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# Evolution of Fledgling Choice

## When to fight for territory?



*a masters project by  
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## Abstract

The 'goal' for any organism is to reproduce, thereby securing the persistence of its genes for the next generation. Many vertebrate species need a territory before reproduction is possible. When good quality territories are not available a fledgling may opt for other routes to breeding. Several theoretical studies have been performed on breeding in low quality territories, delaying dispersal and floating behaviour. 'Squeezing in' a territory, is an active and aggressive option which results in a small and not yet productive territory for the fledgling. Under which circumstances should a fledgling decide to squeeze in a territory?

I used an individual based simulation model in which floaters have two options to become a breeder: through waiting for a territory to become available, or through squeezing in a territory.

The results showed that squeezing is much more prevalent when larger parts of territories are overtaken. In contrast, the chance of succeeding in this squeezing attempt does not influence the evolution of squeezing at all. The mortality of breeders and floaters both influence the occurrence of squeezing, but not in a linear way. Relative high breeder survival promotes squeezing, as does high floater survival. Territory owners defend their territories against squeezing attempts when they could loose a lot of territory, but not if these attempts have a high chance of being made by philopatric offspring.

## Introduction

A lot of behaviour observed in nature seems to be suboptimal or to have downright negative effects on the fitness of the individual. Although some of these observations may be ascribed to misfit individuals, most of these suboptimal behaviours have actual positive effects in the long run. Abandoning a nest, for example, has detrimental effects on that cohort of offspring and therefore on the lifetime reproductive success of the parent. But if abandoning this nest means that the parent will increase its future prospects, the nest abandonment becomes adaptive. For evolutionary biologists the goal is to explain the emergence of these seemingly unadaptive behaviours and traits.

Delaying one's reproduction is in its most straightforward manifestation an offspring-reducing behavioural trait and therefore one could call it unadaptive. On the other hand, what if the individual has no choice? There are several circumstances where the conditions just do not allow you to breed. When no mates are available for example or when there is no room for another nest. Delaying one's reproduction is not so much of a choice then, but forced upon you by the outside world.

What possible choices are left then? An individual could choose to wander around, simply waiting for an opportunity to arise. Instead of wandering, one could also choose to stay with ones parents and wait for a breeding opportunity. This is called 'delayed dispersal'. In birds, 3% of the species that show delayed reproduction also show delayed dispersal (Komdeur & Edelaar 2001). Within this group cooperative breeding has been a much observed phenomenon. Offspring that decided not to disperse make it possible for them to help their parents raise consecutive broods. Since they are related to their siblings they help raising, their own fitness is increased indirectly (Hamilton 1964).

But not all offspring necessarily chooses to stay at home when reproduction is limited. Other strategies are also employed. The already mentioned wandering (usually referred to as 'floating') is one option. Another would be to breed under suboptimal conditions in a territory of low quality. As a last option, one could resort to force, by squeezing a new territory between the existing ones. When part of the natal territory is incorporated into this new territory, the process is also called 'budding'. This way, the individual creates a breeding opportunity for itself and does not have to delay its reproduction.

The most common explanation for delayed dispersal has always been the limited opportunity to breed (as already stated before e.g. by no territory, no mate or high cost of dispersing) (Hatchwell & Komdeur 2000). But a lot of species although confronted with these ecological constraints do not choose to delay dispersal. The ecological constraints theory has therefore only been able to explain variation within a species (Hatchwell & Komdeur 2000). To predict the occurrence of delayed dispersal on a species level, life-history traits become more important. It is argued that especially low adult mortality promotes group living, due to prolonged habitat saturation (Covas & Griesser 2007). A low mortality in the natal territory (together with other benefits provided by the parents) might also be a reason for offspring to postpone their dispersal. With these intrinsic benefits of staying at home, delayed dispersal would occur even in the absence of habitat saturation (Hatchwell & Komdeur 2000).

Theoretical studies have been trying to find out what exactly the factors are that determine the occurrence of delayed dispersal. In most mathematical models individuals

are given a choice between different routes to breeding. The available options however are always variations of floating on one side and delayed dispersal, with or without helping on the other side (Kokko & Sutherland 1998, Pen & Weissing 2000a, Pen & Weissing 2000b, Kokko *et al.* 2001, Kokko & Ekman 2002). An additional option which has not been considered yet in theoretical modelling is trying to squeeze in a new territory. By doing that, the individual would provide itself with a territory on which it can immediately start breeding. Since this is quite an advantage over waiting for an existing territory to become vacant, the question arises why this behaviour is not more widespread. Budding off a territory from the parental territory is in this context especially interesting since part of the costs is burdened by the parents.

Theoretical studies have shown that the occurrence of strategies such as floating or delaying dispersal is bound to environmental and physiological cues (Kokko & Sutherland 1998, Pen & Weissing 2000a, Pen & Weissing 2000b, Kokko & Ekman 2002, Lopez-Sepulcre & Kokko 2005). Nature itself confirms that delayed dispersal is not omnipresent. Territory squeezing is most likely bound to the same type of cues. In this study I hope to find the conditions under which squeezing and budding can and cannot occur. Using computer simulations I hope to gain more insight in the factors contributing to the dynamics of territory budding.

### ***Fledgling choices***

When breeding opportunities are scarce fledglings may have to employ other means by which they can maximize their fitness. Delaying dispersal is only one of several possible strategies a fledgling can choose. Delaying dispersal means staying at the parental nest, potentially waiting for the territory to become vacant. While staying, one can either help in raising subsequent broods, help defending the territory or just do nothing (e.g. (Komdeur 1992, Balshine-Earn *et al.* 1998)). Other possible options are floating – leaving the parental nest and waiting for a vacant territory, queuing and eventually moving into a neighbouring territory, budding – budding off a part of the parental territory, breeding in a low quality habitat or moving into high quality habitat. But these definitions may differ per study done.

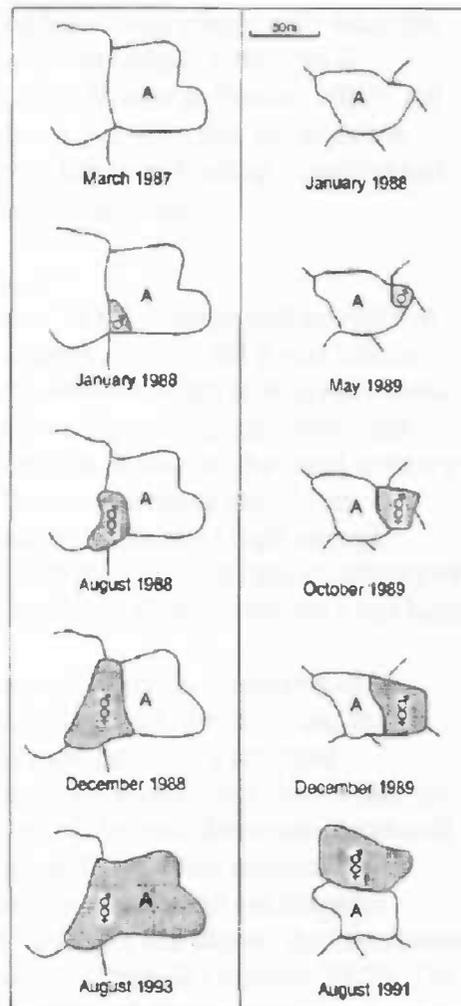


Figure 1. Two examples of territory budding by young male Seychelles warbler. The shaded area represents land taken by the son but originally owned by the parental pair in territory A. The territory grows at the expense of neighbouring territories. The budding males ultimately inherit a neighbouring territory. From (Komdeur & Edelaar 2001)

With many strategies available, evolutionary biologists have been looking for what the optimal strategies are under several conditions (Kokko & Sutherland 1998, Pen & Weissing 2000a, Pen & Weissing 2000b, Kokko *et al.* 2001, Kokko & Ekman 2002). All these mathematical models built differ slightly in their assumptions and the possible coexisting strategies. Most of them look at the dynamics between floating, queuing and the opportunity to breed immediately in a game theoretical approach.

#### *Evolution of delayed dispersal and reproduction*

Why would one choose to delay its reproduction? It has been hypothesized that delayed reproduction was just the best-of-a-bad-job strategy, that is, not a real 'choice' but the only available strategy since the reproducing opportunities are scarce (Hatchwell & Komdeur 2000). The main explanation for this has been the ecological constraints hypothesis (Hatchwell & Komdeur 2000). Offspring decides to stay on the natal territory because of lack of available independent resources. These constraints have been hypothesized to act in four different ways: through lack of territory of high enough quality, through a high mortality risk associated with dispersal, through unavailability of suitable mates or through a low chance of successful breeding after the territory has been established (Hatchwell & Komdeur 2000).

