City Research Online

City, University of London Institutional Repository

This is the accepted version of the paper.

This version of the publication may differ from the final published version.

A temporal model of territorial defence with antagonistic interactions

Tamás Varga[*]
Bolyai Institute
University of Szeged
vargata@math.u-szeged.hu

József Garay[†]
Centre for Ecological Research,
Evolutionary Systems Research Group
Klebelsberg Kuno utca 3, Tihany 8237,
Hungary
garayj@caesar.elte.hu

Jan Rychtář[‡]
Department of Mathematics and Statistics
University of North Carolina at Greensboro
rychtar@uncg.edu

Mark Broom
Department of Mathematics
City, University of London
Mark.Broom@city.ac.uk

Abstract

Territorial behaviour is an important part of the lives of many animals. Once a territory has been acquired, an animal may spend its entire life on it, and may have to repeatedly defend it from conspecifics. Some species make great investments in the defence of a territory, and this defence can be costly, in terms of time, energy and risk of injury. Time costs in particular have rarely been explicitly factored into such models. In this paper we consider a model of territorial defence which includes both population dynamic and time delay elements, building upon recent advances in time constraint models. Populations may divide into two distinct types, where one type makes no effort to control territories. We shall call this type nomads, and the other type territorials. Here the territory owners must divide their time between patrolling and foraging, and this balance is their only strategic decision. We show how to find the evolutionarily stable patrolling strategy and the population composition of territorials and nomads, and consider some examples demonstrating key situations. We see that both time constraints and population density pressure are crucial to influencing behaviour. In particular we find cases with both territorial individuals and nomads where a mixed, either pure or both pure patrolling strategies are evolutionarily stable. In different conditions either nomads or territorials can be absent, and indeed for a significant range of parameter combinations the population can exhibit tristability, with three distinct ecologically stable population compositions: with both nomads and territorials, only nomads or only territorials.

Keywords: evolutionary game theory, territoriality, time constraints, owner-intruder games, density dependence

---

[*]Author for correspondence

[†]Also MTA-ELTE Theoretical Biology and Evolutionary Ecology Research Group, Eötvös Loránd University, Pázmány Péter sétány1/c, H-1117 Budapest, Hungary

[‡]Also Department of Mathematics and Applied Mathematics, Virginia Commonwealth University, Richmond, VA 23284-2014, USA

1 Introduction

Territory is the sociographical area that an animal defends against conspecifics (Adams 2001, Hinsch and Komdeur 2017, Owen-Smith 1977). The evolutionary success of territorial behaviour is determined by the benefits and costs of occupying and defending the territory. Direct benefits include: a) more or less exclusive access to food (Maher and Lott 1995); b) mating opportunities (Sinervo and Lively 1996, Sinervo et al. 2000, Stamps 1987); c) the females deter infanticide (Ostfeld 1990); d) a refuge from predators (Cowlishaw 1997, Everett and Ruiz 1993, Maher and Lott 1995); e) domiciles (e.g. a nest, burrows). There are also indirect benefits, such as the fact that non-owner individuals have limited breeding capability (e.g. Boutin and Schweiger 1988, Stamps 1994) and potentially limited access to food. The cost of territory ownership can be measured in the probability of injury, energy loss and time duration of fighting (Grant et al. 1992) and patrolling. Patrolling can include searching, fighting, scent marking (Schlägel et al. 2017) and any combination of these (Corbet 2004, Golab 2017). Territorial patrolling is costly, requiring both energy and time. For instance, 58% of the total travelling time of chimpanzees is patrolling (Amsler 2010) and dragonflies devote about 20% of their total flight time to patrolling (Parr 1983).

Since all of the costs of territory ownership comes from interaction with conspecifics, only game-theoretical models can give insight into the evolutionary stability of territoriality (for a review see e.g. Hinsch and Komdeur 2017). Fights occur between neighbours and between owners and individuals with no territory ("floaters"), and are often modelled using the Hawk-Dowe game (Hinsch and Komdeur 2010, Kokko et al. 2006, Maynard Smith 1982, Mesterton-Gibbons and Adams 2003, Pereira et al. 2003) including using explicit strategies related to ownership (e.g. the bourgeois strategy, see Maynard Smith 1982, Eshel and Sansone 1995, Grafen 1987). The interaction between neighbours is well studied (Hinsch and Komdeur 2017), for instance when the cost of interaction is high enough, then fights between neighbours occur with low intensity and low cost compared to interactions between owners and intruders (Morrell and Kokko 2005, see also the "dear enemy hypothesis" Getty 1987, Temeles 1994). On the other hand, interactions between owners and floaters can draw our attention to two components of territoriality. Firstly, if the density of floaters is high enough, then irrespective of whether the floaters either avoid fights or are ready to fight, the owner has to spend time and energy either chasing the non-fighter away or beating the aggressive floaters out of its territory. In both cases the owner spends much time defending its territory, consequently the owner has less time for mating and feeding, thus its fitness will be decreased by too many interactions when the intrusion rate is high enough. Furthermore, patrolling also takes extra, e.g. traveling, time. Moreover, territoriality as a competitive behaviour can decrease the total density of the population when owners can monopolize more food than what they really need. Thus, territoriality has a role in population regulation (Brown 1969). Secondly, the density of the non-aggressive floaters depends on whether the owners can or cannot shut floaters out of their territories, and consequently deprive floaters of the chance to breed (Stamps 1994). In this paper we concentrate on these two components of territoriality: the time constraints of owning and defending a territory and the density dependence of interactions (e.g. Both and Visser 2003, Houston and McNamara 2006, Lopez-Sepulcre and Kokko 2005). We discuss these two concepts in turn below.

Time constraints in ecology have important consequences. For instance, in trophic interactions the functional response takes account of time constraints (Holling 1959, Křivan et al. 2008, Garay 2019). Schoener (1987), in the framework of a detailed optimization model, calculates the optimal territory size and patrolling time, as a function of food density and intrusion rate, calling our attention to the importance of the time budget. More recently, time constraints have been considered in game-theoretical models, especially in connection to food-stealing behaviour. Broom and Ruxton (1998) developed a game-theoretic model of kleptoparasitism where individuals could strategically challenge for food, but where contests took time that could be spent searching (e.g. see also Broom et al. 2004, Broom and Rychtář 2011). This model was fitted to a population of foraging

gulls in Spencer and Broom (2018). Such competition over food has similarities and differences to territorial contests. In both cases there is an owner and a challenger (or indeed perhaps more than one challenger, as in Broom and Rychtář 2011) competing for a resource. The value of a territory is likely to be much greater than a food item, leading to more significant (longer, more violent) contests. It may be logical to concede a food item rather than fight, as there is the possibility of finding another uncontested item. For territories, however, there are unlikely to be uncontested ones, and so it is more likely to be better to stay and fight (Morrell and Kokko 2005, Hinsch and Komdeur 2017).

Furthermore, the theory of single-species matrix games under time constraints has been developed (Garay et al. 2017, see also Křivan and Cressman 2017, Cressman and Křivan 2019). Here each interaction has two consequences: a benefit and a waiting time (during which the players are not able to interact) and the concept of a (monomorphic) evolutionarily stable strategy (ESS) in such games was characterized. The common assumption of these game theoretical models is that the individual actions (e.g. fights) exclude each other, e.g., at a particular time each individual is either searching or fighting but cannot do these two activities simultaneously.

As mentioned above, a second important component of the model to understand territoriality is density dependence and its relationship with evolutionary stability. Density dependent evolutionary monomorphic stability for multi-species co-evolutionary ecosystems was introduced in Cressman and Garay (2003a,b). This notion is strictly based on the dynamical perspective; here an ecological equilibrium of a system remains stable when a rare mutant phenotype is introduced in each species and subsequently eliminated according to the population dynamics.

The game theoretical literature of territorial behaviour (starting from the Hawk Dove game) mainly concentrates on the aggressive interactions between owner and intruder (e.g. Morrell and Kokko 2005, Hinsch and Komdeur 2017 and the references within). However, the evolutionary stability of territoriality cannot be fully understood without considering an alternative type of individual, which has no territory and pursues an alternative strategy without striving for territory ownership, and consequently which is free from all costs of the acquisition or ownership of a territory. Whilst the ownership of a territory can guarantee that a male can mate with the females in the territory, the territory owner is not always able to exclude other males from mating with these females.

Fighting over territories will lead to the evolution of enhanced fighting abilities, but these will usually come at some cost, for example larger body size or heavy weapons which require greater resources. Similarly, there can be a range of behaviours that an animal can use in defence of its territory depending upon the value of the territory and the frequency or severity of potential invasions. Often the alternative strategy that we mention above can then become viable; namely not to compete for territories at all, and thus dispense with the extra resources required to be an effective competitor. Some species can then diversify into different types with different physical forms, adapted to either fighting for territories or obtaining resources in an alternative way.

For instance, a well-known example is that of the side-blotched lizard (*Uta stansburiana*). Ultra-dominant orange-throated males establish and control large territories, but are not able to prevent the yellow stripe-throated males ("sneakers") from mating with "their" females (Sinervo and Lively 1996, Sinervo et al. 2000). Here the main point is that the yellow stripe-throated males do not, and never will, have a territory. Similar phenomena take place in the case of sunfish and salmon (e.g. Gross 1984 and references therein, Gross and Charnov 1980). Thus we will consider a non-territorial phenotype, called a nomad, which has no territory and does not get involved in fights.

To summarise, in connection with territorial behaviour two questions arise: (i) How much time and energy is necessary to keep a territory? (ii) Is it worth to keep a territory from the evolutionary aspect at all? This article focuses on both questions and during the development of the model we primarily imagine a territory which mainly provides food for the owner. We can also say that territorial interactions can increase the growth rate of the territorial type through access to the

resource in our model. The model therefore investigates the questions from the energetic aspect so that we focus on two factors mentioned in the introduction during the development of the model: time constraints and density dependence.

We follow the often used methodology of mathematical ecology of separating the time scale of interactions between individuals from the time scale of the population process (e.g. Metz et al. 1992, Geritz et al. 1998, Bolker et al. 2003, Werner and Peacor 2003, Cressman and Garay 2003a,b, Abrams 2005, Vincent and Brown 2005, Dercole and Rinaldi 2008, Abrams 2010)[1]. This also implies that neither of the participants can die in a fight (albeit there are well-known cases of this, for instance, fig wasps (Hamilton 1979) or ungulates (Clutton-Brock 1982)). The territorial interaction (that is the fight for the territory) nevertheless decreases the fitness of both participants in the model introduced in the present article too, but this is considered through loss in intake (energy) and time. This presumption on mortality is realistic for several species. For instance, among songbirds the main territorial behaviour is singing which is chiefly energetically costly (Berg et al. 2005). It seems if there is a fight for the territory then the outcome is rarely death. For example, in the collared flycatcher (*Ficedula albicollis*) males actively defend a small surrounding area of their nesting holes during the mating period, but no mortal interaction has been experienced in over 15 years of experiments in the Pilis Mountains (Hungary) (personal communication by János Török). Numerous studies have shown that in territorial defence threats, song and scent marking have a number of advantages over violent combat, because of e.g. elimination of the risk of injury, and so death (Johnson 1973, Brown 1975, Maynard-Smith 1982, Gosling 2010), lower energetic costs (Brown 1975) or less reduced predator vigilance (Dunn et al. 2004).

The paper is organised as follows. In Section 2 we explain our model. In Section 3 we find the "right" strategy for our population, i.e. find the Nash equilibrium strategy. In Section 4 we consider the stability of such a population against potential invading "mutants" of an alternative type. Finally in Section 5 we discuss our results and future work.

2   The Model

In this section we consider the details of the model, introducing the biological scenario, the mathematical details and the parameters and develop the analysis for a "resident" population where a single strategy (as later defined) occurs.

2.1   The biological scenario

We consider a population in which there are two types of individual that we shall term territorials and nomads. As previously described these could be male individuals who aim to secure mates either by owning a territory which can support a group of females (the territorial individuals) or by an opportunistic strategy which involves mating with females wherever the opportunity arises. Alternatively the resources could be food, and it is the latter case that we shall use in the terminology that follows. In any case, there can be at most one territory owner in a territory, and territories are only left empty if there are insufficient territorials to occupy them all.

Nomad individuals wander through the field regardless of the territory borders looking for prey. If they come across a territory owner they flee. The two styles of living exclude one another. A territorial individual having a territory (i.e. an owner) lives on its territory which it never leaves. It defends the territory against intruding territorials and nomads or hunts for prey inside the territory. A territorial individual without a territory (i.e. an intruder) looks to challenge for a territory and

---

[1]There are now a number of models which do not have such a separation of timescales (Levin 1992, Argasinski 2012, 2013 and 2018, Argasinski and Rudnicki 2017), and where significant differences are demonstrated (Cressman R. and Křivan V. 2013).

4

for prey to consume. If it comes across a territorial individual having a territory then they fight over the territory and the winner gets the territory while the loser becomes/remains an intruder.

An owner can follow one of the two pure strategies:

The *patroller strategy:* the owner looks for intruders. It does not find any prey (if so, then it neglects the prey). Then its intake derives only from a background intake which every owner has (this could be a share of prey captured by subordinate groupmates within the territory). The patroller strategy can be advantageous if the owner successfully defends its territory with a higher probability than the owners following the predator strategy (see below), otherwise it is not worth following the patroller strategy. Therefore we focus on the situation when a territory owner following the patroller strategy wins with a higher probability than when following predator strategy.

The *predator strategy:* the owner looks not only for intruders but also for prey (the term "predator" is used due to the latter). Therefore, an intake from the prey comes in addition to the background intake but (we assume that) the owner successfully defends its territory with a lower probability than when following the patroller strategy. This is, to say, the cost of the predator startegy.

We are interested in which strategy will evolve in the population. To investigate this question we have to calculate the fitnesses of our different types, which will depend upon their densities within the population. We use two approaches, that operate on different timescales. The first is a population dynamic model similar to the Lotka-Volterra equations which describes the evolution of the nomads and territorials by differential equations (the slower process). This involves game-theoretical fitness terms derived following the second approach using the methodology of Garay et al. (2017), which considers a stochastic behavioural dynamics process of individuals moving between population states for any given population composition (the faster process).

2.2 Population terminology and parameters

Here we consider the key terminology and parameters of the model, breaking it down into distinct parts based upon the different aspects of the model.

2.2.1 Population densities

We assume that the population follows a stochastic process moving between a number of states. We shall consider this in detail in Section 2.3. The population density of the nomads is denoted by x and of the territorials is denoted by y, scaled to the number of territories, i.e. the population density of territories is 1. Equivalently y is the number of territorial individuals per territory, and x is the number of nomads per territory. Thus if $y \leq 1$ there are enough territories for all territorials to have one, but if $y > 1$ there are not, and they have to contest them. Then we assume that every territory is possessed by a single territorial (i.e. owner) and the other territorials remained without territory get to intruder position so the density of territorial owners is 1 while that of territorial intruders is $y - 1$. It is x and y which evolve on the slow timescale (we shall see how to find the values of x and y in Section 2.4), and for the purposes of the faster stochastic model, these can be considered fixed.

2.2.2 Events and time constraints

Here we shall introduce some parameters and concepts. Each individual can be involved in a number of different activites, which can provide some reward or cost, and in turn can lead onto other activites. We first describe the activies and their (expected) durations below, before considering the rewards and costs.

Time constraints: If an individual is busy with regeneration after fighting, handling a prey or fleeing, respectively, then it cannot be involved in another activity (fighting or fleeing or hunting),

Table 1: The model parameters and notation

Parameter	Meaning
x, y, z	Density of nomads, resident and mutant territorials
ϱ_n	Proportion of active nomads among nomads
ϱ_o	Proportion of active owners among owners
ϱ_a	Proportion of active patrollers among patrollers
ϱ_r	Proportion of active predators among predators
ϱ_i	Proportion of active intruders among intruders
b	Steady contribution in the intake rate of an owner
i_h	Benefit gained from a pray
c_w, c_l	Cost of injury of the winner/loser in a fight
c_f	Cost of fleeing
t_w, t_l	Duration of regeneration after winning/losing a fight
t_h	Time necessary to handling a prey
t_f	Time necessary for a nomad to fleeing from a territory owner
α_a, α_r	Probability that a patroller/predator wins a fight
d	Cost rate of maintenance
c_{nn}	Nomads on nomads (density dependent Lotka-Volterra) competition coefficient
c_{nt}	Nomads on territorials (density dependent Lotka-Volterra) competition coefficient
c_{tn}	Territorials on nomads (density dependent Lotka-Volterra) competition coefficient
c_{tt}	Territorials on territorials (density dependent) competition coefficient
λ_i	Rate of finding an active intruder
λ_o	Rate of finding an active owner
λ_h	Rate of finding a prey
λ_r	Rate of reconsidering the state without fight
f	Normalized rate of encountering a territory
p, q, r	Probability of choosing the patroller state for residents/mutants at reconsiderations
F	Fitness of an average nomad
G	Fitness of an average resident territorial
H	Fitness of an average mutant territorial

(The aim of the table is just to recall the notations but the definitions given here are necessarily brief. For the precise definitions of the notations, see the relevant text.)

and we assume that it is effectively invisible for individuals searching for a fighting partner or prey. Such an individual is considered to be *inactive* while an individual in the searching state is considered to be *active*. This, for example, means that if a territory owner looks for intruders then it can only encounter those intruders or nomads which are active. Therefore the probability of an encounter with territorial intruders or nomads is proportional to the density of active territorial intruders and nomads rather than the total density of territorial intruders and nomads.

