fights, they emerge from punishment and persistence. Individuals with greater familiarity with a site are more persistent in returning to a site in spite of costly contests. Their persistence is typically eventually rewarded by exclusive use of that site. More aggressive individuals do not necessarily win fights. Even if all contests end in draws, by inflicting repeated punishment, highly aggressive individuals tend to take over a larger area, and coerce less aggressive individuals into using a smaller space.

The models also generate some novel predictions. First, because of the benefits of familiarity, individuals settle into stable territories even without aggressive interactions, and without being 'tethered' to a localized special site, such as a nest site or shelter. More strikingly, after escalated (high punishment) fights, both individuals should tend to avoid the site, regardless of who wins. In particular, when two newcomers fight, under some conditions, even the winner should avoid the site afterwards. Less costly interactions (e.g. chases), however, should be associated with stable, often considerable, ongoing overlap in space use. Most interestingly, individuals can take over space without winning any contests. That is, simply by being persistent in making it costly for another individual to use a site, a 'loser' can gain space. Stamps and Krishnan refer to this as gaining space by 'nagging'. This fascinating phenomenon has indeed been observed in several cases[2].

Stamps and Krishnan emphasize that their models represent only an initial step in a novel approach. Box 1 notes some possible extensions involving other known aspects of learning. Other useful extensions involve accounting for more complex behavioral strategies – for example, adaptations for detecting intruders or for advertising the presence of a resident at greater distances, or conditional aggressive strategies (e.g. be less aggressive towards known neighbors versus towards 'strangers'). Yet another type of possible extension involves more complex representations of habitat heterogeneity.

Finally, it would be useful to explicitly blend cost–benefit game-theory approaches with the modeling approach developed by Stamps and Krishnan. For example, Stamps and Krishnan's models have parameters (set by the modeler) that govern both the degree of punishment inflicted in an interaction and the negative–positive feedback functions that determine how the attractiveness of each site is altered by experiences. These parameters can be treated instead as optimal variables that depend on cost–benefit considerations. For example, existing game theory has addressed when individuals should punish other individuals[9]. An extension could assess and incorporate the optimal degree of punishment to inflict given the costs and benefits of punishment. A further extension might address how the benefits and costs of space use and contests should affect the optimal degree of alteration in site attractiveness following a visit to a site (with or without an aggressive interaction). A marriage of game theory and Stamps and Krishnan's process-based proximate modeling approach should move us towards to a deeper, more integrative understanding of animal space use and territoriality.

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Meeting Report

# The physiology of life histories

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**The Physiological Basis of Life-History Traits and Tradeoffs Symposium of the Comparative section of the American Physiological Society, was held at the Experimental Biology Conference, Orlando, FL, USA, from 31 March to 4 April 2001.**

Life-history studies traditionally address behavior and demography, focussing on measures such as foraging success, reproductive success and survival, which all express the outcome of the interaction between the organism and its environment. Physiological aspects of organism function, including metabolism, immunocompetence and endocrine controls, are seen primarily as supporting, rather than controlling, life-history responses to the environment. A recent symposium at the FASEB meeting, organized by Tony Williams (Simon Fraser University, Vancouver, Canada) and Barry Sinervo (University of California, Santa Cruz, CA, USA) has emphasized that physiology also can have a constraining role in life-history tradeoffs.

A recurring theme of the symposium was that organisms can trade off different physiological functions, such as immune and endocrine responses to environmental challenges. Such physiological functions are often reflected in energy expenditure, which can thus serve as a common currency to gauge the outcome of life-history tradeoffs. It is also evident that constraints might occur because of competing demands for body tissues (e.g. flight versus refueling during long-distance migration) or for control mechanisms (e.g. parental investment versus intraspecific aggression), as well as for time, energy and nutrients.

The participants agreed that experimental manipulation is a powerful tool for understanding the pathways of how physiological constraints occur. Long-term selection and hormone manipulations are particularly good candidates for studying variation in life-history traits[1]. Phenotypic engineering of life-history strategies[2] allows researchers to isolate experimentally individual phenotypic correlations between life-history traits and to study their physiological and fitness consequences. Williams reported that tamoxifen, an antiestrogen, decreases egg size in zebra finches *Taeniopygia guttata*, whilst simultaneously affecting other life-history characteristics, for example, increasing clutch size. Hormonal manipulation might also break the pervasive correlation between egg size and the nutritional state of a female[3]. Such manipulations might help us to understand why egg size and clutch size are genetically correlated in lizards, but not in birds (Sinervo and Williams).

Neil Metcalfe (University of Glasgow, UK) showed that energy allocation underlies the extreme variation in age at maturity of anadromous salmon *Salmo salar*, which can occur between nine months and nine years of age. Standard metabolic rate, which measures the rate of transformation of energy, determines early growth rate, which is correlated with the age at which individuals migrate to sea (and later mature). Interestingly, growth rate is related to metabolic rate relative to other individuals in the same social group rather than to absolute metabolic rate. Thus, energy metabolism and growth rate appear to be affected by social relationships, including aggression and dominance, which in turn influence physiological and life-history traits[4]. An interesting twist on the theme of energy allocation during growth is that individuals that invest in accelerated growth to recover from unfavorable circumstances often pay a cost in terms of reduced fecundity or reduced survival later in life[5].

Energy allocations also appear to underlie seasonal differences in immune function, reported Randy Nelson (Ohio State University, Columbus, OH, USA). Winter conditions might be challenging immunologically, and many animals, including humans, boost their immune system in anticipation of particularly

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