Variation in these ecological constraints between different populations of a species have in the past been enough to explain the occurrence of family-living in one population but the absence in others, or even the same population in a different year (Hatchwell & Komdeur 2000). Experimental breeder removals have shown that the constraints on independent breeding are the actual cause of delayed dispersal (Hatchwell & Komdeur 2000). So cause and effect have been proven, but the fact remains that almost all species are confronted with some ecological constraints and yet disperse immediately (Covas & Griesser 2007). A phylogenetic analysis has shown the distribution of delayed dispersal over the different genera to be patchy (Covas & Griesser 2007). The same analysis also showed that among long-lived birds delayed dispersal occurs more often.

These life-history traits in bird species have proven to be a better predictor for the variances between species (Covas & Griesser 2007). Species with a high survival rate combined with a small clutch size have a higher chance of living in families (Hatchwell & Komdeur 2000). Furthermore, it was found that the higher the proportion of cooperative breeding species in a family, the lower the value of mortality. This strongly suggests that low mortality promotes sociality and not the other way around (Hatchwell & Komdeur 2000).

Recognizing the importance of life-history traits helped understanding the patchy distribution of family living among birds (Covas & Griesser 2007). Still, most long-lived birds do not show delayed dispersal. This shows that the life-history hypothesis can, just like the ecological constraints hypothesis, not be the sole explaining factor of delayed dispersal (Covas & Griesser 2007). Some point out that the life-history and ecological constraints hypotheses are in essence the same; In a population in which individuals have high longevity, turnover of territories is low and habitat saturation emerges fast, which poses ecological constraints on new recruits (Hatchwell & Komdeur 2000, Covas & Griesser 2007). This is in line with findings that low mortality is associated with

increased sedentariness, lower latitudes and reduced environmental fluctuation(Hatchwell & Komdeur 2000).



Figure 2. A group of the cooperatively breeding cichlid *Neolamprologus pulcher* defending their territory against a predatory fish. Subordinates of this group delay their reproduction and instead assist the dominant breeding pair in raising offspring. High predation risk outside the territory is one of the suspected factors contributing to the delayed dispersal of offspring.

From <http://www.zoology.unibe.ch/>

In the above section, delayed dispersal and reproduction have only been considered as a best-of-a-bad-job strategy, a 'plan-B'. But some studies point out that staying at home might provide direct benefits, especially for species with high longevity. Since most long lived species have a low fecundity, the tactic to maximize lifetime reproductive success would be to maximize the number of breeding attempts. Young breeders have several disadvantages; they do not have breeding experience, they have low competitive ability and the chance of settling in a high quality territory is small(Covas & Griesser 2007). These factors increase mortality which decreases the total number of breeding attempts possible. Waiting a few seasons before dispersing will therefore increase the total fitness of an individual(Covas & Griesser 2007). Longevity also makes increased parental investment more feasible. Parents with high a survival can afford to invest in prolonged parental care after offspring independence without increasing their own mortality disproportionately(Covas & Griesser 2007).

The benefits-of-philopatry hypothesis states that these aforementioned intrinsic benefits of the natal territory promote delayed dispersal. So even in the absence of habitat saturation delayed dispersal can occur. One straightforward advantage of staying at home not related to longevity is the increased chance of territory inheritance(Pen & Weissing 2000b).

It has already been said that the ecological constraints and the life-history hypotheses both promote delayed dispersal through habitat saturation. Similarly the main difference between the ecological constraints and the benefits-of-philopatry hypotheses is the emphasis on costs or benefits, respectively(Hatchwell & Komdeur 2000). Altogether the three explanations mentioned should therefore not be seen as mutually exclusive.

### ***Territoriality***

Breeding opportunities are often highly dependent on available territories. Delayed dispersal and cooperative breeding are often observed together with territoriality in an animal's ecology(Komdeur 1992,Balshine-Earn *et al.* 1998,Legge & Cockburn 2000,Campbell *et al.* 2005). Although cooperative breeding does not necessarily imply territoriality(see(Valencia *et al.* 2003)), most models of delayed dispersal also assume

territoriality(Kokko & Sutherland 1998, Pen & Weissing 2000a, Kokko *et al.* 2001, Kokko & Ekman 2002). The number and sizes of available territories could be quite crucial to the decision of offspring. How do these territories come about? What are the important dynamics? And what determines their size?

But let us first try to define a territory. Maher and Lott( 1995) found 48 different definitions of territoriality in the literature. 'Defended space' was the most used term, followed by 'exclusive use' and 'site specific dominance'. Quite a number of papers do not explicitly define territoriality.

#### *Focal residents, neighbour interaction and new comers*

How has territoriality been modelled up to now? Adams( 2001) gives a good overview of the theoretical studies that have been performed on the size of territories. Three different categories can be distinguished in his review.

Focal resident models focus on the optimal territory size an individual should adopt, depending on resource availability and intruder pressure(Adams 2001). Intruders are assumed to be easily chased away by the focal individual. But no distinction is made between foraging floaters and territorial neighbours/potential settlers who will not be chased away so easily. In effect these territories are assumed to be isolated, not bordering any other territories(Adams 2001).

As the name implies, neighbour-interaction models do take neighbours into account. Using the asymmetries in condition of the neighbouring individuals, these models describe how boundaries are settled and what determines their positions and shapes(Adams 2001). To predict boundary positions, modellers use geometric techniques, assuming that the intensity of aggressive defence declines with distance from the central site. Territory shapes can be affected by a heterogeneous distribution of resources causing them to deviate from the simpler forms(Adams 2001). Instead of looking at distinct boundaries, one can also look at territory size as an emergent property from rules on how animals forage, move and react to competitors(Adams 2001).

The third type of models Adams( 2001) identifies consists of the interaction between residents that already have established a territory and newcomers looking to acquire them. The number of individuals that will have a territory in the end determines the average territory size(Adams 2001). To prevent territory loss, neighbours may interact, thereby preventing settlement of newcomers. These models link territorial decisions to population-level phenomena like floaters(Adams 2001). These are the dynamics in which I hold most interest.

#### *Reproductive skew*

If offspring decides to bud off a part of its parental territory, it will swap its parents' reproductive success for its own. This is a special case of reproductive skew in which the central question is how much a parent should reduce its fitness in favour of its offspring(Johnstone 2000). Because I want to study budding behaviour, some theory on skew seems vital.

In an extensive paper Johnstone( 2000) states that a reproductive skew occurs when a dominant individual prevents its subordinates from reproducing thereby monopolizing reproduction. A complete skew arises when only the dominant pair can reproduce. The subordinates can then only help the dominant raising the dominants

offspring, thereby enhancing the dominants reproductive success. In practise, the whole range between a complete skew and free breeding is observed(Johnstone 2000). So why should a dominant pair allow reproduction of its offspring? And in which cases is this advantageous?

According to Johnstone( 2000), there are two ways in which skew can arise. In the first type, the dominant pair is assumed to have total control over reproduction. So it can decide who can breed and to what extent. If it would allow its subordinates no reproduction at all, the subordinate may leave since it might then become more advantageous to breed independently. Since the subordinates help the dominants, the dominant pair wants to prevent them from leaving. The subordinates should be allowed a minimum amount of breeding that makes staying just a bit more advantageous over leaving; this is the so called concession model(Johnstone 2000).

Arguments have been raised over this theory with respect to the control the dominant pair is supposed to have over reproduction. Some claim this to be highly unlikely and propose an opposite theory, dubbed the restraint model by Johnstone( 2000). In this model the dominant pair has no influence on the others' reproduction, but can evict subordinates. Then the subordinates can have a much higher own reproduction, until they 'push it too far' and get evicted from the group. In fact the dominant pair should throw subordinates out once the reproduction that the dominants have given up is not compensated anymore by their helping effort(Johnstone 2000).

## **Research questions**

When immediate breeding is not or hardly possible, two major strategies can be adopted, floating or delaying dispersal. Delaying dispersal might even provide intrinsic benefits to the individual. But other strategies, not yet considered in theoretical studies can be employed. Forcing a breeding window for oneself in the population is one of those options. 'Squeezing' in a territory between the existing territories is a good example of that.