ϱ_o, ϱ_i, ϱ_n, ϱ_a, ϱ_r are the proportion of active (i.e. searching) individuals among the territorial [o]wners, the [i]ntruder territorials, [n]omads, territorial owners in the p[a]troller state and territorial owners in the p[r]edator state (see below for a detailed explanation), respectively. These are not fixed parameters, but depend upon y in our model, and we shall evaluate them explicitly in Section 2.3.5.

Different encounters cost specific expected amounts of time (the so called "waiting time" which might be 0). In each case we assume an exponentially distributed length of time with the following means. We have:

t_h is the expected time length of handling the prey,

t_f the expected time length for a nomad to flee from a territory owner,

t_w (t_l) the expected time length of regeneration after winning (losing) a territory owner versus intruder fight, i.e. the time depends only upon the outcome of the fight, and not the initial state of the individual concerned. For losing this could include some fleeing time, as above. For simplicity the time of the fight itself is assumed to be zero (alternatively this could be non-zero and included in the winning/losing regeneration times).

2.2.3 Rewards and costs

Depending upon whether an individual owns a territory and on what events occur, there are a number of rewards and costs that they can receive. These are as follows:

b is a steady (baseline) contribution in the expected intake rate of an owner. This is the main benefit of having a territory. This can derive from, for example, the fact that the owner knows its territory better or one can imagine the owner as a leader of a group, for instance a male in a pride of lions, and the group provide the significant benefit of a steady supply of food, giving the contribution b in the expected intake rate. An alternative is where the reward is in terms of mating opportunities, and an owning male has (almost) exclusive access to a group of females, and this also applies in the lion example.

i_h is the benefit gained from consuming a prey item.

c_w is the cost of the injury to the winner in a fight.

c_l is the cost of the injury to the loser in a fight.

c_f is the cost of fleeing.

There are also indirect costs which do not relate directly to the interactions, but come about through independent effects.

d is the cost rate (cost per time) of maintenance; all individuals consume resources simply to stay alive, and these are then not available for reproduction.

c_{nn}, c_{nt}, c_{tn} and c_{tt} are the density dependent (Lotka-Volterra) competition coefficients depending on the phenotypes; these are the costs of nomads on nomads, nomads on territorials, territorials on nomads and territorials on territorials , respectively. This derives from the fact that the general environmental resources, such as water, places (like the appropriate nest site, refuge etc. Rodenhouse et al. 1997), used by the individuals are bounded. One can think that the more individuals there are the harder it is to obtain the given environmental resources or the worse the quality of the environmental resources are, and that different types of individuals can have different effects. Moreover, in the case of territoriality, monopolising the resources of a territory can continue to increase the negative effect of the territory owners on the fitnesses of the individuals excluded.

2.3 The stochastic process

In our model we consider an ecological system of two types which evolves over a considerable period of time (following the differential equation model that we shall introduce in Section 2.4), so that the values of x and y change as individuals are born and die. We assume that this process happens on a much slower timescale than that involving interactions between individuals, where it can be assumed that over the course of this process, x and y do not change.

To give the terms deriving from direct interactions we follow the Markov model of Garay et al. (2017). Different events (hunting, fighting etc. depending on the interpretation) can happen to an individual. The events have rates which give how often they can be expected to occur (as if the time between two events of the same type were an exponential random variable) and after every event there is some duration, the waiting time which the individual has to wait and the length of which depends on the event. The waiting time is also assumed to be an exponential random variable; it represents the regeneration time after a fight, the handling time necessary for handling a prey and so on. The event itself is assumed to have zero, negligible duration or one can think that it is included in the waiting time. During waiting time events cannot occur. Furthermore every event leads to some (maybe negative or zero) intake for the individual.

An individual "searches" for events. During this searching state it experiences any given event at some above mentioned rate (some time will elapse before an event occurs). After experiencing an event the individual has to wait the waiting time related to the event and when the waiting time finishes the individual starts to search again (Figure 1). It is important to note, though we speak about "search", it is just an intuitive terminology (and we use the terminology of Garay et al., 2017) how can one interpret the time between two adjacent events. One can call it "waiting for the next event" and so on. Accordingly, the "search" is not an event in our model. Since the rate at which events occur, the duration of waiting times and the intakes derived from the events vary with the events, we calculate an average time length for an event to happen and an associated average intake per event. The expected intake rate is then calculated as the quotient of these two values.
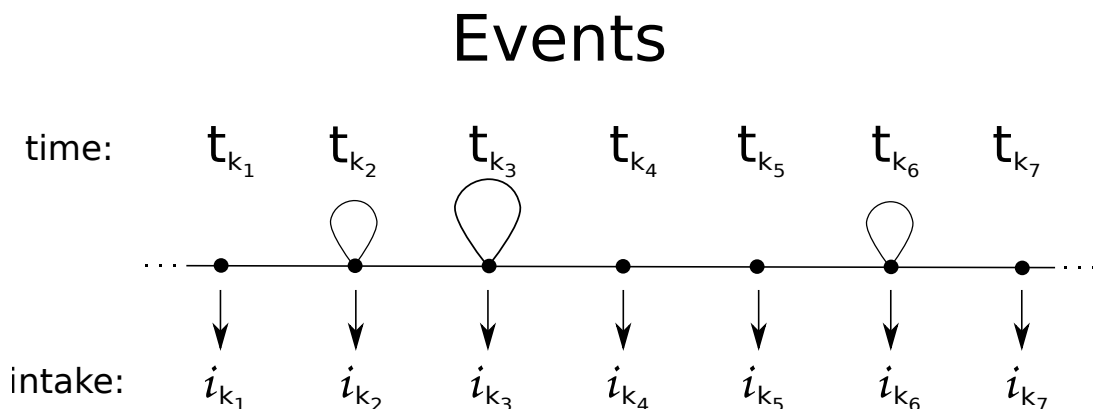

Figure 1: The diagram schematically depicts a part from a life of an individual. The nodes correspond to the events following each other. The loops on the nodes represents the waiting time after the given event. (If there is no loop then the waiting time is 0.) A section between two adjacent nodes corresponds to a "search". $k_1, \dots, k_7$ denotes the serial number of the events. If there are n different kinds of events with rates $\lambda_1, \dots, \lambda_n$ then $k_1, \dots, k_7 \in \{1, 2, \dots, n\}$ and the probability that $k_j = k$ is $\lambda_k / (\lambda_1 + \dots + \lambda_n)$. The length of a section and a loop is an exponential variable but on the figure we use their expected values. This is why the lengths of sections between nodes are equal.

Formally, assume that there are n different events with rates $\lambda_1, \ldots, \lambda_n$ with related waiting times $t_1, \ldots, t_n$ and intakes $i_1, \ldots, i_n$. Denote by Λ the sum $\sum_k \lambda_k$. Then we calculate the fitness as the expected intake per event divided by the expected time between two consecutive events (consisting of the waiting time – the average length of a loop on Figure 1 – after the first event and the search – the length of a section between two consecutive nodes on Figure 1) –), i.e.

$$\frac{\sum_{k=1}^{n} \frac{\lambda_k}{\Lambda} i_k}{\frac{1}{\Lambda} + \sum_{k=1}^{n} \frac{\lambda_k}{\Lambda} t_k} = \frac{\sum_{k=1}^{n} \lambda_k i_k}{1 + \sum_{k=1}^{n} \lambda_k t_k}. \tag{2.1}$$

Note that the (expected) time duration between two adjacent events (not including the waiting time) is just $1/\Lambda$ (the expected value of the sum of exponential random variables with parameters $\lambda_1, \ldots, \lambda_n$). In our heuristic interpretation this corresponds to the average searching time and λ_k/Λ is the probability of the k-th event occurring.

Accordingly, since we know the rewards/costs and times associated with each activity, we can calculate the part of the fitness deriving from direct interactions (owning a territory, consuming prey, fighting and fleeing), which we do in Section 2.4.

2.3.1 Transitions and rewards for territory owners

An owner chooses the **patroller state** with probability p in every reconsideration event (see below). In this state, it only gains rewards through the steady background intake rate b. The value of p is the only strategic element within the model. We consider the possible events which can occur depending on the chosen strategy.

An active patroller can encounter the following events:

To find an active intruder with rate $\lambda_i = f\varrho_i[y - \min(y, 1)]$, where f is the rate at which any given active intruder encounters a territory (we will call f the *unit rate*). Here we assume that if $y \leq 1$, all territorials have a territory and so there can be no intruder; if $y > 1$, the density of territorials without territories is $y - 1$. When they meet, they fight for the territory. The defeated individual will be without a territory and gets injured, which is considered as a negative intake $-c_l$. The winner obtains the territory but also potentially gets injured which means an intake $-c_w$. The waiting time after a fight event can be considered as the regeneration process which is t_w after winning a fight whilst it is t_l after losing a fight (the duration of the fight itself is assumed to be 0). After regeneration, the territory owner (either the original owner or the new owner if the intruder wins) will reconsider its state with duration 0, and will select the patroller state with probability p. We cannot distinguish the winner from the original owner (the owner before the fight). It can be the original owner or the original intruder but this does not matter from the point of view of the territorial population; the winner will always be the owner after the fight, and the loser will always be an intruder. A patroller owner wins with probability α_a.

To find an active nomad with rate $\lambda_n = f\varrho_n x$. For simplicity, we use the same unit rate f as in λ_i (for more explanation see Section 2.3.4) and we assume that the waiting time after the event needs no time and means zero intake for the owner, that is, nomads have no direct effect on territorial owners. Accordingly, no term corresponding to this event occurs in the formula describing the fitness deriving from direct interactions (see Section 2.4.1).

To reconsider the state: the owner can reconsider its search strategy (patroller or predator) with rate λ_r, again choosing patroller with probability p. The waiting time after a reconsideration is 0. We note that this is the second way a reconsideration can happen, as it also happens after a fight (as described above). Hence, the reconsideration rate is $\lambda_r + \lambda_i$ altogether. Note that with the term "reconsediration" we refer to a situation where owner thinks again about its strategy in order to decide if it should be changed or not. So it is not certain that the owner change its strategy even if the word "reconsideration" may suggest that.

9

An owner chooses the **predator state** with probability $1 - p$. The word "predator" refers to the fact that the owner searches not only for intruders but for prey which are a further positive intake in addition to the steady background intake rate b. The disadvantage of the predator strategy derives from the trade-off between vigilance and feeding/foraging/hunting (Lima 1990, McNamara and Houston 1992, Lima and Bednekoff 1999). One can think that the hunt distracts the attention of the owner from the defence of its territory, it is therefore easier to surprise it and so it loses its territory easier than an owner following the patroller strategy. For example, a teal (*Anas crecca*) often uses a feeding method with its eyes beneath the water and so becomes unable to perceive potential attackers above the water (Pöysä H. 1987). Following this reasoning the value of winning a fight is taken to be smaller for the predator state than for the patroller state in our examples (see Section 2.5).

An active predator can encounter the following events:

To find a prey with rate λ_h. The intake is i_h and the (waiting) time necessary for handling the prey is t_h.

To find an active intruder with rate λ_i. The scenario is the same for the patroller case except that the owner wins with probability α_r instead of α_a.

There are two further events each of which occur in an identical way to those for the patroller. Namely:

To find an active nomad with rate λ_n.

To reconsider the state with rate λ_r independently of finding something.

An inactive owner (being in patroller or predator state) is in a waiting time related to one of the events (finding a prey, an active intruder or a reconsideration). Then the individual is invisible for the other members of the population. After the waiting time elapsed the owner becomes active, that is, starts searching.

2.3.2 Transitions and rewards for territory intruders

An active *territorial intruder* looks for prey and for the opportunity to acquire a territory. An intruder encounters the following events:

To find an active owner with rate $\lambda_o = f \varrho_o \min(1, 1/y)y$. The event is discussed above (see the owner in the patroller state).

To find prey with rate λ_h. The intake is i_h and the time necessary for handling the prey is t_h.

To find an active nomad/territorial intruder with rate λ_n and λ_i, respectively. For simplicity, the waiting times are zero and the events mean zero intake for the intruder, that is, nomads/intruders have no direct effect on territorial intruders (accordingly, no term corresponding to these events occurs in the formula describing the fitness for intruders deriving from direct interactions).

An inactive territorial intruder is in a waiting time related to one of the events (finding a prey or an active owner). Then the individual is invisible for the other members of the population. After the waiting time elapsed the intruder becomes active, that is, starts searching.

2.3.3 Transitions and rewards for nomads

A *nomad* looks for prey. If it encounters a territory owner then it first flees, and only after that starts a new searching phase. A nomad can encounter the following events:

To find an active owner with rate λ_o. Then the nomad flees. Fleeing takes a time t_f and costs c_f

To find prey with rate λ_h. The intake is i_h and the time necessary for handling the prey is t_h.

To find an active nomad/territorial intruder with rate λ_n and λ_i, respectively. For simplicity, the waiting times are zero and the events mean zero intake for the nomad, that is nomads/intruders have no direct effect on nomads. Accordingly, no term corresponding to these events occurs in the formula describing the fitness for nomads deriving from direct interactions.

An inactive nomad is in a waiting time related to one of the events (finding a prey or an active owner). Then the individual is invisible for the other members of the population. After the waiting time elapsed the nomad becomes active, that is, starts searching.

2.3.4   Pairwise interactions

In the above, there are a number of possible interactions; each of owners, intruders and nomads can meet others who are owners, intruders or nomads (except that as owners never leave their territory, owners cannot meet other owners). As described above, meetings between intruders or nomads with intruders or nomads have no effect on the payoff. This leaves four key interactions. Owners meeting intruders, owners meeting nomads, intruders meeting owners, and nomads meeting owners.

In the above we have used the same unit rate f in all four of these expressions. In fact this is a natural (and in some cases necessary) assumption. Suppose that f_i was the unit rate for the intruders meeting owners and f_o was the unit rate for the owners meeting intruders. Since the total rate of active owners meeting active intruders must be the same as the total rate of active intruders meeting active owners (if I meet you, you must meet me) we have

$$\underbrace{f_i \varrho_i [y - \min(1, y)]}_{\lambda_i} \varrho_o \min(1, y) = \underbrace{f_o \varrho_o \min(1, y)}_{\lambda_o} \varrho_i [y - \min(1, y)].$$

We infer that $f_i = f_o$.

A similar argument holds for the unit rates for owners meeting nomads and nomads meeting owners. It could be that this meeting rate is different to that from above, but for simplicity we assume that all four unit rates are the same.

2.3.5   Calculating the active state probabilities

We still need to calculate the probability that a given type of individual is active (i.e. is searching). An individual is active with some probability, say ϱ, and we assume if we take a glance at the population then we find that the ϱ part of the population is active as if the individuals were active or inactive independently of each other (there is no synchronization in the population such as everybody is inactive at night), and the size of the population is effectively infinite. This assumption is a theorem (Theorem 1) in the model of Garay et al. (2017). Hence we have that the active proportion of territorial owners being in the patroller state is

$$\varrho_a = \frac{\frac{1}{\lambda_r + \lambda_i}}{\frac{1}{\lambda_r + \lambda_i} + \frac{\lambda_i}{\lambda_r + \lambda_i} t_w} = \frac{1}{1 + \lambda_i t_w}, \qquad (2.2)$$

The numerator $1/(\lambda_r + \lambda_i)$ (of the middle expression) corresponds to the duration of the search between two adjacent reconsiderations while the denominator (of the middle expression) corresponds to the duration of the search between two adjacent reconsiderations $(1/(\lambda_r + \lambda_i))$ and the expected waiting time after the first reconsideration $([\lambda_i/(\lambda_r + \lambda_i)]t_w)$. To get this expected waiting time one can argue as follows: since the waiting time is zero after a reconsideration not related to a fight and t_w after a reconsideration related to a fight and the probability of a reconsediration relating to a fight is $\lambda_i/(\lambda_r + \lambda_i)$ it follows that the expected/average waiting time after a reconsideration is $[\lambda_i/(\lambda_r + \lambda_i)]t_w$. Recall, furthermore, that the new owner and the original owner of a territory cannot be distinguished (see Section 2.3.1). In this sense the owner always appears to win. If the original owner is defeated, from that time it is not an owner any longer and the original intruder becomes the owner. This may seem strange at first sight but we focus on the population of a given phenotype and not a given individual. This approach of recording the cost of winning and losing fights makes the formulas more trtansparent, but one can consider that this does not influence the

formulas with respect for an "average" individual (e.g. (2.11)). Similarly, the active proportion of territorial owners being in the predator state is

$$\varrho_r = \frac{\frac{1}{\lambda_r+\lambda_i}}{\frac{1}{\lambda_r+\lambda_i} + \frac{\lambda_i}{\lambda_r+\lambda_i}t_w + \frac{\lambda_h}{\lambda_r+\lambda_i}t_h} = \frac{1}{1 + \lambda_i t_w + \lambda_h t_h}. \tag{2.3}$$

The numerator is the same as for the patroller state but in the denominator the time necessary for handling the preys, $\lambda_h/(\lambda_r + \lambda_i)$ (the expected number of prey items caught between two adjacent reconsiderations) appears in addition to the sum of the search time between two adjacent reconsiderations and the waiting time after the first reconsideration. The active proportion of territory owners is

$$\varrho_o = \frac{p\frac{1}{\lambda_r+\lambda_i} + (1-p)\frac{1}{\lambda_r+\lambda_i}}{p\left(\frac{1}{\lambda_r+\lambda_i} + \frac{\lambda_i}{\lambda_r+\lambda_i}t_w\right) + (1-p)\left(\frac{1}{\lambda_r+\lambda_i} + \frac{\lambda_i}{\lambda_r+\lambda_i}t_w + \frac{\lambda_h}{\lambda_r+\lambda_i}t_h\right)}$$
$$= \frac{1}{1 + \lambda_i t_w + (1-p)\lambda_h t_h}, \tag{2.4}$$

the active proportion of territorial intruders is

$$\varrho_i = \frac{\frac{1}{\lambda_o+\lambda_h}}{\frac{1}{\lambda_o+\lambda_h} + \frac{\lambda_o}{\lambda_o+\lambda_h}t_l + \frac{\lambda_h}{\lambda_o+\lambda_h}t_h} = \frac{1}{1 + \lambda_o t_l + \lambda_h t_h}, \tag{2.5}$$

the active proportion of nomads is

$$\varrho_n = \frac{1}{1 + \lambda_o t_f + \lambda_h t_h}.$$

2.4 Population dynamics and the fitness functions

As stated in Section 2.2.1, x is the density of nomads (the number of nomad individuals per territory) and y is the density of territorial individuals (the number of territorial individuals per territory).

We interpret the fitness as a reproductive rate. Consider the following model:

$$\dot{x} = xF(x,y) \tag{2.6}$$
$$\dot{y} = yG(x,y)$$

where F and G, respectively, correspond to the fitness of an average nomad and an average territorial, respectively. The fitness functions (F, G) above include the effect of direct interactions (hunting, fighting, fleeing), indirect interactions (using common environmental resources) and maintenance. Note that such a differential equation model focuses on only the biomass of the population but not the different individuals. The individuals of the same type can not be distinguished from each other. The death of an individual hence simply means a decrease of the biomass.

To calculate G and F we follow Garay et al. (2017). As previously stated, we assume that the stochastic process governing direct interactions happens on a faster timescale to the population dynamic process, so that we assume here that x and y are effectively constant. In this period (call it the foraging season), the individuals gather/lose the energy which can be used to reproduce. This time is long enough to reach a stationary state; moreover, the time when the population is not in the stationary state is negligible. After this period comes a period (call it the breeding season) when gained/lost rewards are transformed into births and deaths. The model (2.6) describes the long-term evolutionary consequences of many foraging seasons and breeding seasons in turn. We assume that the fitness of an individual (or the biomass of individuals of the same type) for a given breeding season is determined in the previous foraging season.

2.4.1 The direct interaction fitnesses

By formula (2.1), the term representing the direct interactions in the fitness of a nomad, a component of fitness F, is:

$$\frac{\lambda_h i_h - \lambda_o c_f}{1 + \lambda_o t_f + \lambda_h t_h}. \tag{2.7}$$

Similarly, by (2.1) we get the following terms in the fitness G deriving from direct interactions: The term representing the direct interactions of a territorial owner in the patroller state is

$$D_a = b + \frac{-\lambda_i c_w}{1 + \lambda_i t_w}.$$

The term representing the direct interactions of a territorial owner in the predator state is

$$D_r = b + \frac{-\lambda_i c_w + \lambda_h i_h}{1 + \lambda_i t_w + \lambda_h t_h}.$$

Before giving the term representing the direct interactions of a territorial intruder we need to know the proportion of patrollers and predators, respectively, among the territorial owners. We know that an owner can reconsider its strategy only if there is a reconsideration event, or at the end of a fight (recall that it does not matter who is defeated in the fight because the winner is indistinguishable from the original owner for an outside observer). Hence the time from a reconsideration event until the next reconsideration event in the patroller state is

$$T_a = \frac{1}{\lambda_r + \lambda_i} + \frac{\lambda_i}{\lambda_r + \lambda_i} t_w = \frac{1 + \lambda_i t_w}{\lambda_r + \lambda_i},$$

(cf. the denominator of expression (2.2) for ρ_a) whilst in the predator state, this is

$$T_r = \frac{1}{\lambda_r + \lambda_i} + \frac{\lambda_i}{\lambda_r + \lambda_i} t_w + \frac{\lambda_h}{\lambda_r + \lambda_i} t_h = \frac{1 + \lambda_i t_w + \lambda_h t_h}{\lambda_r + \lambda_i}.$$

(cf. the denominator of expression (2.3) for ρ_r) Therefore, in the stationary state, a randomly chosen owner is in the patroller state with probability

$$\frac{pT_a}{pT_a + (1-p)T_r} = \frac{p\frac{1+\lambda_i t_w}{\lambda_r + \lambda_i}}{p\frac{1+\lambda_i t_w}{\lambda_r + \lambda_i} + (1-p)\frac{1+\lambda_i t_w + \lambda_h t_h}{\lambda_r + \lambda_i}} = \frac{p(1 + \lambda_i t_w)}{1 + \lambda_i t_w + (1-p)\lambda_h t_h} =: \pi \tag{2.8}$$

and it is in the predator state with probability $1 - \pi$. Hence the term representing the direct interactions of a territorial intruder is

$$D_i = \frac{-\frac{\lambda_o}{\lambda_o + \lambda_h} c_l + \frac{\lambda_h}{\lambda_o + \lambda_h} i_h}{\frac{1}{\lambda_o + \lambda_h} + \frac{\lambda_o}{\lambda_o + \lambda_h} t_l + \frac{\lambda_h}{\lambda_o + \lambda_h} t_h} \tag{2.9}$$

$$= \frac{-f\min(1, y)[\varrho_a \pi c_l + \varrho_r(1 - \pi)c_l] + \lambda_h i_h}{1 + \lambda_o t_l + \lambda_h t_h}. \tag{2.10}$$

Note that $\lambda_o = f\min(1, y)\varrho_o = f\min(1, y)[\pi\varrho_a + (1 - \pi)\varrho_r]$. The first term in the denominator of the middle expression is the expected duration between two consecutive events (fight or finding a prey) that is the sum of the duration of search and the average waiting time after the first event which is a fight (encountering an owner) with probability $\lambda_o/(\lambda_o + \lambda_h)$ and finding a prey with probability $\lambda_h/(\lambda_o + \lambda_h)$. The numerator of the middle expression is just the expected intake from an event.

Now that we know D_a, D_r and D_i we can find the term representing the direct interactions in the fitness of a "mean" territorial (which is in owner position with probability $\min(1, y)/y$ and in intruder position with probability $[y - \min(1, y)]/y)$ as

$$D(y) = \frac{1}{y}\{\min(1, y)[\pi D_a + (1 - \pi)D_r] + [y - \min(1, y)]D_i\}$$

$$= \begin{cases} \pi D_a + (1 - \pi)D_r & \text{if } y \leq 1 \\ \frac{1}{y}[\pi D_a + (1 - \pi)D_r + (y - 1)D_i] & \text{if } y > 1 \end{cases} \qquad (2.11)$$

After substitution ($\lambda_i = f[y - \min(1, y)]\varrho_i$, $\lambda_o = f[y - \min(1, y)]\varrho_o = f[y - \min(1, y)][\pi\varrho_a + (1 - \pi)\varrho_r]$) we get, if $y \leq 1$ (note that $\lambda_i = 0$ now) then

$$D(y) = b + (1 - \pi)\frac{\lambda_h i_h}{1 + \lambda_h t_h};$$

if $y > 1$ then

$$D(y) = \frac{b}{y} - \frac{f}{y}(y - 1)\varrho_i\varrho_o(c_w + c_l) + \frac{(1 - \pi)\varrho_r + (y - 1)\varrho_i}{y}\lambda_h i_h$$

$$= \frac{1}{y}\Big(b - f(y - 1)\varrho_i\varrho_o(c_w + c_l) + (1 - \pi)\varrho_r\lambda_h i_h + (y - 1)\varrho_i\lambda_h i_h\Big), \qquad (2.12)$$

where b is the steady (baseline) contribution in the expected intake rate of an owner (the benefit of having a territory), term $f(y - 1)\varrho_i\varrho_o(c_w + c_l)$ describes the costs of fights for territories, term $(1 - \pi)\varrho_r\lambda_h i_h$ gives the benefit of hunting by territory owners in the predator state while term $(y - 1)\varrho_i\lambda_h i_h$ gives the benefit of hunting by territorials in the intruder position. The multiplier $1/y$ is a normalisation factor. It ensures that the expression (2.12) corresponds to the fitness rate of an average territorial. Note when $y \leq 1$ the term D is independent of y.

2.4.2   Evaluating G and F

The simpler part of the fitness derives from the indirect interactions and maintenance. The former is considered as a term $-c_{nt}x - c_{tt}y$ and $-c_{nn}x - c_{tn}y$, respectively, the latter as term $-d$. These terms are present both in F and G.

Now using the stochastic process described in Section 2.3 we can give the concrete shape of G. Note that when we calculate G we would like to get the fitness of an average territorial individual so G can be considered as the expected fitness of a randomly chosen territorial individual.

Using the equations (2.7) and (2.12) we get the following formulae for the fitnesses G and F:

$$G = G(x, y) = -d - c_{nt}x - c_{tt}y + D(y),$$

$$F = F(x, y) = -d - c_{nn}x - c_{tn}y + \frac{\lambda_h i_h - \lambda_o c_f}{1 + \lambda_o t_f + \lambda_h t_h}, \qquad (2.13)$$

where d represents the cost of maintenance or, in other words, the background death rate, the term $-c_{nt}x - c_{tt}y$ and term $-c_{nn}x - c_{tn}y$, respectively, describe the density dependent indirect competitions (e.g. if the the density of nomads is x then the nomads decrease the fitness rate of a territorial by $c_{nt}x$), $D(y)$ is the contribution of direct interactions (benefit of having a territory, hunting, fights) to the fitness rate of a territorial (for details see (2.12)) while $(\lambda_h i_h - \lambda_o c_f)/(1 + \lambda_o t_f + \lambda_h t_h)$ is the contribution of direct interactions (hunting, fleeing) to the fitness rate of a nomad (see (2.7)).

2.4.3 The steady states of the dynamical system

For any particular territorial strategy p, we can now follow the evolution of the system (2.6) to its steady states. As we shall see in the examples in the next section, there can be more than one steady state to the system. In any given steady state, (x^*, y^*), we will have specific values of x and y that can be used in any of the components of the payoff function and we will thus be able to consider the evolutionary stability of the strategy p which led to this steady state. We shall first consider some examples.

2.5 Examples

In this section we consider some examples with a stable interior equilibrium in which both nomads and territorials are present in the system with positive density and with stable equilibria when only one of them are present with positive density. It is important to emphasize that there are no mutants in the territorial population in the present section, the population of territorials is monomorphic and we only investigate whether an ecological equilibrium of nomads and territorials is possible with respect to the dynamics (2.6). Later (in Sections 3 and 4) we analyze what occurs if some mutants appear in the territorial population at the interior equilibrium.

In each example the corresponding differential equation system given in (2.6) has a stable interior ecological equilibrium and, in some cases, there are two further stable equilibria in which there are no nomads or no territorials so these cases together show ecological tristability. In the equilibria (both the interior and the boundary one) containing territorials the density of them is greater than 1 which means that there are both owners and intruders in the territorial population. In this paper we principally focus on the "upper part" of the phase space, that is, when $y \geq 1$. However, to get an example for an equilibrium in which the density of the territorials is zero we have also investigated the $y < 1$ case.

To find appropriate parameters we have used a computer algebra (Mathematica 11.3) which is capable of symbolic calculations. Thus our results are exact. We consider six examples below, each of which demonstrate a distinct situation:

1. Parameters: $f = 1/10$, $\lambda_h = 4/25$, $t_h = t_f = t_w = t_l = 0$, $c_w = 1/15$, $c_l = 1/4$, $c_f = 1/10$, $c_{tn} = 1/100$, $c_{tt} = 1/1000$, $c_{nn} = 1/600$, $c_{nt} = 1/250$, $i_h = 3/10$, $d = 1/1000$, $\alpha_a = 9/10$, $\alpha_r = 1/2$ and $b = 21/100$. The patrolling strategy for this example is $p = 15475/19208$.

2. The parameters are the same as in Example 1, except that $b = 205/1000$ and $p = 0$.

3. The parameters are the same as in Example 1, except that $b = 215/1000$ and $p = 1$.

4. Parameters: $f = 1/10$, $\lambda_h = 4/25$, $t_h = t_f = t_w = t_l = 0$, $c_w = 1/15$, $c_l = 1/4$, $c_f = 1/10$, $c_{tn} = c_{tt} = c_{nn} = c_{nt} = 1/300$, $i_h = 4/10$, $d = 1/500$, $\alpha_a = 9/10$, $\alpha_r = 1/2$ and $b = 1/10$. The patrolling strategy for this example is $p = 25/128$.

5. The parameters are the same as in Example 4, except that $p = 0$.

6. The parameters are the same as in Example 4, except that $p = 1$.

2.5.1 Examples for ecological tristability (Examples 1-3)

As stated above, most parameters for Examples 1-3 are identical. The only distinction in the parameters is in the value of the steady contribution b (by the territory) in the expected intake rate of an owner (although the strategies of the territorials also differ, as we discuss below). As we see, there is no particular qualitative effect of this distinction in the present section in the sense that the corresponding equilibrium points of Examples 1-3 and Examples 4-6, respectively are of

the same stability type (see column "Stability" in Table 2) but the significance will be seen when the resistance to mutants is investigated in Sections 4.3.1 and 4.3.2. Actually, b determines the value of a territory. The larger the value of b the larger the value of the territory is. Therefore one can expect that if b is large enough then the patroller strategy is evolutionary stable. This conjecture is supported by Examples 1-3: as b varies from $205/1000$ to $215/1000$ the evolutionarily stable strategy varies from the pure predator strategy to the pure patroller strategy through mixed strategies (see Section 4.3.1).

The corresponding phase portraits are shown on Figure 2-4: Figure 2 belongs to Example 1, Figure 3 belongs to Example 2 and Figure 4 belongs to Example 3. The strategy of the territorial individuals p varies with the example considered, and has always been chosen in such a way that the population of individuals following this strategy can, at the ecological equilibrium, resist mutants of any kind (see Section 4.3.1).

The three diagrams are very similar, each having five hyperbolic[2] equilibria (see Table 2): an asymptotically stable equilibrium on the y-axis, two interior unstable equilibria, an interior asymptotically stable equilibrium and an asymptotically stable equilibrium on the x-axis, so there is an ecological tristability. We can see later (see Section 4.3.1), the stable interior equilibrium (which is our main interest) remains stable with respect to the extended dynamics (4.4) in all of the three examples.
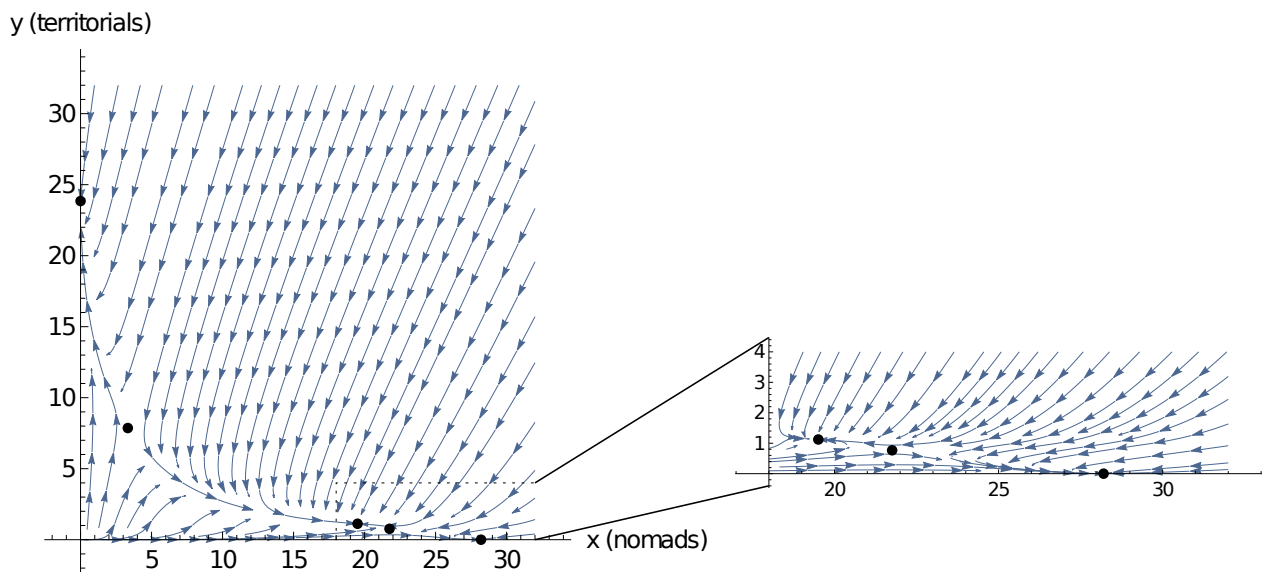

Figure 2: The phase portrait of the system (2.6) with parameters of Example 1 (see the main text) when $b = 21/100$, $p = 15475/19208$ and where x is the density of nomads (average number of nomads per territory) and y is the density of territorials (average number of territorials per territory). There are five equilibria marked by black discs on the diagram; each of them is hyperbolic and three of them are stable, that is, there is an ecological tristability. The coordinates of the equilibria in the ascending order of the first coordinates are $(0\,,23.85)$, $(3.33\,,7.86)$, $(19.51\,,1.12)$, $(21.76\,,0.77)$, $(28.2\,,0)$. At the stable interior equilibrium the system mainly consists of nomads. Among the territorials, the owners are in the majority. In the other two stable equilibria one of the two types (nomad and territorial) is missing. If there are no nomads, the density of the territorial intruders is much greater than that of the territorial owners.