As already has been shown, delaying dispersal is not the always the optimal choice for a fledgeling (Pen & Weissing 2000b, Kokko & Ekman 2002) and can therefore only evolve under specific circumstances. In the same line of reasoning I expect that the decision to actively (and most of the times aggressively) chase away others for an own piece of territory will not always be beneficial, but bound to certain restrictions. To identify these restrictions I ask myself:

***Under which circumstances should a fledgling decide to create a new territory instead of wait for a territory to become available?***

Squeezing in a territory is an interesting strategy for a fledgling. The individual can breed immediately, even though possibly with a low chance of success (e.g. (Komdeur & Edelaar 2001)). In some cases, its chance to overtake a neighbouring territory increases dramatically (e.g. (Komdeur & Edelaar 2001)). But it is probably much more costly than staying at home in a familiar, already protected area.

In reality, part of the squeezing success depends on the willingness of the neighbouring territory holders. If these fiercely resist the establishment of a new territory, squeezing will not be a viable option. But by doing so, they might deny their own offspring a breeding opportunity. The question therefore arises:

***Do territory owners resist the establishment of a new territory?***

The strategy of offspring to bud off part of the parental territory is a special and very interesting case of territory squeezing; budding offspring will always try to overtake part of the parental territory. From the parents perspective this is an interesting situation. If they allow a son to take part of their territory to use as its own, the parents evidently loose part of their territory which comes with a loss of reproductive success. On the other hand this loss might be compensated by the fact that their offspring can now produce grandchildren. One instinctively expects that parents will have lower resistance against territory squeezing if the chances are high that it concerns their own offspring. This could perhaps arise when offspring chooses familiar terrain when looking for own territory. I wonder if this would lead to a higher degree of territory squeezing, due to decreased resistance of territory owners. So my final question is:

***Does philopatry of offspring promote territory squeezing?***

## Previous work

Theoretical work on different routes to breeding, like delayed dispersal, has been trying to unravel the factors responsible for the existence of these phenomena. Most of the studies try to explain the occurrence of floaters. Only a few are on the evolution of group living or helping. I could find no theoretical work covering the strategy of territory squeezing or budding.

### *Optimal territory choice*

Under which conditions should an individual refrain from breeding, but wait instead for better quality territories to become available? What would be the minimal expected lifetime reproductive success an individual should aim for? Kokko and Sutherland( 1998) tried to answer this question using a model in which two strategic choices are available to the individuals: in their model an individual has the option to either be a floater which enables it to compete for any available free territory, or to become a breeder on a territory (assuming a vacant territory is available). The territories differ in quality (which corresponds to estimated future LRS), but can not shrink in size or split. Once a territory is chosen, the breeder stays there until it dies. It might therefore be advantageous to not start breeding on the first territory available but wait for a better quality site to become vacant. The model variable is the minimal LRS a territory should provide ( $V^*$ ) for a floater to decide competing for it. In a different version of their model floaters can not compete for all vacancies, but have to queue for a specific territory.

The evolutionarily stable minimal LRS the floaters should adopt is 1 for both models(Kokko & Sutherland 1998). Therefore both models predict that the non-breeding population will be maximized (floaters for the first model and queuers for the second), thereby decreasing the total population size. The ratio breeding-non breeding population size is linearly dependent on the average breeding habitat quality.(Kokko & Sutherland 1998)

Two assumptions of the model are that individuals can perfectly assess territory quality and that habitat choice would be ideal (individuals would choose the best of available sites, as long as it exceeds the minimal quality)(Kokko & Sutherland 1998, Pen & Weissing 2000a). The presence of ideal habitat selection in the model presented by Kokko and Sutherland( 1998) has been questioned; mutants that have a lower  $V^*$  (territory quality acceptance threshold) are condemned to this lower quality sites and will therefore never have an LRS higher than unity, a consequence of modelling in continuous time(Pen & Weissing 2000a). This might occur in saturated habitats(Kokko *et al.* 2001) although even there these mutants with lower  $V^*$  are expected to first compete with the other floaters for higher quality sites(Pen & Weissing 2000a).

Pen and Weissing( 2000a) propose a model that is quite similar, with the exception that breeder mortality depends on site quality and that breeding occurs in periodic discrete time intervals(Pen & Weissing 2000a). They implement two different scenarios of site competition: in one, first the best territory has a floater assigned to it randomly, as long as its  $V^*$  is lower, followed by the second best territory etc., corresponding to seasonal territoriality. In the other scenario the sites are randomly picked and assigned to a randomly picked floater (with a fitting  $V^*$ ), which would be more in correspondence to a year round breeder. In the first scenario the ESS has the minimal LRS  $V^*$  reduced to  $1-\mu_f$  (=floater mortality). At this acceptance threshold the number of floaters will not be maximized. In the second scenario a variety of  $V^*$  co-occur(Pen & Weissing 2000a).

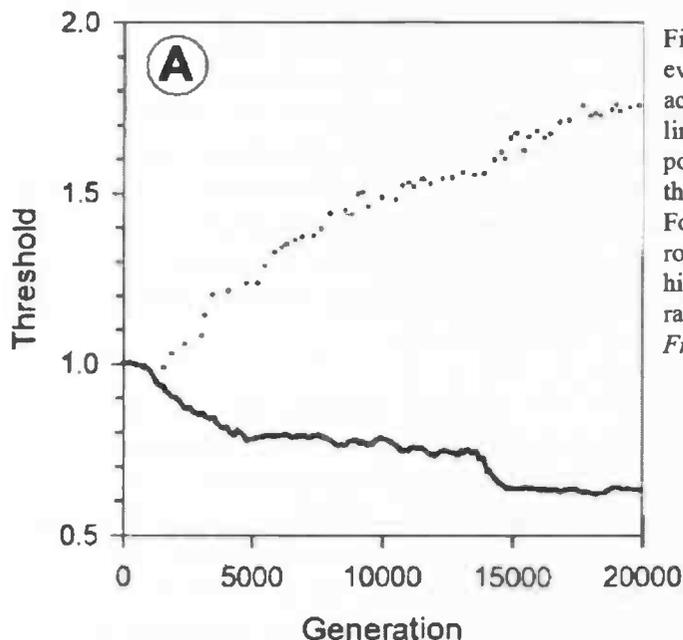


Figure 3. A simulation showing the evolutionary trajectories of the average acceptance threshold. Scenario 1 (solid line) represents seasonal territoriality. The population evolves towards an acceptance threshold of 0.6, corresponding to  $1-\mu_f$ . For scenario 2 (dotted line) with year round breeders, the population evolves to a highly polymorphic state were a broad range of acceptance thresholds exists. From (Pen & Weissing 2000a)

In contrast to Kokko and Sutherland( 1998), this model shows that a territory quality acceptance threshold below one would evolve(Pen & Weissing 2000a). This seems to be the main point of their article. But in fact the outcome of their second scenario is a better comparison to the system modelled by Kokko and Sutherland, since it does not involve the seasonality. The conclusion that model outcomes can markedly differ depending on how time dynamics are modelled is still a valid one(Pen & Weissing 2000a).

#### *The invasion of helping*

One step before what to do when floating a fledgling has to decide whether to float at all. Delaying dispersal and helping at the nest are both behaviours observed in nature(e.g. (Komdeur 1994,Balshine-Earn *et al.* 1998,Valencia *et al.* 2003)). In a paper from 2000, Pen & Weissing( 2000b) ask which conditions determine the evolutionary success of the helping strategy.

In their model the chance that offspring will opt for helping is the evolving trait. The number of helpers a breeding individual has positively influences the number of offspring produced that season. When offspring choose not to help, they become floaters

instead, looking for a free breeding opportunity. The population size is assumed to be fixed and the chance for a floater to find a breeding spot is independent of the number of breeders.

If territories are not inherited, neither ecological constraints on breeding, nor breeder survival affect the occurrence of cooperative breeding. The occurrence of territory inheritance itself does affect the occurrence of cooperative breeding. Even when helpers are not helping at all, but imply a small cost, still the 'helping' behaviour can invade the population as long as the helpers can inherit the territory. Providing benefits of philopatry therefore seems to be a crucial factor in the evolution of cooperative breeding (Pen & Weissing 2000b).

Under the regime of territory inheritance and if density dependence acts on floater success, breeder mortality affects occurrence of cooperative breeding (negatively), while ecological constraints on breeding have no such influence. The authors state that exactly this has been confirmed in phylogenetic analyses (Pen & Weissing 2000b). The often expected influence of ecological constraints on occurrence of cooperative breeding were only seen when the density dependence acted on reproductive output. Breeder mortality was in this case positively related to cooperative breeding. In contrast, in the previous scenario low mortality increased the benefits when the territory was inherited and therefore the occurrence of helping. Determining the mechanism of density dependence therefore seems crucial in predicting cooperative breeding.

#### *Direct benefits of group living*

Is helping behaviour necessary for the evolution towards group living? The roles of ecological constraints, life history traits and the benefits of philopatry are closely examined in a paper by Kokko and Ekman (2002). In a mathematical model they design several routes to breeding without any helping involved; all the fitness advantages will be due to direct benefits. In the continuous-time model offspring has three options of becoming a breeder: as a philopatric subordinate it can wait to (possibly) inherit its parental territory, or it can shift to a nearby territory that has become vacant. As a floater it can inspect a much larger range of territories, but it has a higher mortality. Local subordinates may have a competitive advantage because they know their territory which increases their chance on territory inheritance, or they have a disadvantage due to incest avoidance. Floaters can have a competitive disadvantage because they know the area less well. Local subordinates are not given an advantage or disadvantage at neighbouring sites. If offspring stays, they join a queue which can vary in strictness of order of who inherits the territory.

Mathematical analysis reveals the forming of groups by delayed dispersal when territorial inheritance and local shifting are present. Even when the chance on territorial inheritance is low, benefits of staying still let delayed dispersal prevail (Kokko & Ekman 2002). This so called 'safe haven' mechanism reduces in effect for lower ranking subordinates, making it for them more likely to disperse, especially when mortality differences between stayers and floaters is small (Kokko & Ekman 2002).

The strength of competition for breeding sites does not influence the development of groups. But the influence of ecological constraints should not be discarded completely (Kokko & Ekman 2002). If the strength of competition increases due to, for

example, more competitors, this will affect some life history trait values, like floater mortality, which does influence delayed dispersal(Kokko & Ekman 2002). No difference in territory quality is implemented in this model. Both variation in territory quality and helping behaviour of offspring therefore do not seem to be obligatory for the development of delayed dispersal(Kokko & Ekman 2002).

#### *Territory compression*

In many models, territories are seen as discrete entities with a fixed size. The carrying capacity of such a model equals the number of territories available. What determines carrying capacity of a territorial population when territories are considered fluid quantities? So the number of territories a certain habitat encompasses and their sizes are not fixed, but rather depend on the number of individuals breeding. In a model by Lopez-Sepulcre and Kokko( 2005) territory size depends on the defence effort an individual expends. Reproductive success is positively influenced by the size of the territory, breeder mortality by defence effort. An individual in the model can squeeze in its own territory until a minimum territory size is reached. The excess of individuals adopts a floater strategy. The number of floaters, which equals the number of potential intruders, increases the defence effort of a territory holder.

A small equilibrium territory size can be the result of two processes. If fecundity is high and has a steep dependency on territory size, a maximum number of territories is created and the surplus of individuals becomes floaters. The population obeys regulation by floaters while territory size remains fixed(Lopez-Sepulcre & Kokko 2005). If fecundity is low and its relation with territory size is weak, large territories will create offspring that will squeeze between the other territories, which reduces per capita reproduction, until equilibrium is reached. So the carrying capacity of a habitat is determined by life history traits of a species(Lopez-Sepulcre & Kokko 2005). When these results are compared with a non-territorial model, the territorial population yields lower population sizes. This shows that conflict over space use often leads to sub-optimal performance of a population(Lopez-Sepulcre & Kokko 2005).

## Hypotheses

What will be the important processes influencing territory squeezing? What makes an individual choose to fight aggressively for a new territory? The first condition which will be important is that there should be a certain degree of saturation of territories in the area. This poses an ecological constraint on the new fledglings which only now have to decide how to acquire a breeding position. In principle the need of this choice arises immediately after the first breeder has settled. Should a future breeder wait for the first breeder to leave its territory, bud off part of that territory or start breeding in a lower quality territory. The last option will be the most likely in the beginning since 'lower quality' will still be good.

When there is no difference in territory quality but only in quantity (as for example in the model of this paper), territory squeezing will be pointless as long as the empty area left is bigger than the tiny territory acquired through squeezing in a territory. Delaying dispersal or floating are therefore already applicable at lower saturation levels than squeezing; when inheriting a big territory later compensates for the loss that had to be incurred by not opting for immediate breeding in the smaller left over area. The point is that squeezing will only occur when a qualitatively uniform area is practically saturated. As also pointed out for the ecological constraints hypothesis (Hatchwell & Komdeur 2000) this will be a prerequisite for squeezing behaviour to evolve, not a predictor of its evolution.

From a squeezers perspective, floating and delaying dispersal are the same. They both wait for a territory to become available. Floaters just check a larger number of territories than the delayed dispersers, though this is more a matter of definition. For a fledgling the question is, why should I wait for a territory when I can have one now? Of course this 'instant territory' is only small, with a low chance of reproduction and it is very costly to expand this territory. How can these costs be compensated?

For short-lived species, squeezing could provide a fitness advantage over waiting. First of all no time should be wasted when one has not long to live; any breeding opportunity should be tried, even when it only provides a small chance of reproduction. Secondly, as a breeder this individual now has a higher than average chance of overtaking a neighbouring territory which has lost its owner (which is more likely due to this low longevity). Thereby it acquires a decently-sized territory. A relation between a life history trait such as longevity and delayed dispersal has already been found, theoretically and empirically (Pen & Weissing 2000b); long lived species showed a higher chance of delaying their dispersal.

Another potentially important cause for the evolution of squeezing behaviour is when owning a territory provides intrinsic benefits, next to the possibility to breed. For instances if the life of a floater is risky and a territory provides a place where the individual can safely retreat. This could push towards the evolution of acquiring a territory as quickly as possible by squeezing between others. Though the same argument can (and has) been used to explain the evolution of delayed dispersal (Kokko & Ekman 2002).

## Material and methods

### Model

I used an individual based simulation model to answer my research questions. Two types of individuals are present: breeders and floaters. Floaters have two different possible pathways available for becoming a breeder: either through taking an empty territory ('squatting') or through forcing in a new territory between existing ones ('squeezing'). Breeders never return to the status of floaters.

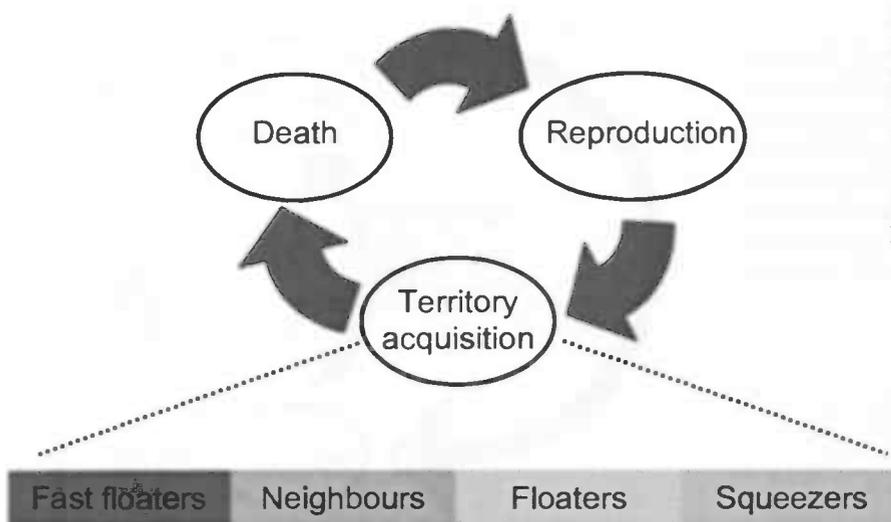


Figure 4. A schematic representation of a yearly cycle. The zoom shows from left to right the sequence of processes during the territory acquisition phase

### *The yearly cycle*

The model runs in discrete years: every year has the same build up of several stages or seasons. The year starts in the breeding season. For simplicity, and to circumvent the problems associated with models with continuous time (Pen & Weissing 2000a), every year there will be only one breeding season. Successful breeders produce offspring to which they pass on their traits  $\beta$  and  $\rho$ . Once the offspring has left its parent's nest and become a floater, the 'harsh season' starts. For every breeder and floater it is determined whether they live through this year. All casualties are removed from the population.

In the following pre-breeding season every floater has to decide whether to get a territory through the squeezing or squatting tactic. Some vacant territories will be discovered by fast, vigilant squatters before the neighbours have found out. All the other territories are incorporated by the neighbours. Squatters then take the empty territories that are still left. Squeezers are the last to make their squeezing attempt. For the successful attempts a new territory is generated. Squatters move into any empty territories that casualties of squeezing attempts have left behind.