---

[2]Recall that an equilibrium is hyperbolic with respect to a dynamics if the Jacobian matrix of the dynamics at the equilibrium has no eigenvalues with zero real parts. Then the stability of the equilibrium can simply be determined from the signs of the real parts of the eigenvalues.
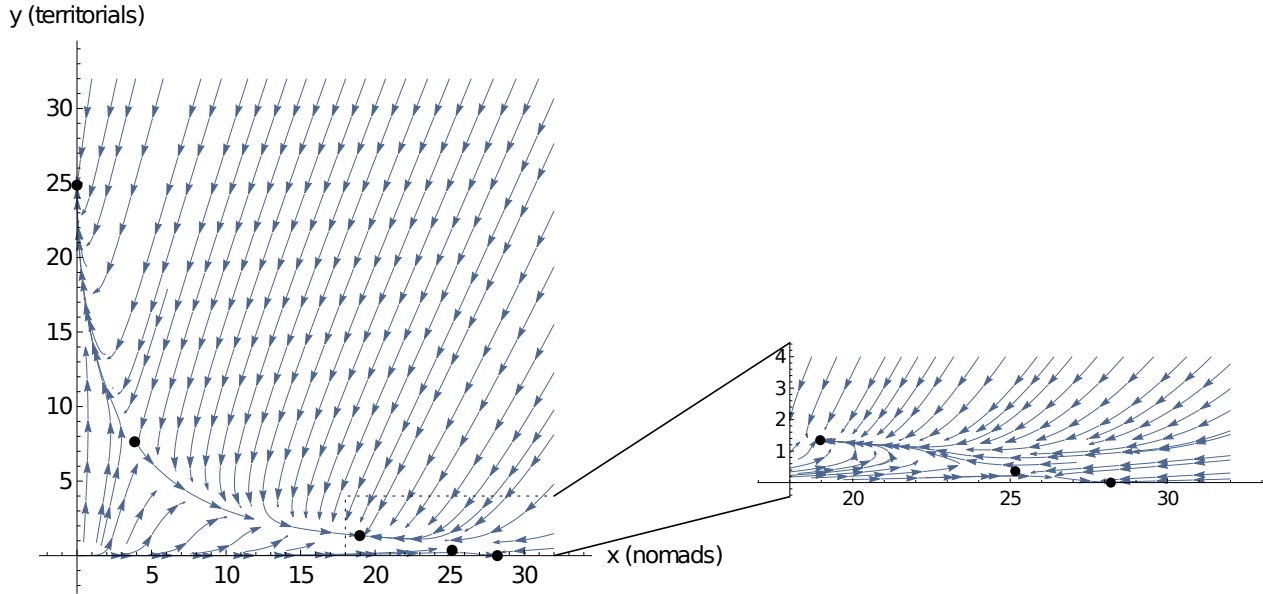
Figure 3: The phase portrait of the system (2.6) with parameters of Example 2 (see the main text) when $b = 205/1000$, $p = 0$ and where x is the density of nomads (average number of nomads per territory) and y is the density of territorials (average number of territorials per territory). There are five equilibria marked by black discs on the diagram; each of them is hyperbolic and three of them are stable, that is, there is an ecological tristability. The coordinates of the equilibria in the ascending order of the first coordinates are $(0, 24.85)$, $(3.87, 7.64)$, $(18.97, 1.35)$, $(25.16, 0.36)$, $(28.2, 0)$. The situation is similar to that of Figure 2.
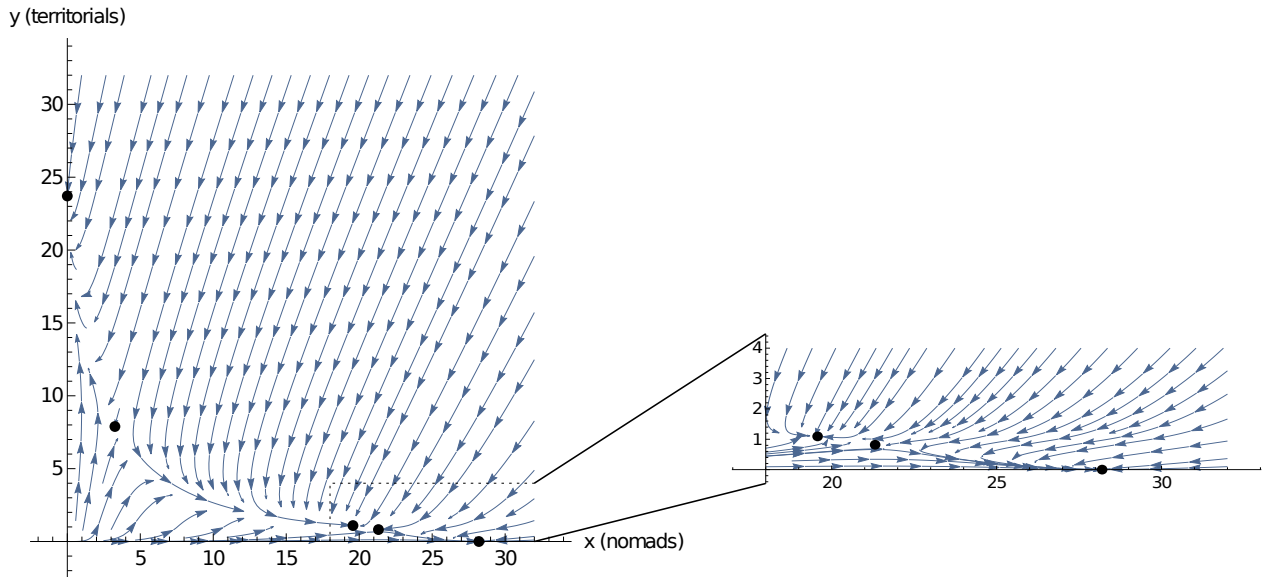

Figure 4: The phase portrait of the system (2.6) with parameters of Example 3 (see the main text) when $b = 215/1000$, $p = 1$ and where x is the density of nomads (average number of nomads per territory) and y is the density of territorials (average number of territorials per territory). There are five equilibria marked by black discs on the diagram; each of them is hyperbolic and three of them are stable, that is, there is an ecological tristability. The coordinates of the equilibria in the ascending order of the first coordinates are $(0, 23.71)$, $(3.26, 7.89)$, $(19.57, 1.09)$, $(21.32, 0.82)$, $(28.2, 0)$. The situation is similar to that of Figure 2.

Example	Equilibrium density		Eigenvalues		Stability
	x^*	y^*	λ_1	λ_2	
1.	0	23.85	-0.77	-0.058	l.a.s.
	3.33	7.86	-0.42	0.14	unstable
	19.51	1.12	-0.64	-0.20	l.a.s.
	21.76	0.77	-0.070	0.033	unstable
	28.2	0	-0.067	-0.047	l.a.s.
2.	0	24.85	-0.85	-0.062	l.a.s.
	3.87	7.64	-0.46	0.14	unstable
	18.97	1.35	-0.60	-0.23	l.a.s.
	25.16	0.36	-0.062	0.020	unstable
	28.2	0	-0.047	-0.030	l.a.s.
3.	0	23.71	-0.76	-0.058	l.a.s.
	3.26	7.89	-0.42	0.14	unstable
	19.57	1.09	-0.64	-0.20	l.a.s.
	21.32	0.82	-0.071	0.034	unstable
	28.2	0	-0.068	-0.047	l.a.s.
4.	0	12.06	-0.60	0.012	unstable
	10.1	5.5	-0.47	-0.085	l.a.s.
	18.6	0	-0.062	0.0875	unstable
5.	0	12.31	-0.64	0.011	unstable
	9.52	6.08	-0.47	-0.084	l.a.s.
	18.6	0	-0.062	0.10	unstable
6.	0	10.95	-0.47	0.015	unstable
	12.48	3.12	-0.56	-0.063	l.a.s.
	18.6	0	-0.062	0.036	unstable

Table 2: The ecological equilibria (x^*, y^*) of Examples 1-6 in the non-negative quadrant with respect to differential equation (2.6) with right-hand side defined in (2.13) with at least one types (nomad or territorial) where x^* is the equilibrium density (average number of nomads per territory) of nomads and y^* is the equilibrium density (average number of territorials per territory) of territorials. As we can see, the linearization has non-zero eigenvalues at every equilibrium, that is, every equilibrium is hyperbolic. Abreviation: l.a.s. – locally asymptotically stable.

2.5.2 Ecologically stable coexistence of nomads and territorials (Examples 4-6)

Here again three examples are investigated. As stated above, the parameters are the same, even in the case of parameter b, the only distinction being in the strategy of the territorial individuals. The corresponding phase portraits of the differential equation system (2.6) with respect to these parameters are depicted in Figure 5-7. The phase portraits essentially agree with each other. There are three hyperbolic equilibria (see Table 2): two unstable equilibria on the axes and an interior locally asymptotically stable equilibrium. In the stable equilibrium the proportion of territorials and nomads is more balanced compared to Examples 1-3. Figure 5 shows the case when $p = 25/128$, Figure 6 when $p = 0$ and Figure 7 when $p = 1$. The value of p gains more significance if we investigate the resistance to mutants as we can see later (see Section 4.3.2).
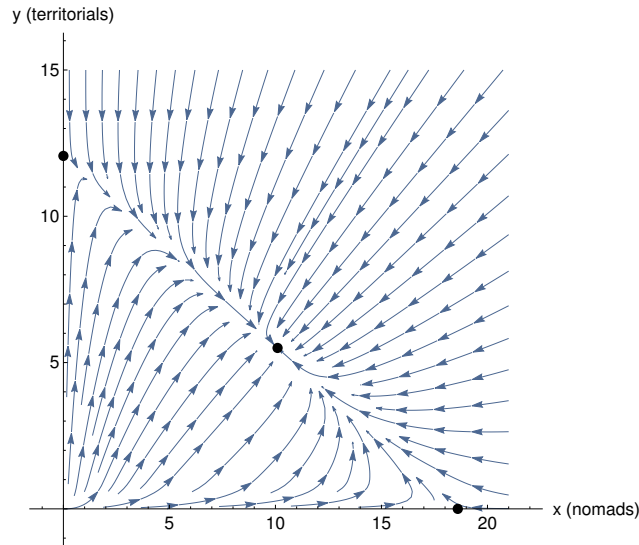

Figure 5: The phase portrait of the system (2.6) with the parameters of Example 4. Here x is the density of nomads (average number of nomads per territory) and y is the density of territorials (average number of territorials per territory). There are three equilibria marked by black discs on the diagram; each of them is hyperbolic. The coordinates of the equilibria in the ascending order of the first coordinates are $(0\,,\,12.06)$, $(10.1\,,\,5.5)$, $(18.6\,,\,0)$. The interior equilibrium is stable. The density of territorials and nomads are similar compared to that in the stable equilibrium in Examples 1-3 (see Figure 2-4). There is no interior unstable equilibrium. However, the equilibria on the axes are unstable, contrary to Examples 1-3.
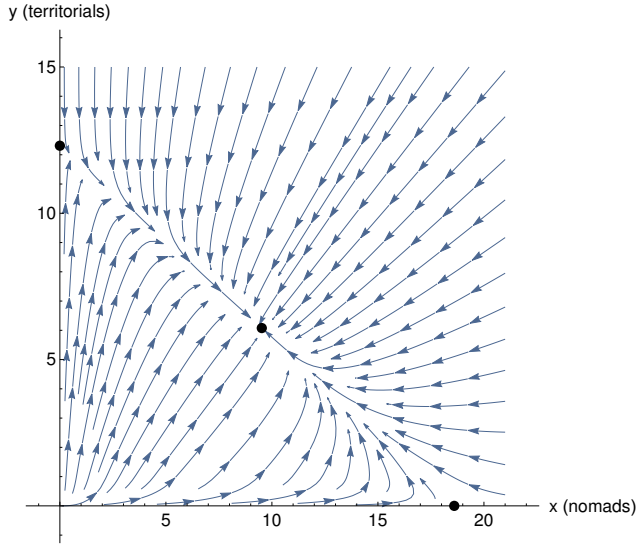
Figure 6: The phase portrait of the system (2.6) with parameters of Example 5. Here x is the density of nomads (average number of nomads per territory) and y is the density of territorials (average number of territorials per territory). There are three equilibria marked by black discs on the diagram; each of them is hyperbolic. The coordinates of the equilibria in the ascending order of the first coordinates are $(0\,,12.31)$, $(9.52\,,6.08)$, $(18.6\,,0)$. The situation is similar to that of Figure 5.
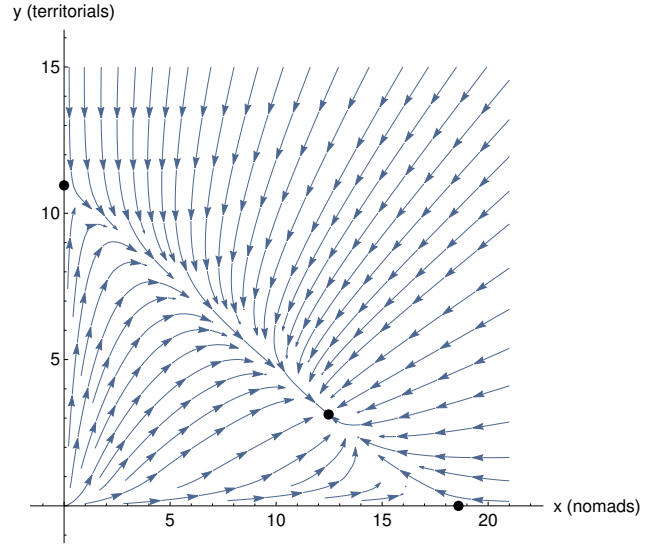

Figure 7: The phase portrait of the system (2.6) with parameters of Example 6. Here x is the density of nomads (average number of nomads per territory) and y is the density of territorials (average number of territorials per territory). There are three equilibria marked by black discs on the diagram; each of them is hyperbolic. The coordinates of the equilibria in the ascending order of the first coordinates are $(0\,,10.95)$, $(12.48\,,3.12)$, $(18.6\,,0)$. The situation is similar to that of Figure 5.

3 Finding the Nash equilibrium

In Section 2.5 we have considered a population where all territorial individuals play the strategy p in the owning position which gives the probability of choosing the patroller state in a reconsideration event. This is the only strategic element in the model (to be a nomad or territorial is not a strategic choice) and it manifests itself only in territorial individuals in the owner position (it has no effect in the intruder position). The fitness F of an "average" nomad and the fitness G of an "average" territorial individual is then calculated by (2.13). With the fitnesses in hand one can investigate the dynamics (2.6). This in turn leads to specific stable values for each of x and y (the three stable equilibrium points of Examples 1-3 in Section 2.5.1 and the stable equilibrium point of Examples 4-6 in Section 2.5.2, furthermore, see Table 2). So far a single strategy (the strategy p which can be called the resident strategy) has been shown in the population. We now consider invasion of the population by a different type of territorial which selects strategy q. Recall that the strategy is just the probability of choosing the patroller state in a reconsideration event. Since the probability of winning a fight is generally distinct for the patroller and predator states, it follows that the proportion of time spent in the owner position (thereby the benefit deriving from the territory) varies with the strategy. Therefore the fitnesses of different strategies also differ in general leading to the question: When can p resist invasion from such a q? A necessary condition for this to occur is for p to be a Nash equilibrium, a concept we discuss in more detail in Section 3.4.

3.1 The mutant fitness function

We consider the fitness of a p individual and a q individual in an infinitely large population of resident p individuals in which a q individual appears.

We have found the fitness $G(x, y)$ of a p individual above. We get the fitness of a q individual if ϱ_a and ϱ_r with respect to p are replaced by ϱ_a and ϱ_r with respect to q which are denoted by $\hat{\varrho}_a$ and $\hat{\varrho}_r$ throughout this section. Generally, we use the notation "^" if the given function belongs to the q territorials, e.g. $\hat{G}(x, y)$ denotes the fitness of a q territorial.

The distinction between $\hat{G}$ and G derives from the fact that the time spent in the patroller/predator state is distinct for a q and a p territorial. Note that we again calculate an expected fitness for the q territorial in a foraging season because the q individual spends a part of the foraging season in intruder position and the other part in the owner position.

For our q individual, its mean fitness will be determined by the proportion of time that it spends in the owner and intruder positions, and its mean payoff rate in each of these positions. A q territorial and a p territorial are indistinguishable in the intruder position, so the fitness of a q territorial in the intruder position is the same as that of a p territorial in the intruder position. However, the ratio of time spent in the intruder position to that spent in the owner position can be different with respect to p and q territorials. Therefore we calculate the expected duration from becoming an intruder until acquiring a territory and the expected duration from becoming an owner until losing the territory.

Specifically we have: *the fitness of a q territorial:*

$$\hat{G}(y) = \frac{\hat{T}_i \hat{G}_i + \hat{T}_o \hat{G}_o}{\hat{T}_i + \hat{T}_o}, \tag{3.1}$$

where:
$\hat{T}_i$ is the expected length of time a q-individual spends in the intruder position from becoming an intruder after losing a fight in the owner position until the first winning fight, that is, getting to the owner position again. This time includes the waiting time after losing the fight in the owner position but the waiting time after the first winning fight is already assigned to the owner position (recall the text after the formula for ϱ_a in Section 2.3.5).
$\hat{T}_o$ is the expected length of time a q-individual spends in the owner position from becoming an owner after winning a fight in the intruder position until the first losing fight, that is, getting to the intruder position again. This time includes the waiting time after winning the fight in the intruder position but the waiting time after the first losing fight in the owner position is already assigned to the intruder position (recall the text after the formula for ϱ_a in Section 2.3.5).
$\hat{G}_i$ is the expected payoff per unit time for a q-individual in the intruder position;
$\hat{G}_o$ is the expected payoff per unit time for a q-individual in the owner position.

3.2 The four fitness components

Accordingly, we calculate the expected time spent in the intruder position from losing a territory until acquiring a new territory and the time that passes from acquiring a territory until losing it.

3.2.1 Time in the intruder position

An intruder searches for an (active) owner or a prey item. It encounters an owner (call this an owner event) with rate λ_o and finds a prey item (call this prey event) with rate λ_h so it encounters an owner or finds a prey item with rate $\lambda_o + \lambda_h$. Hence the probability that the intruder encounters an owner is $\lambda_o/(\lambda_o + \lambda_h)$ and the probability that the intruder finds a prey item is $\lambda_h/(\lambda_o + \lambda_h)$. Recall that an intruder can only experience owner or prey events and not other kinds of event (see Section 2.3.2). Therefore, if we consider an intruder just after losing a fight then the probability

that the first owner event is the n-th event (after losing the fight) is $[\lambda_h/(\lambda_o + \lambda_h)]^{n-1}\lambda_o/(\lambda_o + \lambda_h)$ (since before the owner event has to occur $(n-1)$ prey events). So the expected number of events until the first owner event is

$$\sum_{n=1}^{\infty} n \left(\frac{\lambda_h}{\lambda_o + \lambda_h}\right)^{n-1} \frac{\lambda_o}{\lambda_o + \lambda_h} = \frac{\lambda_o + \lambda_h}{\lambda_o}.$$

Since every event is a prey event until the first owner event the expected length of time that passes until the end of the first owner event is

$$\sum_{n=1}^{\infty} \left(\frac{\lambda_h}{\lambda_o + \lambda_h}\right)^{n-1} \frac{\lambda_o}{\lambda_o + \lambda_h} \left[\frac{n}{\lambda_o + \lambda_h} + (n-1)t_h + t_l\right]$$

$$= \frac{1}{\lambda_o} + \frac{\lambda_h}{\lambda_o} t_h + t_l.$$

Here, $n/(\lambda_o + \lambda_h)$ corresponds to the duration of n "searches", that is, n sections from Figure 1; $(n-1)t_h$ corresponds to n waiting times after finding n prey items, that is, $n-1$ loops with length t_h on Figure 1 and t_l is the waiting time after the losing fight from which we start to consider the intruder position. Whereas the waiting time after the first owner event in which the intruder wins, so becoming an owner, is not considered here (cf. the text after the formula for ϱ_a in Section 2.3.5). Note that this result is natural: If we start a clock when the territorial becomes an intruder the owner event happens on average at time $1/\lambda_o$. During the length of time $1/\lambda_o$ a prey event occurs λ_h/λ_o times.

Recall that λ_o is the rate of encountering an active owner (see Section 2.3.2). An active owner is in the patroller state with probability $\pi\varrho_a/[\pi\varrho_a + (1-\pi)\varrho_r]$ which is just p by (2.8), (2.2) and (2.3). It is therefore in the predator state with probability $(1-p)$. Accordingly, the probability that the intruder wins is

$$p(1 - \alpha_a) + (1 - p)(1 - \alpha_r),$$

so the intruder has on average $1/[p(1-\alpha_a)+(1-p)(1-\alpha_r)]$ fights until its first win. Then it becomes an owner. Therefore, the time (denoted by $\hat{T}_i$) spent in the intruder position from becoming an intruder until becoming an owner is

$$\hat{T}_i = \frac{1}{p(1 - \alpha_a) + (1 - p)(1 - \alpha_r)} \left(\frac{1}{\lambda_o} + \frac{\lambda_h}{\lambda_o} t_h + t_l\right).$$

3.2.2 Time in the owner position

In the owner position, the territorial can be in the patroller or in the predator state, respectively. First, we have to determine the time spent in the different states. The probability of winning a fight in the patroller state is α_a while, in the predator state, it is α_r. If a q-territorial is active (so is searching) then it is in the patroller state with probability q. Accordingly, when it gets involved in a fight, it loses its territory with probability $q(1 - \alpha_a) + (1 - q)(1 - \alpha_r)$ and, consequently, the expected number of fights until this occurs is $1/[q(1 - \alpha_a) + (1 - q)(1 - \alpha_r)]$. A reconsideration event is due to a fight with probability $\lambda_i/(\lambda_r + \lambda_i)$ (recall that reconsideration can occur not only spontaneously with rate λ_r but a reconsideration is always related to every fight so the total rate of reconsideration is $\lambda_r + \lambda_i$, see Section 2.3.2), so there are on average

$$\hat{R} := \left(\frac{\lambda_r + \lambda_i}{\lambda_i}\right) \frac{1}{q(1 - \alpha_a) + (1 - q)(1 - \alpha_r)}$$

reconsiderations from becoming an owner until losing the territory.

We now calculate the time taken from becoming an owner until losing the territory. The expected time between two reconsiderations is $1/(\lambda_r + \lambda_i)$ if the owner is in the patroller state and there is no fight, and $1/(\lambda_r + \lambda_i) + \lambda_h t_h/(\lambda_r + \lambda_i)$ if the owner is in the predator state and there is no fight (if there is a fight then the expected duration t_w of the regeneration should be added to the previous durations). Since there are $\hat{R}$ reconsiderations until losing the territory from which on average $q\hat{R}$ end up with a choice of the patroller strategy and there are on average $1/[q(1-\alpha_a)+(1-q)(1-\alpha_r)]$ fights, the expected time $\hat{T}_o$ from becoming an owner until losing the territory is

$$
\begin{aligned}
\hat{T}_o &= q\hat{R}\frac{1}{\lambda_r + \lambda_i} + (1-q)\hat{R}\frac{1+\lambda_h t_h}{\lambda_r + \lambda_i} + \frac{1}{q(1-\alpha_a)+(1-q)(1-\alpha_r)}t_w \\
&= \frac{\hat{R}}{\lambda_r + \lambda_i} + (1-q)\hat{R}\frac{\lambda_h t_h}{\lambda_r + \lambda_i} + \frac{t_w}{q(1-\alpha_a)+(1-q)(1-\alpha_r)} \\
&= \frac{1}{q(1-\alpha_a)+(1-q)(1-\alpha_r)}\left[\frac{1}{\lambda_i} + (1-q)\frac{\lambda_h}{\lambda_i}t_h + t_w\right].
\end{aligned}
\tag{3.2}
$$

Here, $q\hat{R}/(\lambda_r + \lambda_i)$ corresponds to the time of searching in the patroller state until losing the territory; $(1-q)\hat{R}(1+\lambda_h t_h)/(\lambda_r + \lambda_i)$ corresponds to the time of searching in the predator state including the handling (waiting) times after finding prey items until losing the territory; $t_w/(q(1-\alpha_a)+(1-q)(1-\alpha_r))$ corresponds to the waiting times related to the winning fights before losing the territory.

3.2.3 Fitness in the intruder position

Since there is no distinction between a p and a q territorial in the intruder position their fitnesses are identical. So, by (2.9) and (2.13), we have

$$
\hat{G}_i = -d - c_{nt}x - c_{tt}y + D_i.
$$

3.2.4 Fitness in the owner position

In this case the distinctions between the fitnesses of p and q individuals derive from the distinctions in the direct interactions. The cost of maintenance and indirect interactions is the same for both strategies, $-d - c_{nt}x - c_{tt}y$.

To get the term in the fitness deriving from the direct interactions we should only repeat the calculation made for the p territorials but with respect to the time that passes from becoming an owner until losing the territory. The constant background intake rate b is present now too. We have seen previously there are $1/[q(1-\alpha_a)+(1-q)(1-\alpha_r)]$ winning fights with negative intake $-c_w$. When a territorial owner is defeated, the negative intake of the defeat is already considered in the intruder position; also, when an intruder wins a fight, the negative intake of the winning fight is considered in the owner position. In addition to this negative intake the intake from hunting in the predator position must be considered; this is

$$
(1-q)\hat{R}\frac{\lambda_h i_h}{\lambda_r + \lambda_i}.
$$

So the fitness in the owner position is

$$\hat{G}_o = -d - c_{nt}x - c_{tt}y + b + \frac{-\frac{1}{q(1-\alpha_a)+(1-q)(1-\alpha_r)}c_w + (1-q)\hat{R}\frac{\lambda_h i_h}{\lambda_r + \lambda_i}}{\frac{1}{q(1-\alpha_a)+(1-q)(1-\alpha_r)}\left[\frac{1}{\lambda_i} + (1-q)\frac{\lambda_h}{\lambda_i}t_h + t_w\right]}$$

$$= -d - c_{nt}x - c_{tt}y + b + \frac{-c_w + (1-q)\frac{\lambda_h i_h}{\lambda_i}}{\frac{1}{\lambda_i} + (1-q)\frac{\lambda_h}{\lambda_i}t_h + t_w}$$

$$= -d - c_{nt}x - c_{tt}y + b + \frac{-\lambda_i c_w + (1-q)\lambda_h i_h}{1 + (1-q)\lambda_h t_h + \lambda_i t_w}.$$

Observe that $\hat{G}_o + d + c_{nt}x + c_{tt}y$ agrees with $\pi D_a + (1-\pi)D_r$ if q is replaced by p in $\hat{G}_o + d + c_{nt}x + c_{tt}y$.

3.3 Calculating the fitness

We now substitute the above four terms into the fitness function (3.1) to obtain (3.3). We note that this is a linear rational function in q. Indeed,

$$\hat{G} = -d - c_{nt}x - c_{tt}y + \frac{\hat{T}_i D_i}{\hat{T}_i + \hat{T}_o} + \frac{\hat{T}_o}{\hat{T}_i + \hat{T}_o}\left(b + \frac{-\lambda_i c_w + (1-q)\lambda_h i_h}{1 + (1-q)\lambda_h t_h + \lambda_i t_w}\right)$$

$$= b - d - c_{nt}x - c_{tt}y + \frac{\hat{T}_i(D_i - b) + \hat{T}_o \cdot \left(\frac{-\lambda_i c_w + (1-q)\lambda_h i_h}{1 + (1-q)\lambda_h t_h + \lambda_i t_w}\right)}{\hat{T}_i + \hat{T}_o}$$

$$= b - d - c_{nt}x - c_{tt}y + \frac{\hat{T}_i(D_i - b)[q(1-\alpha_a) + (1-q)(1-\alpha_r)] + \left[-c_w + (1-q)\frac{\lambda_h}{\lambda_i}i_h\right]}{\hat{T}_i[q(1-\alpha_a) + (1-q)(1-\alpha_r)] + \left[\frac{1}{\lambda_i} + (1-q)\frac{\lambda_h}{\lambda_i}t_h + t_w\right]}, \quad (3.3)$$

which immediately shows that $\hat{G}$ is a linear rational function in q.

3.4 Nash equilibria

In what follows we write $\hat{G}(q,p)$ instead of $\hat{G}$ defined in the previous section where p denotes the resident strategy and q denotes the mutant strategy.

Consider a strategy p. Let (x^*, y^*) be an asymptotically stable equilibrium of the dynamics (2.6) with territorials following strategy p. Then the triplet (p, x^*, y^*) or, by abuse of notation, p, is a (density dependent) **Nash equilibrium** (NE for short) if $\hat{G}(q,p) \leq \hat{G}(p,p)$ for every $q \neq p$ close enough to p (cf. the last paragraph on p.527 in Cressman and Garay (2003b)). If the inequality is strict, then p is said to be a **strict NE**. (Note that $\hat{G}(q,p) = \hat{G}(q,p,x^*,y^*)$, that is, $\hat{G}$ should be considered at $x = x^*$ and $y = y^*$ when the relation between $\hat{G}(q,p)$ and $\hat{G}(p,p)$ is investigated.) Table 3 summarizes the type of evolutionary stability of the strategies with the corresponding densities in Examples 1-6.

The Nash equilibrium is a central notion of game theory. It is a best response to itself. If the players are rational then they can retain their strategies. Therefore if one of the players uses a Nash equilibrium strategy then its opponent is forced to use a best response in order to have maximal profit. Generally, the best response can be the Nash equilibrium strategy or an alternative best response. If there is no alternative best response we speak about a strict Nash equilibrium. From the biological aspect when the players' strategy is not a result of a rational decision but an inheritable property and the opponent is generally an individual randomly chosen from a population, a non-strict Nash equilibrium is not necessarily stable because small perturbation by mutation can dislodge the population from the Nash equilibrium strategy (for example $p = 25/128$ at densities $x^* = 101/10$ and $y* = 11/2$ is an unstable NE of Example 4, see Table 3). Thus the Nash equilibrium

strategy is not sure to be the most remunerative in the population any longer. However, a strict Nash equilibrium can resist small perturbations giving it biological significance. Nevertheless, the strictness often proves a strong condition which is rarely satisfied. This leads to the weaker (but more complicated) conditions of evolutionary stability (see Section 4).

Rearranging the numerator and the denominator of the quotient in (3.3) according to the powers of q we can re-write expression (3.3) as

$$\hat{G}(q,p) = \frac{a_{11}(p) + a_{12}(p)q}{a_{21}(p) + a_{22}(p)q} + a_3 \tag{3.4}$$

where $a_{11}(p) = \hat{T}_i(D_i - b)(1 - \alpha_r) - c_w + \lambda_h i_h/\lambda_i$, $a_{12}(p) = \hat{T}_i(D_i - b)(\alpha_r - \alpha_a) - \lambda_h i_h/\lambda_i$, $a_{21}(p) = \hat{T}_i(1 - \alpha_r) + 1/\lambda_i + t_w + \lambda_h t_h/\lambda_i$, $a_{22}(p) = \hat{T}_i(\alpha_r - \alpha_a) - \lambda_h t_h/\lambda_i$ and $a_3 = b - d - c_{nt}x - c_{tt}y$. (Note that a_{11}, a_{12}, a_{21} and a_{22} all depend on p since $\hat{T}_i, D_i, \lambda_i$ depend on p.)

A Nash equilibrium is a best response to itself, and so equation (3.4) must be maximised over q at $q = p$. We thus have:

$p = 0$ is a Nash equilibrium if $a_{12}(0)a_{21}(0) - a_{11}(0)a_{22}(0) \leq 0$,

$p = 1$ is a Nash equilibrium if $a_{12}(1)a_{21}(1) - a_{11}(1)a_{22}(1) \geq 0$,

$0 < p < 1$ is a Nash equilibrium if $a_{12}(p)a_{21}(p) - a_{11}(p)a_{22}(p) = 0$. This condition is equivalent to having $\frac{\partial}{\partial q}\hat{G}(q,p)_{q=p} = 0$ due to the fact that $\hat{G}$ is a linear rational function in q so that the derivative w.r.t q can be 0 only if the numerator of $\hat{G}$ is a constant multiple of the denominator. The potential problem of the denominator of $\hat{G}$ having a root on $[0, 1]$ does not arise, since from (3.3) we see that the denominator of $\hat{G}$ is positive for any $q \in [0, 1]$.

4 Evolutionary stability

Below we consider two concepts of stability for our solutions, which we introduce in Section 4.1. The second of these, in terms of its definition and assumptions, is more realistic for our system.

4.1 Mixed solutions

All mixed strategy solutions p must satisfy

$$a_{12}(p)a_{21}(p) - a_{11}(p)a_{22}(p) = 0. \tag{4.1}$$

4.1.1 Convergence stability

We borrow the first concept for evolutionary stability from adaptive dynamics (Metz 2012, Chapter 13 in Broom and Rychtář 2013) which describes the evolution of a population through small mutation. One of the important stability concept of adaptive dynamics is convergence stability. If the average strategy of the population is close enough to a convergence stable strategy then only the strategies closer to the convergence stable strategy than the average strategy have an advantage, thereby one can expect that the average strategy of the population (moreover the strategy of the individuals) of the consecutive generations tends to the convergence stable strategy. Therefore, if some mutants appeared in a population of individuals following a convergence stable strategy it can be expected that the average strategy of the population returns to the convergence stable strategy. For differentiable fitness functions convergence stability can be characterised by the help of first and second order derivatives (Eshel 1983, Meszéna et al. 2001). We use this characterisation (see (4.2) below) for our model.

Consider a mixed strategy p. Let (x^*, y^*) be an interior equilibrium of the dynamics (2.6) with respect to the strategy p, that is, $x^* > 0, y^* > 0$ and $F(p, x^*, y^*) = G(p, x^*, y^*) = 0$. Then by the implicit function theorem (see e.g. Theorem 9.28 (p. 224) in Rudin 1976) there is a neighbourhood

$\mathcal{N}$ of p and a unique (continuously differentiable) function $(x^*(q), y^*(q))$ defined on $\mathcal{N}$ such that $x^*(p) = x^*$, $y^*(p) = y^*$ and $F(x^*(q), y^*(q)) = G(x^*(q), y^*(q)) = 0$ for every $q \in \mathcal{N}$ (Lemma 2 in Cressman and Garay, 2003b). In our context, the function $(x^*(q), y^*(q))$ is called the **stationary density surface**[3].

The mixed strategy p (more precisely the triplet (p, x^*, y^*) if we emphasize the density dependence) is *convergence stable* if and only if the equilibrium condition (4.1) is satisfied, together with

$$\frac{\mathrm{d}}{\mathrm{d}r}\left(\left.\frac{\partial}{\partial q}\hat{G}(q,r)\right|_{q=r}\right)_{r=p} < 0. \tag{4.2}$$

This is equivalent to having (4.1) satisfied and

$$\frac{\mathrm{d}}{\mathrm{d}r}\left(a_{12}(r)a_{21}(r) - a_{11}(r)a_{22}(r)\right)_{r=p} < 0. \tag{4.3}$$

This means that within some neighbourhood the population strategy would evolve towards any strategy that satisfies the above conditions, and so in any case with a unique NE which is convergence stable, evolution would take a population starting from any strategy other than p to p.

It is important to emphasize when we investigate the convergence stability of a strategy p that we consider the function $\hat{G}$ on the stationary density surface $(x^*(r), y^*(r))$ defined in a neighbourhood of p even if this is suppressed in the notation, that is, $\hat{G}(q, r) = \hat{G}(q, r, x^*(r), y^*(r))$ in (4.2).

We shall consider an alternative definition of resistance to invasion by mutant strategies.