### Life-history

The population is assumed to be haploid, asexual and reproducing parthenogenetically. Between the breeding seasons individuals have a type-specific mortality (floater mortality  $\mu_f$ ; breeder mortality  $\mu_b$ ). If a breeder survives until the breeding season, it may reproduce. The chance for an individual to reproduce successfully depends on the size of its territory. If successful, one offspring is produced. The offspring is assumed always to be raised successfully into sexual maturity, so the chance to reproduce is actually equal to the chance to produce a new, live fledgling. These newly produced individuals immediately leave their parent's territory and join the floating population.

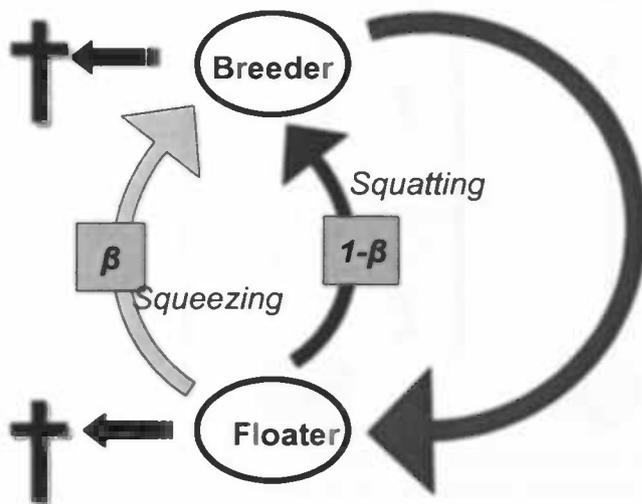


Figure 5. The life cycle of an individual. Breeders reproduce, thereby creating floaters. A floater has to choose between two strategies in order to become a breeder. With chance  $\beta$  it opts for squeezing. Both breeders and floaters have a certain mortality chance.

### Territory

Territories and their sizes play an important role in the model. The essence of squeezing is that it can start with a much smaller territory than average and then grow larger. Therefore territory size is not a fixed value. Rather each territory has a certain amount of area, which is taken from the total stack of area available. For simplicity space is modeled as a 1-dimensional ring. All territories are therefore bordered by two neighbouring territories.

Only breeders can own a territory, or to put it otherwise, once an individual owns a territory, that individual becomes a breeder. If a breeder dies the territory does not disappear automatically but remains lingering.

Every vacated, lingering territory has a chance of being discovered by a squatter before the neighbours do (chance  $d$ ). When this is the case, a randomly picked squatter will be assigned to that territory. Otherwise vacated territories are incorporated by the neighbours into their territories. Neighbours split a territory evenly between them, unless one has reached its maximum size ( $T_{max}$ ). If so, the other neighbour may take the remaining area. If both neighbours reach the maximum territory size before the territory is used up a random squatter quickly takes the remaining bit of area left as its own territory.

Incorporating neighbouring, vacant territories is the only available mechanism for growth of territories in this model. A large territory is important because it provides

resources (food) needed to raise offspring. An increase in territory size therefore increases reproductive success. The chance for successful reproduction is described by

$$O = \frac{T^2}{T^2 + R} \quad (1)$$

where  $O$  is the chance of producing one offspring in a certain year,  $T$  is the size of the breeders territory and  $\sqrt{R}$  is the territory size on which  $O = 0.5$ . (1) is a function of diminishing returns; at a certain point an increase in territory size does not produce any significant increase in chance of producing offspring; one does not need an infinite amount of resources. Since physical constraints make it impossible to maintain arbitrarily large territories I set a maximum territory size  $T_{max}$ .

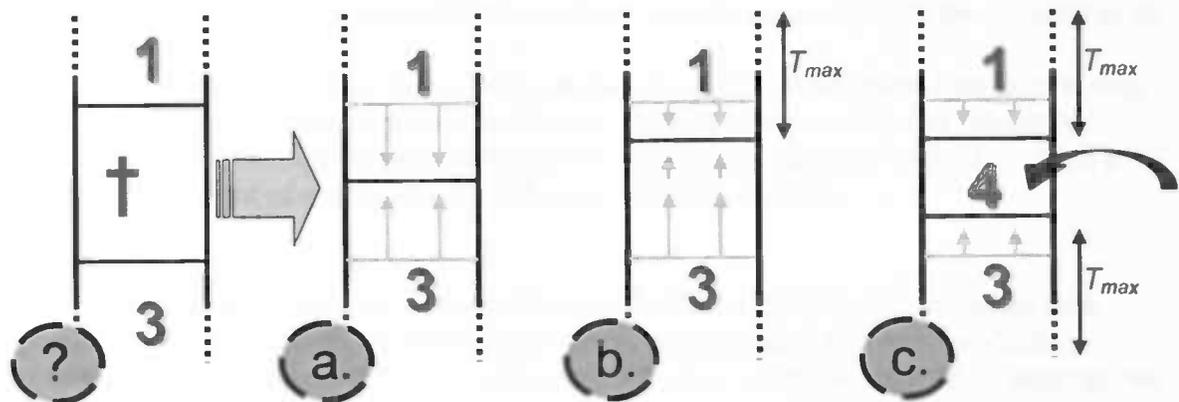


Figure 6. Three possible outcomes of territory incorporation: '?' shows the starting point with three territories, the top one occupied by individual 1, the bottom one by individual 3 and the middle territory has just lost its owner. 'a': Both neighbours share equally. 'b': neighbour 1 reaches its maximum territory size, 3 receives what is left. 'c': both neighbours reach their maximum, a squatter takes the left over space.

### Strategy

Every year, each individual in the floating population chooses one of two pathways to breeding. With chance  $\beta$  an individual decides to make a 'squeezing' attempt that season. It forces its territory between already existing territories, thereby taking over part of its neighbouring territories areas. These victim-territories can be two randomly chosen, neighbouring territories, which will be referred to as 'general squeezing'. In a different version of the model, the victim territories consist of the parental territory and a random neighbour thereby simulating 'budding'. If in this version of the model the parental territory does not exist anymore, the individual adopts the 'general squeezing' tactic.

The victim territories can resist the squeezing attempt made by the floater. Resisting consists of two parts. First the territory owner decides whether it wants to resist, determined by chance to resist  $\rho$ . If so, the chance that the squeezer wins the subsequent fight is determined by  $w$ . If the two residents do not resist or the squeezer wins both fights, the squeezer gets to create a territory between the defeated neighbours.

'Creating' or 'squeezing in new territory' are a bit misleading terms in this case since they suggest that the intruder forces new area between two territories which only have to move to the side. In reality these two territories lose part of their area to the new

one. Once the intruder has beaten both neighbours it 'steals' a percentage  $b$  of both their territories which it uses for its own territory between them. No additional space is therefore created; borders have been merely shifted and in the area between them a new territory was founded.

Note that for every fight both contestants have to pay a mortality cost  $\mu_c$ . This cost should not necessarily be seen as a direct result of the fight, but more as an indirect cause of a premature death later in the season. So a defending resident may die because of a fight, but still have won that fight, thereby preventing the squeezer from settling. Floaters that fail but survive their squeezing attempt will return to the floating population at the end of the season.

If a floater decides not to make a squeezing attempt (a chance of  $1 - \beta$ ), it will instead wait and try to take a vacated territory that season, a behaviour dubbed 'squatting'. For every discovered empty territory a random squatter will be assigned as its owner.

$\beta$  and  $\rho$  are heritable traits. They can mutate slightly when passed on to offspring. The chance a trait mutates is determined by  $M$ , the size of the mutation is randomly picked from a continuous uniform distribution between the range of  $-\Delta\beta/\Delta\rho$ ..  $\Delta\beta/\Delta\rho$ . An infinite amount of strategies of  $\beta$  and  $\rho$  are therefore possible.

#### *Density dependence*

It has been shown that the occurrence of helping is greatly influenced by how population density acts on its dynamics. If density dependence acts on reproductive success, ecological constraints have a positive influence on the occurrence of helping (Pen & Weissing 2000b). In this model reproductive success is necessarily density dependent; when there are a lot of breeders, territory sizes will be small which causes reproduction to be low.

Floater success is also necessarily density dependent. The chance of a floater obtaining a territory diminishes with an increasing number of floaters. Number of floaters has also a positive effect on breeder mortality (assuming  $\beta > 0$  and  $\rho > 0$ ) since the breeders have to fight more intruders, paying the mortality cost  $\mu_c$  every time they do so. Another possible density dependent effect of number of floaters could be through food competition on both floater and breeder mortality; more floaters means more competition for less food. For the sake of simplicity, I chose to leave this population regulation mechanism out.

#### *Starting conditions*

In tables 1 to 3 are the different parameter values used for the simulations. Table 1 shows the constants which are kept the same for all simulations. All other parameters of the simulation are variables, which can be seen in table 2. The two mortalities are based on values used in other simulation models (e.g. (Kokko & Ekman 2002), (Pen & Weissing 2000a)). Three values around 0.5 will be used for  $w$ . The two values of  $b$  represent two different possible processes during squeezing. Either  $b = 0.05$  and the squeezer has succeeded in getting a small foothold in his surroundings. Or  $b = 0.33$  where the squeezer has succeeded immediately the first year in getting a foothold and expanding it at the expense of his two neighbours; his territory is now the average size of the neighbouring territories.

Two other aspects of the simulations are varied between simulations. The first is the starting population size. To keep the model balanced, it is necessary to modify two other parameters as well, with the starting population size as to increase the total carrying capacity of the model; decreasing  $R$  actually increases the carrying capacity, making smaller territories already productive (the total area is always scaled to one). To make the largest territory possible as productive as in the less populated model,  $T_{max}$  is decreased. These three parameters in table 3 only vary together.

The last variation between simulations is the absence or presence of philopatry.

All different parameter combinations have run in ten replicates per combination. This would add up to  $(3 * 3 * 3 * 2 * 2 * 2 * 10 =)$  2160 simulations. Due to time constraints, one variable has been thrown out in half of the simulations. Since win chance  $w$  showed hardly any effect, I chose to leave that one out in future simulations. The small starting population with no philopatry and the large population with philopatry have therefore been run with one variable,  $w$ , less.

Every simulation starts by assigning every individual of the starting population a territory. All individuals therefore start as a breeder and all territories have the same size. The for every individual, the traits  $\beta$  and  $\rho$  are assigned random value between 0 and 1.

Table 1. The constant parameter values

Constant	Description	Value
$d$	chance to detect empty territory	0.003
$M$	mutation chance	0.001
$\Delta\beta / \Delta\rho$	mutation step	0.05
$\mu_c$	combat mortality	0.05

Table 2. The simulation variables

Variable	Description	Value		
$\mu_b$	breeder mortality rate	0.1	0.3	0.6
$\mu_f$	floater mortality rate	0.1	0.3	0.6
$w$	chance to win a conflict as a squeezer	0.3	0.5	0.7
$b$	part of territory stolen by successful squeezer	0.05		0.33

Table 3 Parameters associated with starting population size

Variable	Description	Value	
$P$	starting population size	1000	10,000
$R$	squared territory size for reproduction chance = 0.5	$10^{-6}$	$10^{-8}$
$T_{max}$	maximum territory size	0.005	0.0005

### Data analysis

In total 1480 simulations have been done. To analyze the progression of every simulation is a time consuming enterprise. Therefore I only used the end state of every simulation. I assumed that after a 100,000 simulation-years equilibrium would have been reached. This was checked by sampling several simulations. The characteristics of these end states were then pooled in a dataset.

Per simulation several characteristics are stored; all the starting values, the number of territories, breeders and floaters after 100,000 simulation-years, the average  $\beta$  and  $\rho$  and their standard deviations at the end of the simulation. Simulations with zero breeders at the end of the simulation were considered extinct and were left out of the analysis.

## Results

Within the used parameter space several scenarios provided suitable conditions for the successful evolution of squeezing. Between these simulations the frequency of squeezing varied up to a maximum of  $\beta = 0.634$  ( $\mu_b = 0.1$ ,  $\mu_f = 0.6$ ,  $b = 0.05$ ,  $w = 0.5$ ,  $P = 1000$ , non-philopatric). In most scenarios though  $\beta$  decreased immediately at the start of the simulation until  $\beta = 0$  was reached. The evolved resistance level was more variable. All values of resistance from  $\rho = 0$  (never resist) to  $\rho = 1$  (always resist) could be observed.

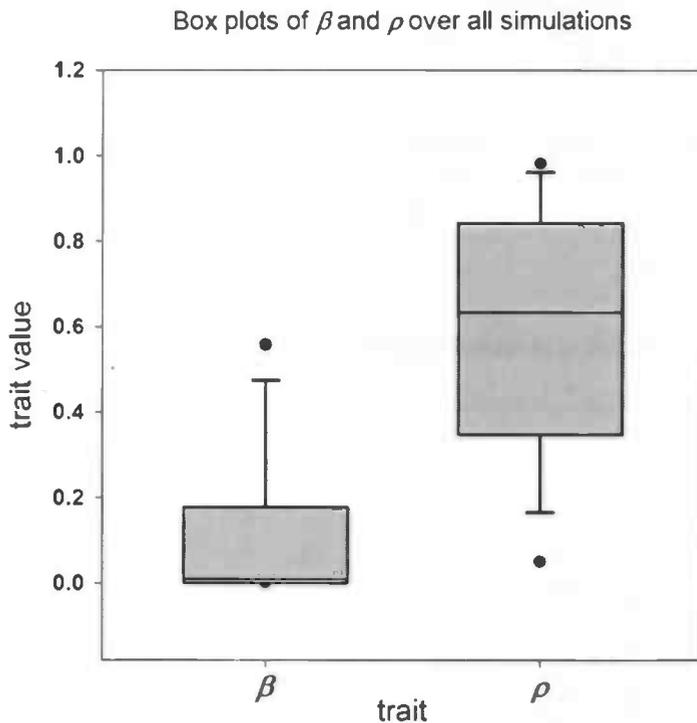


Figure 7. Distribution of the average values of squeezing frequency  $\beta$  and resistance chance  $\rho$  of all simulations with  $P = 1000$  and no philopatry. Median: middle line, box: 25-75 percentile range, whisker: 10-90 percentile range, black dots: outer 5-95% values.

### *Influence of population size*

The effect of population size was quite strong. When the large populations are compared to the same scenario with lower population size, the frequency of squeezing dropped considerably with population growth, ranging from a factor 4 to a factor 50.

Resistance did not show a large change in level when population size changed, except when the squeezing frequency would drop below 0.003 which happened more often in the large population scenario. This resulted in random resistance levels across simulations.

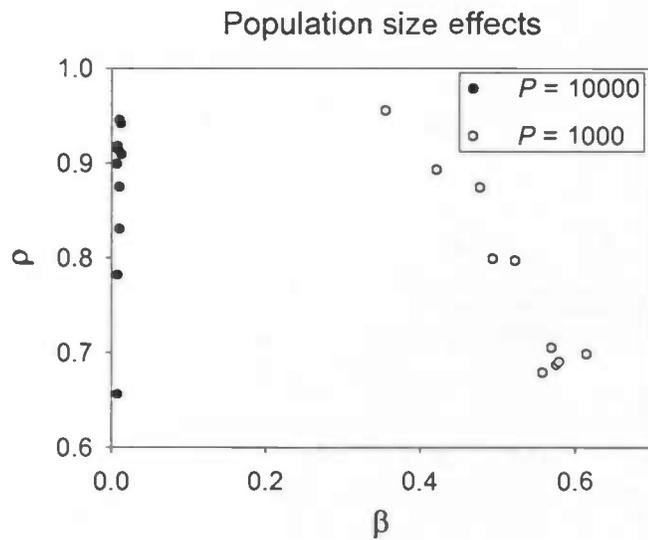


Figure 8. A comparison between a large ( $P = 10,000$ ) (filled dots) and a small ( $P = 1000$ ) (open dots) population size. All other parameter values are constant ( $\mu_b = 0.1$ ,  $\mu_f = 0.6$ ,  $b = 0.33$ ,  $w = 0.5$ , non-philopatric).