4.1.2 Density dependent ESSs (DDESS)

In the above definitions, we have not considered the population dynamics explicitly, only through the stationary density surface. We do this below.

The definition of density dependent ESS is a dynamic approach to stability. Our definition here follows the work of Cressman and Garay (2003b) in which a possible extension of the notion of the one species frequency dependent ESS (Maynard Smith, 1982) is discussed for the multi species density dependent system.

Consider a resident system of nomads and territorials. Let p be the strategy of the resident territorials. As before, denote by x and y, respectively, the density of nomads and resident territorials, with fitness functions F and G, respectively. Assume that some mutant territorials using strategy q appear in the population with density z and fitness function H (see the definition of F, G and H for $z > 0$ in Appendix A.1). Then the evolution of this system is described by the extended dynamics

$$\dot{x} = xF(x, y, z), \tag{4.4}$$
$$\dot{y} = yG(x, y, z),$$
$$\dot{z} = zH(x, y, z).$$

From this point of view, the dynamics (2.6) can be called the resident system. Let $x^* = x^*(p)$, $y^* = y^*(p)$ be a positive equilibrium of the resident system (2.6). (p, x^*, y^*) is a *density dependent evolutionarily stable strategy* (DDESS) if

(i) (x^*, y^*) is an asymptotically stable state of the resident dynamics (2.6) and

(ii) whenever q is a strategy close enough to p but different from p, then $(x^*, y^*, 0)$ is an asymptotically stable rest point of the extended dynamics (4.4),

---

[3]There is in general more than one equilibrium for a given p and parameters. The stationary density surface can be considered at any of the equilibria (if the condition of the implicit function theorem are satisfied) but it is clear from the context where the stationary density surface is considered.

where "close enough to p" means the existence of a $\delta > 0$ such that $|q - p| < \delta$. Thus an equilibrium density (x^*, y^*) is always associated with a DDESS but if this density is clear from the context we often suppress it and only say that p is a DDESS. We demonstrate how to show that a strategy is a DDESS in Appendix A.2.

4.2   Pure solutions

For the pure strategies $p = 0$ and $p = 1$ we have the following conditions for a strict Nash equilibrium. Strict Nash equilibra are also convergence stable and DDESS solutions as described above. Note that for pure strategies the non-strict equilibria are *non-generic* (see e.g. Broom and Rychtář, 2013) and so we do not consider these here further. $p = 0$ is a strict Nash equilibrium if

$$a_{12}(0)a_{21}(0) - a_{11}(0)a_{22}(0) < 0. \tag{4.5}$$

$p = 1$ is a strict Nash equilibrium if

$$a_{12}(1)a_{21}(1) - a_{11}(1)a_{22}(1) > 0. \tag{4.6}$$

It is possible to have one, both or neither of these solutions, as we see in Section 4.3.

4.3   Examples

Here we return to the examples given in Section 2.5. We have seen that each of the examples have an interior equilibrium. We investigate what occurs if a small amount of mutant territorials appear in the ecosystem of nomads and territorials at the interior equilibrium. We calculate the fitness of mutants according to Section 3.1. This intuitively describes the case when the resident population is infinitely large compared to the mutant subpopulation, so the density of mutants is practically zero. Furthermore, we get a suggestion of what one should expect in relation to the stability introduced in Section 4.1.1 and 4.1.2.

4.3.1   Evolutionary stability of a strategy in the ecologically stable interior equilibrium (Examples 1-3)

We proceed as follows. We investigate each example at three values of the resident strategy, namely, when the resident strategy is either of the two pure strategies ($p = 0$ or 1, that is, the pure predator or the pure patroller strategy, respectively) and when the resident strategy is a mixed strategy suitably chosen in the sense that the strategy will be a DDESS in Example 1. Then we plot the mutant fitness calculated according to Section 3.1 as a function of the mutant strategy q. Consequently, a figure related to a given example depicts three graphs. Comparing the slope of the graphs we can infer the stability property of a given resident strategy from the evolutionary viewpoint. We get that depending on the value of b (note that Examples 1-3 differ from each other only in the value of b) either the mixed strategy (Example 1) or pure strategy $p = 0$ (Example 2) or pure strategy $p = 1$ (Example 3) proves to be evolutionarily stable.

In Example 1 (when $b = 21/100$) the chosen mixed resident strategy is $p = 15475/19208$. At this value of the resident strategy any mutant proves neutral since its fitness agrees with the fitness of a resident, that is, the graph of the mutant fitness as a function of q is constant (the green solid line on Figure 8). Actually, starting from the formula (3.3) we have solved an equation for p to find a resident mixed strategy for which the mutant strategies are neutral if the residents are at the interior ecological equilibrium found in Section 2.5. This also means that p is a (density dependent) NE.

If the resident strategy is the pure predator strategy, that is, $p = 0$ then the graph of the mutant fitness increases in q as shown in Figure 8 (the blue dashed graph). So any kind of mutant can invade into the population of pure predators.

If the resident strategy is the pure patroller strategy, that is, $p = 1$ then the graph of the mutant fitness decreases in q as it shown on Figure 8 (the orange dotted graph). So any kind of mutant can invade into the population of pure patrollers.

Comparing the three values of the resident strategy one can expect that the resident population of individuals following the mixed strategy p can resist (a small amount of) mutants. Indeed this is the case as the line slopes of any p smaller (larger) than this critical value are positive (negative) in q, so that we have convergence stability. We can also check formally that the strategy is both convergence stable and a DDESS. To see convergence stability we substitute appropriate values into (4.2) to get

$$\frac{\mathrm{d}}{\mathrm{d}r}\left(\frac{\partial}{\partial q}\hat{G}(q,r)\Big|_{q=r}\right)_{r=p} \approx -0.0010 < 0,$$

that is, the condition of convergence stability is satisfied. As regards density dependent stability we follow the process described after Lemma A.1 in the Appendix and get that

$$\frac{\partial}{\partial q}B(q)|_{q=p} = 0 \quad \text{and} \quad \frac{\partial^2}{\partial q^2}B(q)|_{q=p} \approx -0.018 < 0,$$

that is, strategy p is also a DDESS (see Table 3).

We remark that the stable equilibrium with no nomads proves unstable from an evolutionary point of view. It can be invaded by any mutant with strategy $q > p$ (see Table 3).
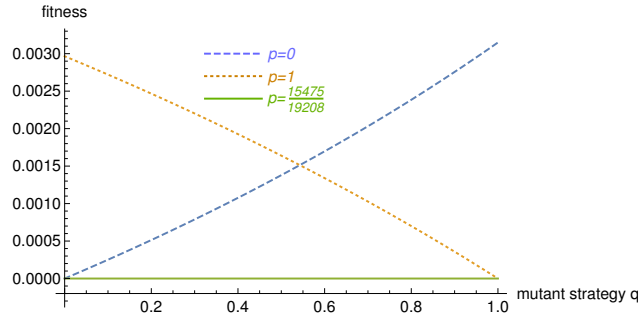

Figure 8: The fitness of mutants in the resident monomorphic population of individuals following strategy p at the stable interior ecological equilibrium of Example 1 ($b = 21/100$, see Section 2.5 and Figure 2). The fitness of a mutant following strategy q is calculated by formula (3.3). If the strategy of resident individuals is $p = 15475/19208$ then every kind of mutant has the same fitness, that is, every mutant type is neutral against the resident phenotype. Therefore the fitness is constant in q (green solid graph). If the strategy of the resident population is the pure predator strategy then the fitness of mutants is increasing in q (blue dashed graph) which shows that any mutant type can invade the resident population. Also, if the strategy of the individuals of the resident population is the pure patroller strategy then the fitness of mutants is decreasing in q (orange dotted graph), so the resident population cannot resist any kind of mutant again. The three graphs together suggest that the mixed strategy p is an evolutionarily stable strategy.

In Examples 2 and 3 as well, the fitness of the mutants as a function of q has been compared with respect to the previous three values of the resident strategy. The only distinction in Example 2 compared to Example 1 is that the value of parameter b is a little smaller, being $205/1000$. This means that the steady contribution of having a territory is smaller than in Example 1. Therefore it seems rewarding to hunt more and this conjecture is supported by the three graphs on Figure 9. Every graph is decreasing in q. Consequently, the predator strategy always proves the most remunerative independently of the strategy of the resident individuals.

The situation in Example 3 is similar in form to that in Example 2, but yielding the reverse outcome. Here $b = 215/1000$, that is a bit greater than in Example 1. Therefore one can expect that it is worth hunting to a lesser extent and patrolling instead. Indeed, the graphs on Figure 10 support this expectation, for the fitness of mutants as a function of q increases in q independently of the strategy of the resident individuals. As a consequence, the highest fitness always belongs to the pure patroller strategy.

Accordingly, Examples 2 and 3 are examples when a pure strategy resists mutants. As Table 3 shows both equilibria are not only convergence stable and DDESS, but strict NE.

We remark that the stable equilibrium with no nomads is unstable in Example 2 (it can be invaded by any mutants following a strategy $q > 0$) while it is a strict NE in Example 3.
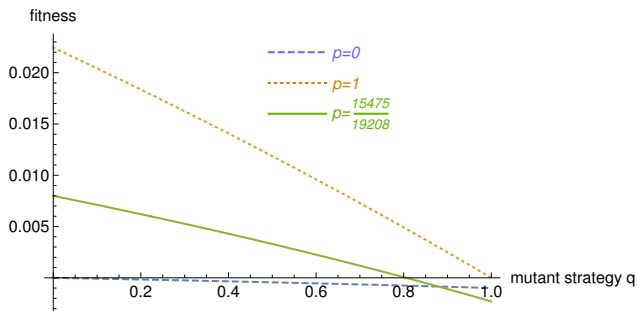

Figure 9: The fitness of mutants in the resident monomorphic population of individuals following strategy p at the stable interior ecological equilibrium of Example 2 ($b = 205/1000$, see Section 2.5 and Figure 3). The fitness of a mutant following strategy q is calculated by formula (3.3). The fitness of mutants is a decreasing function of q independently of the strategy of individuals of the resident population. Consequently, the most rewarding strategy is always the pure predator strategy suggesting not only the evolutionary stability of this strategy but that it is a strict NE.
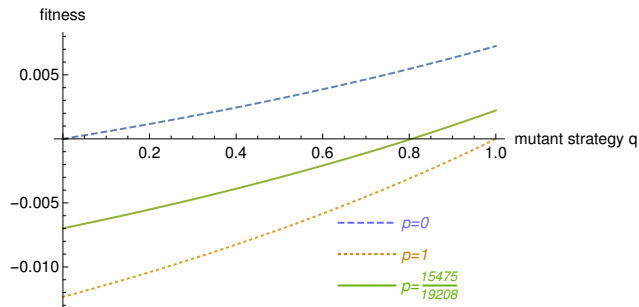
Figure 10: The fitness of mutants in the resident monomorphic population of individuals following strategy p at the stable interior ecological equilibrium of Example 3 ($b = 215/1000$, see Section 2.5 and Figure 4). The fitness of a mutant following strategy q is calculated by formula (3.3). The fitness of mutants is an increasing function of q independently of the strategy of individuals of the resident population. Consequently, the most rewarding strategy is always the pure patroller strategy suggesting not only the evolutionary stability of this strategy but that it is a strict NE.

4.3.2 Evolutionarily instability of a mixed strategy in an ecologically stable interior equilibrium (Examples 4-6)

As in Examples 1-3, the fitness of mutants is investigated with respect to three distinct values of the strategy of resident individuals: for the two pure strategies and for the mixed strategy $p = 25/128$. The mixed strategy has again been chosen in such a way that every kind of mutants proves neutral against the resident population of individuals following p at the ecological equilibrium found in Section 2.5 (green horizontal graph on Figure 11). This also means that strategy $p = 25/128$ is a (density dependent) NE. However, contrary to Example 1, if the resident strategy is the pure predator strategy ($p = 0$) then the fitness of the mutant as a function of q is decreasing in q (blue dashed graph on Figure 11), so the resident pure predators have the highest fitness showing that the population of pure predators resists small amount of mutants. This is also true for all resident strategies below the critical value of $25/128$. Also, if the resident strategy is the pure patroller strategy ($p = 1$) then the fitness of mutants as a function of q is increasing in q (orange dotted graph on Figure 11), so the resident pure patrollers have the highest fitness showing that the population of pure patrollers resists small amount of mutants. This is again also true for all resident strategies above the critical value. In summary, Examples 4-6 provide a set of parameters with a

Example	Strategy p	Equilibrium density x^*	y^*	$\frac{\partial}{\partial q}\hat{G}(q,p)\big|_{q=p}$	$\frac{\mathrm{d}}{\mathrm{d}r}\left(\frac{\partial}{\partial q}\hat{G}(q,r)\big|_{q=r}\right)\big|_{r=p}$	$\frac{\partial^2}{\partial q^2}B(q)\big|_{q=p}$	Evolutionary stability
1.	0.806	0	23.85	$0.0019 > 0$	-	-	us. from the right
	0.806	19.51	1.12	0	$-0.010 < 0$	$-0.018 < 0$	CSS, DDESS
2.	0	0	24.86	$0.00026 > 0$	-	-	us. from the right
	0	18.97	1.35	$-0.0037 < 0$	-	-	strict NE
3.	1	0	23.71	$0.0045 > 0$	-	-	strict NE
	1	19.57	1.09	$0.041 > 0$	-	-	strict NE
4.	$\frac{25}{128}$	$\frac{101}{10}$	$\frac{11}{2}$	0	$0.0020 > 0$	$0.0012 > 0$	unstable NE
5.	0	9.52	6.08	$-\frac{1}{1975} < 0$	-	-	strict NE
6.	1	12.48	3.12	$\frac{103}{5075} > 0$	-	-	strict NE

Table 3: Investigation of the evolutionary stability of the stable ecological equilibria (x^*, y^*) in which the density of territorials is positive where x^* is the equilibrium density (average number of nomads per territory) of nomads in the resident system (2.6) and y^* is the equilibrium density (average number of territorials per territory) of territorials in the resident system (2.6). p denotes the strategy of the resident territorials. We recall that in Example 1 $b = 21/100$, in Example 2 $b = 205/1000$ while in Example 3 $b = 215/1000$. We note that in all cases above we have $y^* > 1$, as otherwise there are no contests between territorials, and the value of p, and any corresponding mutant q, would be irrelevant. Abbreviations: NE – Nash equilibrium, CSS – convergence stable strategy, DDESS – density dependent evolutionary stable strategy. "us. from the right" means that the resident system can only be invaded by mutants following a strategy $q > p$ (us. - unstable).)

mixed strategy which is unstable from an evolutionary perspective; its stable resident equilibrium can be invaded by any mutants following a strategy q distinct from 25/128, and pure strategies which are evolutionarily stable (see Table 3).
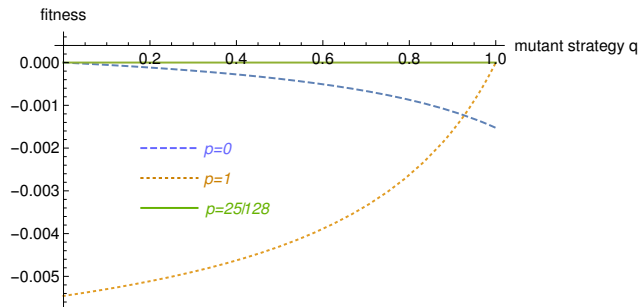

Figure 11: The fitness of mutants in the resident monomorphic population of individuals following strategy p at the stable interior ecological equilibrium values of Examples 4-6 (see Section 2.5 and Figures 5-7). The fitness of a mutant following strategy q is calculated by formula (3.3). If the strategy of resident individuals is $p = 25/128$ then every kind of mutant has the same fitness, that is, every mutant type is neutral against the resident phenotype. Therefore the fitness is constant in q (green solid graph). If the strategy of the resident population is the pure predator strategy then the fitness of mutants is decreasing in q (blue dashed graph) contrary to Examples 1-3 which shows that the resident population can resist any kind of mutant. If the strategy of the individuals of the resident population is the pure patroller strategy then the fitness of mutants is increasing in q (orange dotted graph) contrary to Examples 1-3, so the resident population again resists any kind of mutant. The three graphs together suggest that the mixed strategy $p = 25/128$ is evolutionarily unstable while the pure strategies are both evolutionarily stable, moreover, strict NE. Indeed this is so, as any resident strategy below (above) the critical value $p = 25/128$ is also decreasing (increasing) in q.

5   Discussion

In this paper we have considered a model of territorial behaviour, where territory owners must defend their territories from intruders who in turn wish to take over the territory. A territory has a value to its owner while it is occupied, but defence comes at a cost both in terms of time and risk of injury/energy cost. Owners have a choice of a more active patrolling defence, which was more costly, but have a greater chance of repelling intruders, or a less active defence, the "predator" state, where their priority is foraging. The effectiveness of each strategy depends upon the rewards available compared to the different costs, but also crucial is the density of the population, influenced by indirect intractions caused by underlying environmental quality. The population also consists of an alternative type of individual, nomads, who do not fight for territories, but nonetheless have an important indirect impact through their use of resources.

    We note that the nomad phenotype resembles the dove strategy in the classical Owner-Intruder game (e.g. Maynard-Smith and Parker 1976, Chapter 8 in Maynard Smith 1982) in the sense that a nomad never fights against a territory owner though encountering a territorial owner can decrease the nomad's fitness (the cost of fleeing). The analogy between nomads and doves is not perfect though, because a nomad can never have a territory even if there are territories without an owner. The nomad (not keeping a territory) way of life is an alternative to the territorial (keeping or striving to have a territory) way of life and depending on the assumptions either of the two ways can be eliminated from the ecological system. In our model, territorials represent different "hawkish" strategies depending on how an individual divides its time between hunting and patrolling, thereby

influencing the frequency of fights and the probability of winning a fight. Hence, in future works, the territorial behaviour can be extended incorporating dove and bourgoies strategies (Maynard-Smith and Parker 1976, Chapter 8 in Maynard Smith 1982) or a probaility pair indicating the probability of playing hawk in the owner position and in the intruder position, respectively ("aggressiveness" in Kokko et al. 2006).