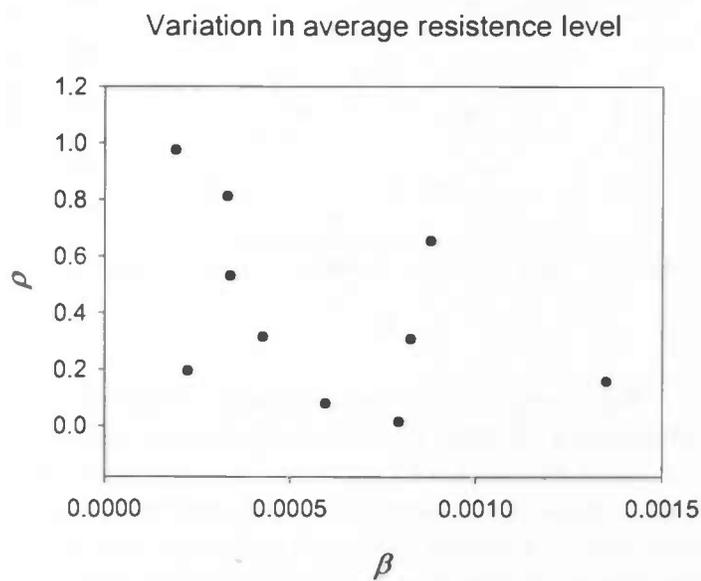


Figure 9. An example of variable average values of resistance from different replicates in a large population ( $\mu_b = 0.1$ ,  $\mu_f = 0.6$ ,  $b = 0.05$ ,  $w = 0.5$ ,  $P = 10,000$ , non-philopatric)

#### *Influence of philopatry*

Offspring that would always squeeze in a territory next to their parents (old) territory resulted in a clear decrease of resistance shown by the parents in small populations, but a decrease in squeezing frequency in large populations (though this frequency was already very small). Consequence of both was that high squeezing rates would never accompany high resistance levels. The breeder population sizes increased with philopatry.

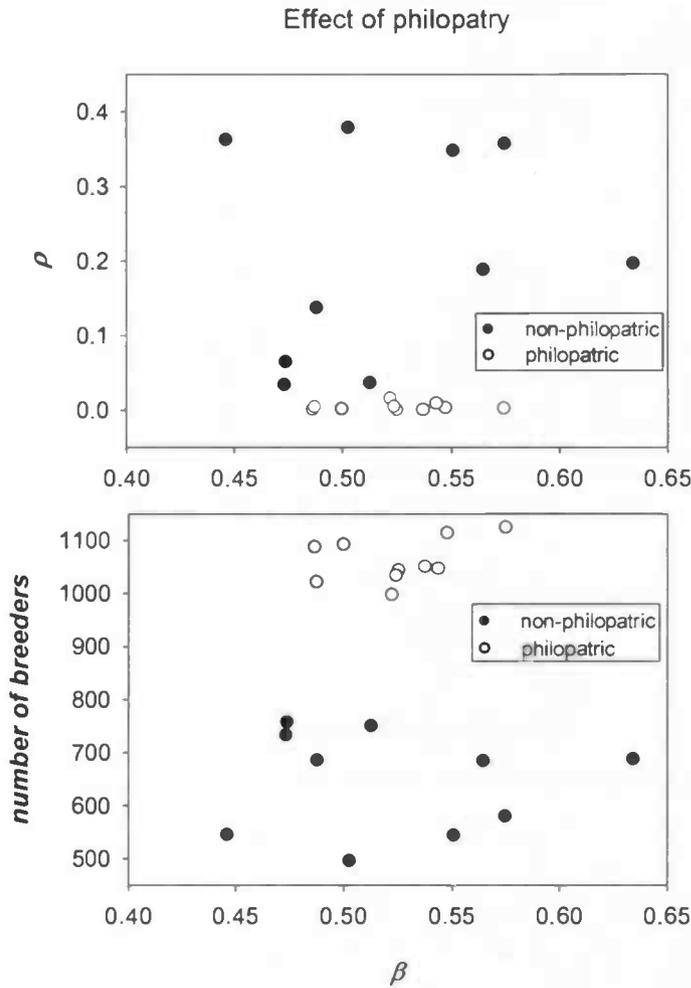


Figure 10. The effect of philopatry: filled dots show values for offspring that squeezes in at random locations, the open dots show the values for offspring squeezing in at the natal territory. The graphs show marked differences in resistance level  $\rho$  (upper graph) and the number of breeders (lower graphs) between the two scenarios. Other parameter settings are  $\mu_b = 0.1$ ,  $\mu_f = 0.6$ ,  $b = 0.05$ ,  $w = 0.5$ ,  $P = 1000$ .

#### *Influence of percentage of stolen territory b*

The percentage of territory taken by a successful squeezer was of great influence on the occurrence of squeezing. If a squeezer would receive a smaller part of the defenders territory,  $\beta$  would decrease or in some cases stay level, but never increase. Any considerable squeezing frequency occurs 3.5 times more often in scenarios with  $b = 0.33$ . Resistance seems to increase as well with increasing stolen territory. Though this relation is weak at best. At larger mortality rates the relation can even inverse.

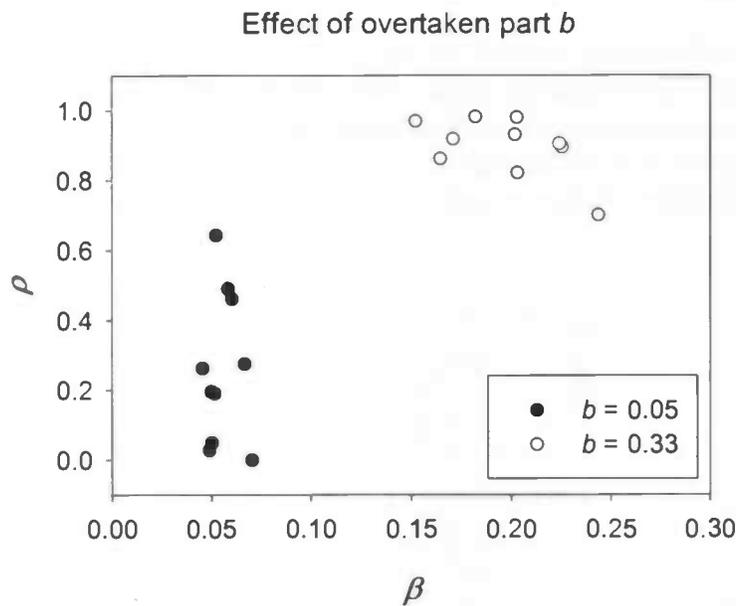


Figure 11. The effect of overtaken part  $b$ : filled dots ( $b = 0.05$ ) show a lower frequency of squeezing and less resistance compared to open dots ( $b = 0.33$ ). Other parameter settings are:  $\mu_b = 0.1$ ,  $\mu_f = 0.3$ ,  $w = 0.5$ ,  $P = 1000$ , no philopatry.

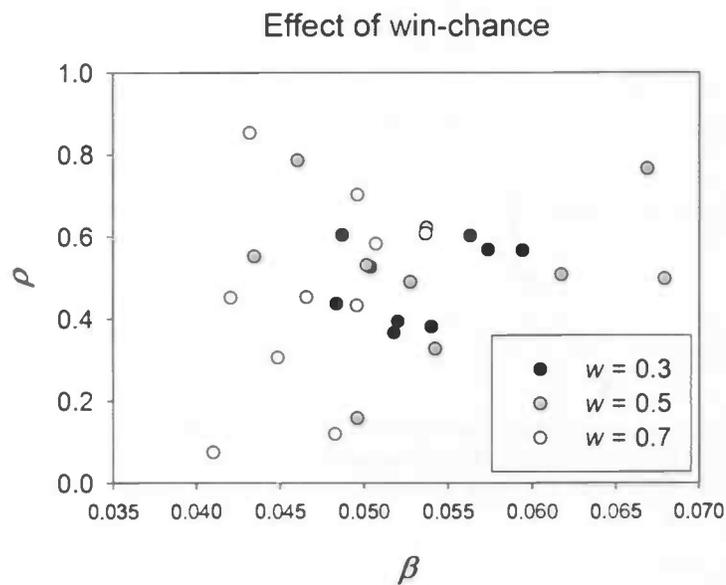


Figure 12. The effect of win chance: For the black dots  $w = 0.3$ , the gray dots  $w = 0.5$ , for the open dots  $w = 0.7$ . Other parameter settings are:  $\mu_b = 0.1$ ,  $\mu_f = 0.3$ ,  $b = 0.33$ ,  $P = 1000$ , philopatry.

*Influence of chance to win  $w$*

The expected benefits of squeezing are also increased by increasing the chance for a squeezer to win a conflict. Yet the expected positive influence of  $w$  on squeezing frequency was minimal. The effect of  $w$  on  $\beta$  is in all cases small.

### Influence of mortality $\mu$

The effect of mortality among floaters and breeders is hard to qualify. The main effect of one of the two mortality values on squeezing changes with the modification of the other mortality. When floater mortality is kept constant at  $\mu_f = 0.1$ , increasing breeder mortality increases the occurrence of squeezing. If  $\mu_f = 0.6$ , increasing breeder mortality induces the opposite. The effect of floater mortality also changes sign.