We have seen that the strategies adopted by the owners affect the population size (see Figures 4-6), caused by a reduction in their resource intake level, and thus has an indirect influence on the effectiveness of the owner strategy. Depending upon the parameters, we thus saw cases where there is a stable pure defensive strategy, where both pure strategies are stable, or where a mixed defensive strategy, sometimes patrolling and sometimes not, is stable. Similarly, there are cases where the nomads are extinct, and others where there is a large population of this type.

The main novelty of our work is that in the framework of game theoretical modelling, we take account not only of energetic cost of the defence of a territory but also the time constraints of different activities and the density dependence of the interactions, as well. The time constraints and the density dependence of fitness are linked, since the time duration of territory defence depends upon the density of intruders. For instance, European Jays (*Garrulus glandarius L.*) in Sweden occupy territories which exhibit the highest breeding success (Henrik 1990), but in the Maremma Natural Park in Italy this species is non-territorial. In the latter case the resources are very abundant, and the density of birds is high, thus the cost of defending the territory against all intruders would be higher than the benefit of owning a territory (Rolando et al. 1995).

In each of the following paragraphs we introduce a scenario, and give real biological cases for which it applies.

Territorials outperform nomads: In the ecological tristable examples, one of the locally asymptotically stable rest points of the population density dependent dynamics is an equilibrium where there are no nomads (Figure 2-4). This occurs, for example, when the territory is necessary for reproduction, like the spotted hyena (Kruuk 1972), Tengmalm's owl (Korpimaki 1988) and eurasian beaver (Rosell et al. 1998).

Nomads outperform territorials: Territoriality is only shown by a minority of species, for instance some well-known examples from non-territorial animals are migratory ungulates (e.g. wildebeest, reindeer), herding fish (e.g. herring) and colony breeding birds (Burger and Gochfeld 1994). Moreover, the home range is not always defended, for instance Grant et al. (1992) reported 11 undefending carnivores species from 23 species and 23 undefending ungulates from 62 species. So territoriality is not always evolutionarily stable behaviour.

Coexistence of territorials and nomads: In the ecological tristable examples and in the example with a single stable equilibrium there is a locally asymptotically stable interior rest point of the population density dependent dynamics, where the territorial and nomad phenotypes coexist. We already mentioned some biological examples for this situation, namely the side-blotched lizard (*Uta stansburiana*) (Sinervo and Lively 1996, Sinervo et al. 2000), sunfish and salmon (e.g. Gross 1984 and references therein, Gross and Charnov 1980). In each case the territorial phenotype belongs to our patroller phenotype, moreover in these species the nomads have different genetically determined phenotypes to the territorials ones. For instance, male bluegill sunfish has two alternative mating strategies: cuckoldry or parental care. Cuckolder males first mature at age two and follow a developmental sequence of sneaking and then mimicking female behavior to deceptively gain access to spawnings. Males who become parental (construct and defend nests) delay maturation until age seven (Gross and Charnov 1980). Although common cuckoos (*Cuculus canorus*) do not show parental care, the males are territorial and aggressively defend their territories. According to the "dear enemy phenomenon" (Fisher 1954) the territory owners tolerate familiar male neighbours living on adjacent territories more than unfamiliar "floating" males. Here the owners are the older males and floaters younger males who try to copulate with the females living on the owners' territories (Moskát et al. 2017).

From the perspective of evolution, we point out that in these cases in the interior equilibrium, there are either mixed territorial ESS, i.e. the ESS is a mixture of the patrolling and predator strategy, see Figure 8, or a unique pure territorial ESSs, i.e. either patrolling see Figure 9 or predator see Figure 10). Moreover, it can be possible to have evolutionary bistability when both the pure patroller and the pure predator strategies are strict NE. There are many biological examples for the case of the mixed ESS, e.g. lions (Schaller 1972) wolves (Hayes 2010), and damselflies (Golab et al. 2017). As regards the pure ESSs, from a biological point of view, the difference between our patroller and predator pure strategies is that the former has an extra cost in territorial defence such as birds' song, which has various behavioural patterns, depending upon the ecological conditions. For example, tropical birds use song for breeding and non-breeding territorial defence. But in other species the song has two different functions: Song restricted to males is used for the defense of breeding territories and to attract females (females may be unable to range male song). Different songs are used to defend non-breeding territories. Moreover, where songs are used for non-breeding territorial defense both sexes sing (Morton and Stutchbury 2012). Finally, we mention an example which corresponds to our "predator" strategy: the red-footed falcon (*Falco vespertinus*) defends its territory, but does not sing (Purger 2001).

In our model the fitness is the average growth rate of the different phenotypes, which is defined by the average energy intake and energy lost per unite time. We use real life examples to show that some predictions of our model (considering the time constraints and density dependence of the phenotypes) are not artificial, calling the attention of other researchers to the fact that this kind of model has some biological insight to understand evo-ecological phenomena such as territoriality. Of course, as a starting step (when considering time constraints and density dependence of the phenotypes) in this direction we must use several simplifying assumptions, but for a more concrete example one can build more mechanistic models taking more details into account in the future.

Our theoretical model draws attention to the fact that we should take time constraints and the density dependence of fitness into account to gain a deeper understanding of territoriality. In future work there are two potential main directions. Firstly a more detailed adaptive dynamic analysis could be applied to our model. Indeed, the exact relationship between convergence stability and density dependent stability for the model is still an open question. Secondly, in the second direction, more detailed mechanistic models based on the fact that a territory can provide benefits of different types for owner (e.g. food, mating opportunities) could be developed, potentially with different consequences. Using these biological details in a framework of mechanistic models, the competitive feature of territoriality can be investigated more fully. Three possible generalizations are: allowing the mortality rate of a non-owner to depend upon the ability of an owner to defend food; considering the classic side-blotched lizard population incorporating density-dependence; incorporating signalling behaviour of the owner, such as scent-marking and singing. In this latter case, there is the possibility of intruders being discouraged, depending upon the signal and if they trust that it is "honest"; this thus introduces strategic decisions for the intruders. There are a number of other possibilities, so there is much opportunity to develop the model further.

A Appendix

A.1 The definition of the fitness functions with respect to a population with mutants

To investigate density dependent evolutionary stability one needs to investigate the extended equation (4.4) in which the following functions can be found: $F(x,y,z)$, $G(x,y,z)$ and $H(x,y,z)$ where F is the fitness of a nomad individual, G is the fitness of a resident territorial individual and H is the fitness of a mutant territorial individual in an ecological system in which the density of the nomads is x, the density of the resident territorials is y and the density of the mutant territorials is z. We shall assume that every mutant individual follows the same strategy. We give the definitions of the three functions here, which are similar to those when there are no mutants, the functions in dynamics (2.6); in particular, they are the extensions of those to $z \geq 0$.

Consider an ecological system in which the density of nomads is x, the density of territorial individuals following strategy p is y while those following strategy q is z. One can think of p as the resident strategy and q as the mutant strategy but their roles from a mathematical point of view are symmetric.

The case with more territorials than territories

First, we deal with the case where there are more territorial individuals than available territories, i.e. $y + z > 1$.

Denote by y_o the density of territorial owners following strategy p in the stationary state (we give below how to calculate y_o). Then the density of territorial owners following strategy q is $1 - y_o$ because the density of territories is 1 and it is assumed that every territory is possessed by a territorial if the density of territorials is greater than 1 (see Section 2.2.1).

The probability γ that a randomly chosen active owner loses in a fight is

$$\gamma = \frac{y_o \varrho_{o,p}}{y_o \varrho_{o,p} + (1-y_o)\varrho_{o,q}}[p(1-\alpha_a)+(1-p)(1-\alpha_r)] + \frac{(1-y_o)\varrho_{o,q}}{y_o \varrho_{o,p}+(1-y_o)\varrho_{o,q}}[q(1-\alpha_a)+(1-q)(1-\alpha_r)]$$

where $(y_o \varrho_{o,p})/(y_o \varrho_{o,p} + (1-y_o)\varrho_{o,q})$ is the probability that an active owner is a resident while $((1-y_o)\varrho_{o,q})/(y_o \varrho_{o,p}+(1-y_o)\varrho_{o,q})$ is the probability that an active owner is a mutant. Consequently, an intruder has expectation of being involved in $1/\gamma$ losing fights before it wins (this $1/\gamma$ includes the fight in which the intruder gets to intruder position when losing the territory in owner position). The expected time passing from a losing fight until the next fight is

$$t_l + \frac{1}{\lambda_o} + \frac{\lambda_h}{\lambda_o}t_h$$

where t_l is the waiting time after a losing fight, $1/\lambda_o$ is the expected time necessary to encounter an active owner and $\frac{\lambda_h}{\lambda_o}t_h$ is the expected additional time which is spent handling prey items found before this encounter.

Hence the expected time passing from becoming an intruder until the first win is

$$T_i = \frac{1}{\gamma}\left(\frac{1+\lambda_h t_h}{\lambda_o} + t_l\right).$$

Recall that the waiting time after a defeat in the owner position (which implies that the owner loses its territory and becomes an intruder) is already allocated to the intruder position while the waiting time after a win in the intruder position is already allocated to the owner position. (In the intruder position there is no distinction between the two strategies so it is not necessary to introduce separate functions $T_{i,p}$ and $T_{i,q}$. They are both equal to T_i.).

34

Similarly, we get the expected time passing from becoming an owner until the first defeat is

$$T_{o,p} = \frac{1}{p(1-\alpha_a)+(1-p)(1-\alpha_r)} \left(\frac{1+(1-p)\lambda_h t_h}{\lambda_i} + t_w \right)$$

if the owner follows strategy p and

$$T_{o,q} = \frac{1}{q(1-\alpha_a)+(1-q)(1-\alpha_r)} \left(\frac{1+(1-q)\lambda_h t_h}{\lambda_i} + t_w \right)$$

if the owner follows strategy q (the factors $(1-p)$ and $(1-q)$ before λ_h are derived from the fact that the owner reconsiders its state $(\lambda_r + \lambda_i)/\lambda_i$ times during the search for an active intruder and decides to be a predator in proportions $(1-p)$ and $(1-q)$, respectively, of the reconsiderations).

The value of y_o, if $y+z>1$, is determined by the following equation:

$$\frac{T_{o,p}}{T_{o,p}+T_i} y + \frac{T_{o,q}}{T_{o,q}+T_i} z = 1. \tag{A.1}$$

Recall that T_i depends on y_o through γ so the previous equation is really an equation in y_o.

Since the active proportion of a population agrees with the quotient of the time spent in the active state and the sum of the times spent in the active and inactive states we have

$$\varrho_i = \frac{\frac{1}{\gamma}\frac{1}{\lambda_o}}{\frac{1}{\gamma}\left(\frac{1}{\lambda_o}+\frac{\lambda_h}{\lambda_o}t_h+t_l\right)} = \frac{1}{1+\lambda_o t_l + \lambda_h t_h}, \tag{A.2}$$

$$\varrho_{o,p} = \frac{1}{1+\lambda_i t_w + (1-p)\lambda_h t_h}, \tag{A.3}$$

$$\varrho_{o,q} = \frac{1}{1+\lambda_i t_w + (1-q)\lambda_h t_h}, \tag{A.4}$$

where

$$\lambda_o = f \cdot (y_o \varrho_{o,p} + (1-y_o)\varrho_{o,q}),$$
$$\lambda_i = f \cdot (y+z-1)\varrho_i.$$

(Thus we have an equation system of equations (A.1)-(A.4) with the four unknowns y_o, ϱ_i, $\varrho_{o,p}$, $\varrho_{o,q}$.)

The expected intakes during the times $T_i, T_{o,p}$ and $T_{o,q}$ in turn are

$$I_i = \frac{1}{\gamma}\left(\frac{\lambda_h}{\lambda_o} i_h - c_l \right),$$

$$I_{o,p} = \frac{1}{p(1-\alpha_a)+(1-p)(1-\alpha_r)} \left(\frac{(1-p)\lambda_h}{\lambda_i} i_h - c_w \right),$$

$$I_{o,q} = \frac{1}{q(1-\alpha_a)+(1-q)(1-\alpha_r)} \left(\frac{(1-q)\lambda_h}{\lambda_i} i_h - c_w \right).$$

Hence the fitness of a territorial following strategy p is

$$G(x,y,z) = -d - c_{nt}x - c_{tt}\cdot(y+z) + \frac{y_o}{y}\frac{I_{o,p}}{T_{o,p}} + \frac{y-y_o}{y}\frac{I_i}{T_i}$$

while the fitness of a territorial following strategy q is

$$H(x,y,z) = -d - c_{nt}x - c_{tt}\cdot(y+z) + \frac{1-y_o}{z}\frac{\hat{I}_{o,q}}{T_{o,q}} + \frac{1+z-y_o}{z}\frac{I_i}{T_i}.$$

As regards the nomads we get the same formula as in (2.13), though λ_o depends not only on y, but also now z. In particular,

$$F(x,y,z) = -d - c_{nn}x - c_{tn}(y+z) + \frac{\lambda_h i_h - \lambda_o c_f}{1 + \lambda_o t_f + \lambda_h t_h}.$$

We remark that one can easily check that $H(x,y,0) = \hat{G}$ in (3.3), $F(x,y,0) = F(x,y)$ and $G(x,y,0) = G(x,y)$ in (2.13).

The case where there are not more territorials than territories

Here we consider the simpler case when $y + z \leq 1$. Then every territorial is in the owner position and, consequently, there is no direct interactions among the territorial individuals, i.e. $\lambda_i = 0$. We have

$$\varrho_{o,p} = \frac{1}{1 + (1-p)\lambda_h t_h},$$

$$\varrho_{o,q} = \frac{1}{1 + (1-q)\lambda_h t_h},$$

$$\lambda_o = (y\varrho_{o,p} + z\varrho_{o,q})f,$$

$$F(x,y,z) = -d - c_{nn}x - c_{tn}(y+z) + \frac{\lambda_h i_h - \lambda_o c_f}{1 + \lambda_o t_f + \lambda_h t_h},$$

$$G(x,y,z) = -d - c_{nt}x - c_{tt}(y+z) + b + \frac{(1-p)\lambda_h i_h}{1 + (1-p)\lambda_h t_h},$$

$$H(x,y,z) = -d - c_{nt}x - c_{tt}(y+z) + b + \frac{(1-q)\lambda_h i_h}{1 + (1-q)\lambda_h t_h}.$$

A.2 Investigation of the evolutionary stability of a strategy

To check that a strategy is a DDESS means that we should investigate the asymptotic stability of infinitely many equilibria (to check that (x^*, y^*) is an asymptotic stable rest point of the resident system (2.6) and that $(x^*, y^*, 0)$ is an asymptotic stable rest point of the extended system (4.4) for any q close to p). The simplest case is when the resident ecological equilibrium (x^*, y^*) is hyperbolic with respect to the resident dynamics (2.6) while the equilibrium $(x^*, y^*, 0)$ is hyperbolic with respect to the extended dynamics (4.4). In our case this just means the hyperbolicity of (x^*, y^*) with respect to the resident dynamics and that $H(x^*, y^*, 0) < 0$.[4] The situation is somewhat more difficult if the hyperbolicity does not hold somewhere. In this paper, we will meet such cases when the equilibrium (x^*, y^*) is hyperbolic with respect to the resident dynamics but $(x^*, y^*, 0)$ is not hyperbolic with respect to the extended dynamics any longer because $H(x^*, y^*, 0) = 0$, that is, the invading mutant strategy is selectively neutral with respect to the resident population. Then we can appeal for help to the following lemma.

Lemma A.1 (Lemma 2, Cressman and Garay (2003b)) *Assume that (x^*, y^*) is a locally asymptotic stable hyperbolic equilibrium with respect to the resident system (2.6) and $H(x^*, y^*, 0) = 0$. If*

$$\partial_z H - (\partial_x H, \partial_y H) \cdot \begin{pmatrix} \partial_x F & \partial_y F \\ \partial_x G & \partial_y G \end{pmatrix}^{-1} \cdot \begin{pmatrix} \partial_z F \\ \partial_z G \end{pmatrix} \Bigg|_{(x,y,z)=(x^*,y^*,0)} < 0, \qquad (A.5)$$

then $(x^*, y^*, 0)$ is also asymptotic stable with respect to the extended dynamics (4.4).

If the direction of the inequality in (A.5) is reversed, then $(x^*, y^*, 0)$ is unstable.

---

[4]One can readily check that the eigenvalues of the Jacobian matrix of the extended dynamics (4.4) at the equilibrium $(x^*, y^*, 0)$ is just the two eigenvalues of the Jacobian matrix of the resident dynamics (2.6) at the equilibrium (x^*, y^*) and the value of $H(x^*, y^*, 0)$.

We can use the lemma to prove that a hyperbolic equilibrium (x^*, y^*) is a DDESS. Denote by $B(q)$ the left-hand side of formula (A.5) for a given q. (p, x^*, y^*) is a DDESS, if $B(p) = 0$ and B has a strict maximum in $q = p$. To see this, it is enough to check that $\partial_q B(q)_{q=p} = 0$ and $\frac{\partial^2}{\partial q^2} B(q)_{q=p} < 0$. If $\frac{\partial^2}{\partial q^2} B(q)_{q=p} > 0$, then (p, x^*, y^*) is evolutionarily unstable in the sense that any kind of mutant with strategy close enough to p can invade the resident population. We proceed this way in our examples.

If one of the densities in the resident equilibrium (x^*, y^*) is zero and the other is not, that is, $x^* = 0$ and $y^* > 0$ or $x^* > 0$ and $y^* = 0$, then the previous lemma changes as follows.

Lemma A.1' *Assume that $(0, y^*)$ is a hyperbolic equilibrium of the resident dynamics (2.6) that is $F(0, y^*) < 0$ and $\partial_y G(0, y^*) < 0$. If*

$$\left. \partial_z H - \frac{\partial_y H \partial_z G}{\partial_y G} \right|_{(x,y,z)=(0,y^*,0)} < 0,$$

then $(0, y^*, 0)$ is a locally asymptotic stable rest point of the extended dynamics (4.4). (The case $(x^*, 0)$ is similar, with only the role of x and y and the role of F and G, respectively, exchanged.)

The relationship between convergence stability and density dependent evolutionary stability is partially investigated in Section 3.3 in Cressman and Garay (2003b). However, in their assumptions there is an essential distinction to those of this article. To explain this distinction denote the stationary density surface defined in Section 4.1.1 as being of type I. We define the stationary density surface of type II as follows. Fix strategy p and strategy q such that $q \neq p$. Let (x^*, y^*) be an interior equilibrium of dynamics (2.6) with respect to p, that is, $F(x^*, y^*) = 0$, $G(x^*, y^*) = 0$ and introduce some mutants of strategy q with density $z(\geq 0)$ into this resident system. If the equilibrium (x^*, y^*) is hyperbolic, then, by the implicit function theorem, there is a $\delta = \delta(q) > 0$ and a unique function $(x_q^*(z), y_q^*(z))$ on $(-\delta, \delta)$ such that $F(x_q^*(z), y_q^*(z), z) = G(x_q^*(z), y_q^*(z), z) = 0$ for any $z \in (-\delta, \delta)$ (Lemma 2 in Cressman and Garay, 2003b). This function is the stationary density surface of type II with respect to q. Note that this function depends on q as emphasized by the subscript. While there is a single stationary density surface of type I which is a function of q, there is a continuum of stationary density surface of type II (namely one for every possible strategy different from the resident strategy) and each of them is a function of z.

Cressman and Garay (2003b) fixed a mutant strategy q and considered the polymorphic population of resident individuals following strategy p and mutant individuals following strategy q. Denote by y the density of the residents and by z the density of the mutants. Depending on the densities the mean strategy of the population is $r = r(y, z)$. Our function $\hat{G}$ in the definition of convergence stability (in Section 4.1.1) measures the fitness of a mutant individual following strategy q in the monomorphic population of individuals following strategy r at the density pair $(x^*(r), y^*(r))$ where $(x^*(r), y^*(r))$ is the stationary density surface of type I. Conversely, the function of Cressman and Garay (2003b) measures the fitness of a mutant individual following strategy q in the polymorphic population of resident individuals following strategy p and mutant individuals following strategy q at the density triplet $(x_q^*(z), y_q^*(z), z)$ where $(x_q^*(z), y_q^*(z))$ is the stationary density surface of type II with respect to strategy q. So their function in convergence stability agrees with our function H on the stationary density surface of type II with respect to strategy q. They showed that in this case convergence stability is equivalent to the asymptotic stability of $(x^*, y^*, 0)$ with respect to the extended dynamics (4.4) when the strategy of invaders is q. But this does not prove the equivalence of the convergence stability defined in Section 4.1.1 and density dependent evolutionary stability, since our function in convergence stability is distinct from that of Cressman and Garay (2003b). In addition, we would like $(x^*, y^*, 0)$ to be stable with respect to the extended dynamics (4.4) with respect to a continuum of q-s instead of a single q which is fixed in advance. So, the relationship of convergence stability and the density dependent evolutionary stability is an open question for our model.

References

Abrams P. A. (2005) 'Adaptive Dynamics' vs. 'adaptive dynamics'. J. Evol. Biol. 18:1162–1165.

Abrams P. A. (2010) Implications of flexible foraging for interspecific interactions: lessons from simple models. Funct. Ecol. 24:7–17.

Adams E. S. (2001) Approaches to the study of territory size and shape. Annu. Rev. Ecol. Syst. 32:277-303.

Amsler S. J. (2010) Energetic costs of territorial boundary patrols by wild chimpanzees. Am. J. Primatol. 72:93-103.

Argasinski K. (2012) The dynamics of sex ratio evolution dynamics of global population parameters. J. Theor. Biol. 309:134-146.

Argasinski K. (2013) The dynamics of sex ratio evolution: from the gene perspective to multilevel selection. PLoS. 8(4):e60405. doi: 10.1371/journal.pone.0060405.

Argasinski K. (2018) The dynamics of sex ratio evolution: the impact of males as passive gene carriers on multilevel selection. Dyn. Games Appl. 8(4):671-695.

Argasinski K. and Rudnicki R. (2017) Towards a mechanistic model of population growth suppressed by the availability of nest sites. J. Theor. Biol. 420:279-289.

Berg M. L., Beintema N. H., Welbergen J. A. and Komdeur J. (2005) Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler Acrocephalus australis. J. Avian Biol. 36: 102-109.

Bolker B., Holyoak M., Křivan V., Rowe L. and Schmitz O. J. (2003) Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84:1101–1114.

Both C. and Visser M. E. (2003) Density dependence, territoriality, and divisibility of resources: from optimality models to population processes. Am. Nat. 161:326-336.

Boutin S. and Schweiger S. (1988) Manipulation of intruder pressure in red squirrels (Tamiasciurus hudsonicus): effects on territory size and acquisition. Canadian Journal of Zoology 66:2270-2274.

Broom M., Luther R. M. and Ruxton G. D. (2004) Resistance is useless? – extensions to the game theory of kleptoparasitism. B. Math. Biol. 66:1645-1658.

Broom M. and Ruxton G. D. (1998) Evolutionarily Stable Stealing: Game Theory applied to Kleptoparasitism. Behav. Ecol. 9:397-403.

Broom M. and Rychtář J. (2011) Kleptoparasitic melees – modelling food stealing featuring contests with multiple individuals. B. Math. Biol. 73:683-699.

Broom M. and Rychtář J. (2013) Game-Theoretical Models in Biology. Chapman and Hall.

Brown J. L. (1969) Territorial Behavior and Population Regulation in Birds: A Review and Re-Evaluation. The Wilson Bulletin 81:293-329.

Brown J. L. (1975) The Evolution of Behaviour. New York: W.W. Norton.

Burger J. and Gochfeld M. (1994) Predation and effects of humans on island-nesting seabirds. In Seabirds on islands: threats, case studies, and action plans. Edited by D.N. Nettleship, J. Burger, and M. Gochfeld. Birdlife International, Cambridge. pp. 39-67.

Clutton-Brock T. H. (1982) The functions of antlers. Behaviour 79:108-124.

Corbet P. (2004) Dragonflies: behaviour and ecology of Odonata. Harley Books.

Cowlishaw G. (1997) Refuge use and predation risk in a desert baboon population. Anim. Behav. 54(2):241-253.

Cressman R. and Garay J. (2003a) Evolutionary stability in Lotka-Volterra systems. J. Theor. Biol. 222:233-245.

Cressman R. and Garay J. (2003b) Stability N-species coevolutionary systems. Theor. Pop. Biol. 64:519-533.

Cressman R. and Křivan V. (2013). Two-patch population models with adaptive dispersal: the effects of varying dispersal speeds. J. Math. Biol. 67(2):329-58.

Cressman R. and Křivan V. (2019). Bimatrix games that include interaction times alter the evolutionary outcome: The Owner–Intruder game. J. Theor. Biol. 460:262-273.

Dercole F. and Rinaldi S. (2008) Analysis of evolutionary processes. The adaptive dynamics approach and its applications. Princeton University Press, Princeton.

Dunn M., Copelston M. and Workman L. (2004) Trade-offs and seasonal variation in territorial defence and predator evasion in the European Robin Erithacus rubecula. IBIS 146:77-84.

Eshel I. (1983) Evolutionary and continuous stability. J. Theor. Biol. 103(1):99-111.

Eshel I. and Sansone E. (1995) Owner-intruder conflict, Grafen effect and self-assessment. The bourgeois principle re-examined. J. Theor. Biol. 177:341-356.

Everett R. A. and Ruiz G. M. (1993) Coarse woody debris as a refuge from predation in aquatic communities. An experimental test. Oecologia 93(4): 475-486.

Fisher J. (1954) Evolution and bird sociality. In Huxley J., Hardy A. C. and Ford E. B. (Eds.), Evolution as a process (pp. 71–83) London, U.K.: Allen and Unwin.

Garay J. (2019) Technical review on derivation methods for behavior dependent functional responses. Commun. Ecol. 20(1):28-44.

Garay J., Csiszár V. and Móri F. T. (2017) Evolutionary stability for matrix games under time constraints. J Theor. Biol. 415:1-12.

Geritz S. A. H., Kisdi É., Meszéna G. and Metz J. A. J. (1998) Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evol. Ecol. 12:35–57.

Getty T. (1987) Dear enemies and the prisoners dilemma: why should territorial neighbors form defensive coalitions? Am. Zool. 27:327-336.

Golab M. J., Golab P. A., Contreras-Garduño J., Zajac T. and Sniegula S. (2017) The Effects of Habitat Deterioration and Social Status on Patrolling Behavior in the Territorial Damselfly Calopteryx splendens. Polish Journal of Ecology 65(1):122-131.

Gosling L. M. (2010) A Reassessment of the Function of Scent Marking in Territories. Ethology 60:89-118.

Grafen A. (1987) The logic of divisively asymmetric contests: respect for ownership and the desperado effect. Anim. Behav. 35:462-467.

Grant J. W. A., Chapman C. A. and Richardson K. S. (1992) Defended versus undefended home range size of carnivores, ungulates and primates. Behav. Ecol. Sociobiol. 31:149-161.

Gross M. R. (1984) Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In Fish reproduction: strategies and tactics ed. R. Wootton and G. Potts, Academic Press London p. 55-75.

Gross M. R. and Charnov E. L. (1980) Alternative male life histories in bluegill sunfish. Proceedings of the National Academy of Sciences Nov, 77(11):6937-6940.

Hamilton W. D. (1979) Wingless and fighting males in fig wasps and other insects. In: Blum M. S. and Blum N. A. (eds) Sexual selection and reproductive competition in insects. Academic Press, New York, pp 167-220.

Hayes B. (2010) Wolves of the yukon. Wolves of the Yukon Publishing.

Henrik A. (1990) Despotic Distribution, Unequal Reproductive Success and Population Regulation in the Jay Garrulus Glandarius L. Ecology 71:1796-1803.

Hinsch M. and Komdeur J. (2010) Defence, intrusion and the evolutionary stability of territoriality. J. Theor. Biol. 266:606-613.

Hinsch M. and Komdeur J. (2017) What do territory owners defend against? Proc. R. Soc. B. 284:20162356. https://doi.org/10.1098/rspb.2016.2356

Holling C. S. (1959) Some characteristics of simple types of predation and parasitism. Can. Entom. 91:385-98.

Houston A. I. and McNamara J. M. (2006) John Maynard Smith and the importance of consistency in evolutionary game theory. Biol. Phil. 20:933-950.

Johnson R. P. (1973) Scent marking in mammals. Anim. Behav. 21:521-535.

Kokko H., Lopez-Sepulcre A. and Morrell L. J. (2006) From hawks and doves to self-consistent games of territorial behavior. Am. Nat. 167:901-912.

Korpimaki E. (1988) Effects of Territory Quality on Occupancy, Breeding Performance and Breeding Dispersal in Tengmalm's Owl. J. Animal Ecol. 57:97-108.

Křivan V. and Cressman R. (2017) Interaction times change evolutionary outcomes: Two-player matrix games. J. Theor. Biol. 416:199-207.

Křivan V., Cressman R. and Schneider C. (2008) The ideal free distribution: a review and synthesis of the game-theoretic perspective. Theor. Pop. Biol. 73(3):03-425.

Kruuk H. (1972) The Spotted Hyena: A Study of Predation and Social Behaviour. University of California Press, ISBN 0226455084.

Lima S. L. (1990) The influence of models on the interpretation of vigilance. In Bekoff M. and Jamieson D. (Eds.) Interpretation and Explanation in the Study of Animal Behavior: Vol. 2. Explanation, Evolution and Adaptation (pp. 246-267.) Boulder, Colorado: Westview Press.

Levin S. A. (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Lima S. L. and Bednekoff P. A. (1999) Temporal variation in dangerdrives antipredator behaviour: the predation risk allocation hypothesis. Am. Nat. 153:649–659.

Lopez-Sepulcre A. and Kokko H. (2005) Territorial Defense, Territory Size, and Population Regulation. Am. Nat. 166:317-329.

Maher C. R. and Lott D. F. (1995) Definitions of territoriality used in the study of variation 415 in vertebrate spacing systems, Anim. Behav. 49:1581-1597.

Maynard Smith J. (1982) Evolution and the theory of games. Cambridge University Press.

Maynard Smith J. and Parker G. A. (1976) The logic of asymmetric contests, Anim. Behav. 24:159-175.

McNamara J. M. and Houston A. I. (1992) Evolutionary stable levels of vigilance as a function of group size. Anim. Behav. 43:641–658.

Mesterton-Gibbons M. and Adams E. S. (2003) Landmarks in territory partitioning: A strategically stable convention? Am. Nat. 161(5):685-697.

Meszéna G., Kisdi É., Dieckmann U., Geritz S. A. H. and Metz J. A. J. (2001) Evolutionary optimisation models and matrix games in the unified perspective of adaptive dynamics. Selection 2(1): 193-220.

Metz J. A. J. (2012) Adaptive dynamics. In Encyclopaedia of theoretical ecology Hastings A and Gross L (eds.), California University Press. Chap 2, 7-16.

Metz J. A. J., Nisbet R. and Geritz S. A. H. (1992) How should we define 'fitness' for general ecological scenarios? Trends Ecol. Evol. 7:198-202.

Morrell L. J. and Kokko H. (2005) Bridging the gap between mechanistic and adaptive explanations of territory formation. Behav. Ecol. Sociobiol. 57:381-390.

Morton E. S. and Stutchbury B. J. (2012) Vocal Communication in Androgynous Territorial Defense by Migratory Birds. ISRN Zoology doi:10.5402/2012/729307

Moskát C., Elek Z., Bán M., Geltsch N. and Hauberc M. E. (2017) Can common cuckoos discriminate between neighbours and strangers by their calls? Anim. Behav. 126:253-260.

Ostfeld R. S. (1990) The ecology of territoriality in small mammals. Trends Ecol. Evol. 5:411-415.

Owen-Smith N. (1977) On Territoriality in Ungulates and an Evolutionary Model. The Quarterly Review of Biology 52(1):1–38. doi:10.1086/409720

Parr M. (1983) An analysis of territoriality in libellulid dragonflies (Anisoptera: Libellulidae) Odonatologica 12(1):39-57.

Pereira H. M. Bergmann A. and Roughgarden J. (2003) Socially stable territories: The negotiation of space by interacting foragers. Am. Nat. 161(1):143-152.

Piper W. H., Walcott C., Mager J. N. and Spilker F. J. (2008) Fatal battles in common loons: a preliminary analysis. Anim. Behav. 75:1109-1115.

Pöysä H. (1987) Feeding-Vigilance Trade-Off in the Teal (*Anas Crecca*): Effects of Feeding Method and Predation Risk. Behaviour 103 (1-3):108-122.

Purger J. J. (2001) Defence behaviour of Red-footed Falcons Falco vespertinus in the breeding period and the effects of disturbance on breeding success. Ornis Fennica 78(1):13-21.

Rodenhouse N. L., Sherry T. W. and Holmes R. T. (1997) Site-Dependent Regulation of Population Size: a New Synthesis. Ecology 78(7):2025-2042.

Rolando A., Cavallini P., Cursano B. and Olsen A. (1995) Non-Territorial Behaviour and Habitat Selection in the Jay Garrulus glandarius in a Mediterranean Coastal Area during the Reproductive Period. J. Avian Biol. 26:154-161.

Rosell F., Bergan F. and Parker H. (1998) Scent-Marking in the Eurasian Beaver (Castor fiber) as a Means of Territory Defense. J. Chem. Ecol. 24:207-219.

Schaller G. B. (1972) The Serengeti lion: A study of predator-prey relations. Chicago: University of Chicago Press.

Schlägel U. E. Merrill E. H. and Lewis M. A. (2017) Territory surveillance and prey management: Wolves keep track of space and time. Ecology and evolution. 7:8388-8405.

Schoener T. W. (1987) Time Budgets and Territory Size: Some Simultaneous Optimization Models for Energy Maximizers. Amer. Zool. 27:259-291.

Sinervo B. and Lively C. M. (1996) The rock-scissors-paper game and the evolution of alternative male strategies. Nature 380:240-243.

Sinervo B., Svensson E. and Comendant T. (2000) Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985-988.

Spencer R. and Broom M. (2018) A game-theoretical model of kleptoparasitic behaviour in an urban gull (Laridae) population. Behav. Ecol. 29:60-78.

Stamps J. A. (1994) Territorial behavior: testing the assumptions. Advances in the Study of Behavior 23:173-232.

Stamps J. A. (1987) The effect of familiarity with a neighbourhood on territory acquisition. Behav. Ecol. Sociobiol. 21:273-277.

Temeles E. J. (1994) The role of neighbours in territorial systems: when are they 'dear enemies'? Anim. Behav. 47:339-350.

Vincent T. L. and Brown J. S. (2005) Evolutionary game theory, natural selection, and Darwinian dynamics. Cambridge University Press, Cambridge.

Werner E. E. and Peacor S. D. (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.