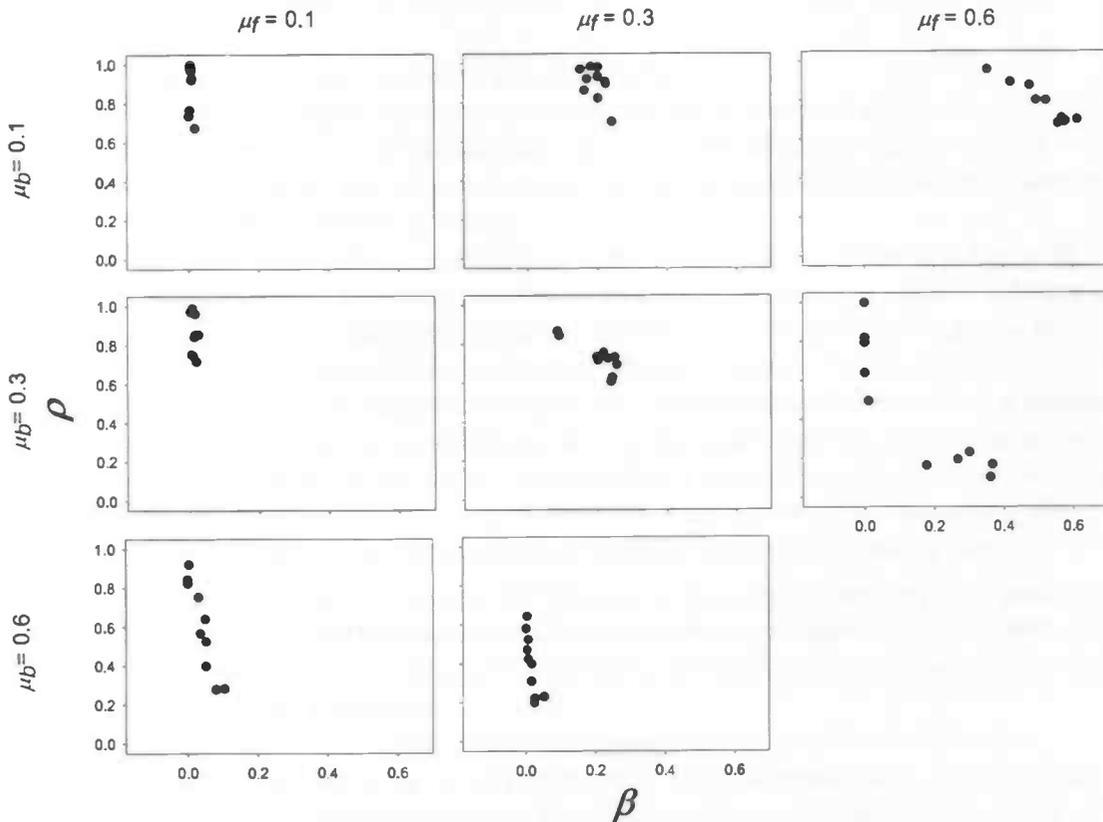


Figure 13. The effect of mortality: Graphs are arranged by mortality; from left to right floater mortality  $\mu_f$  increases, from top to bottom breeder mortality  $\mu_b$  increases. The x-axis of every graph represents  $\beta$ , the y-axis represents  $\rho$ . Other parameter settings are  $b = 0.33$ ,  $w = 0.5$ ,  $P = 1000$ , no philopatry.

## Discussion

In none of the simulations did squeezing ever evolve to  $\beta=1$ . This is in accordance with expectations since such a population would have been susceptible for invasion by squatters; every piece of empty territory left after processes like territory incorporation by neighbours, or territory owners deceased after conflict would be assigned to a squatter. Therefore the chance that a squatter would acquire a territory in a certain season would practically be as large as a squeezer, without paying the mortality cost of conflict. A squatter free society is therefore impossible.

### *In large populations squeezing rarely develops*

Why does it in larger populations hardly pay off to follow a squeezing tactic? The process of squeezing in does not differ between large and small populations. It is a local process, not influenced by any global factors, but purely based on how two neighbours act on intrusion of the potential squeezer.

The process of squatting an empty territory is also expected not to differ with different population sizes. The total number of floaters who have to compete is larger in larger populations, but the number of available territories is expected to likewise be more abundant. The relative competition for territory should therefore remain equal.

If the chance of acquiring a territory is not expected to differ for either a squeezer or a squatter in different sized populations, why is the squeezing frequency then so much lower when population sizes are high? The payoff of a squeezed territory must be smaller in those cases. In the simulation the population size was increased by increasing the starting population, decreasing the maximum territory size and decreasing the 'reproductive rate'  $\sqrt{R}$  all by a factor 10. Therefore the average territory size would have been ten times as small, but breeders would have had the same reproductive output since their fertility increased tenfold. A squatted territory is therefore as much worth in a large population as in a small population.

For squeezers the situation is different though. Once they have acquired a territory, expanding that territory is very important. This becomes much more difficult though in the larger populations scenario. For the population of floaters is ten times as large, while the chance that a potential squatter discovers a certain territory before a neighbouring breeder does, detection chance  $d$ , remains the same for the two scenarios. So compared to the less populated model, the chance of a territory remaining unnoticed by any squatter had been raised to the power of ten

$((1-d)^{f^{large}} = (1-d)^{10 f^{small}} = \{(1-d)^{f^{small}}\}^{10})$  which is much more than a tenfold decrease.

Owners of relatively small territories (e.g. former squeezers) cannot expand their territory as easily in a large population, which makes squeezing a less desirable trait. So to get any considerable squeezing in a population, the effective size of this population should not be too large.

After concluding this, the question remains what would happen if the detection chance of territories by floaters would decrease accordingly with an increase in population size? The vigilance of a single floater is expected to be the same, but if an individual has a larger area to cover, it has to divide its attention more or inspect less territories. The chance to detect a certain single empty territory would thereby decrease. Would this make squeezing more successful again?

### *Consequences of philopatry*

Philopatry increases the chance of parent-offspring interaction. In reaction to this we saw that either resistance or squeezing frequency dropped. Both of these reactions are expected to reduce the number of conflicts that arise; either the parents decide not to resist that often, or the offspring decides to fight less for their territory. The breeding population was considerably larger in scenarios with philopatry. This model therefore shows that philopatry makes squeezing attempts more successful.

Staying at home does not dramatically promote squeezing behaviour though. In most scenarios the frequency of squeezing is only slightly higher in the philopatry version. In one case ( $\mu_b = 0.1$   $\mu_f = 0.3$ ) the squeezing frequency even drops in the philopatry model. But whether this frequency drops or increases, the breeding population size seems only to increase when offspring does not wish to leave. Philopatry has therefore a positive influence on the population size; a population with budders is more successful than a population where floaters fight for a random patch of territory.

Will squeezing therefore promote staying at home? A population of philopatric budders that encounter no resistance would be susceptible for a cheater who does not squeeze in a territory at his parents', but someone else's. I can not answer these questions using these data though. What I can say is that in a situation where offspring has the tendency to stay around their natal territory, perhaps because of direct benefits, their choice to squeeze in a territory would meet less resistance.

### *The mechanism of territorial growth*

The factor that has one of the biggest impacts on the success of squeezing is the percentage of territory taken after the conflict is won. It is in line with expectations that a higher reward for a squeezer will result in more squeezing. The more interesting result is that squeezing even occurs when the reward for it is relatively low. The overtaken part of territory can be as small as  $b = 0.05$  and still half of the floating population opts for this tactic. We can therefore safely say that large instant benefits are not required for 'squeezing in' to be a successful strategy.

The benefits for the squeezer must then lie in the fact that it owns a territory and can now increase it by slowly expanding its border into neighbouring territories. The choice for a fledgling is the choice between immediately getting a small and useless territory but with potential, or wait for a productive territory to become available with the risk of dying without offspring.

I showed that if the part of territory overtaken by a squeezer is not so small (and thus not so useless), more scenarios provide suitable conditions for high frequencies of squeezing. As already said, this makes sense; when benefits are increased one can expect to see more of that behaviour. The assumption behind  $b = 0.33$  was that the squeezer still starts with a small territory, but that it succeeds in expanding that territory during the first season to more useful proportions at the expense of its neighbours. This implies much more conflict for the individual than in the scenario with  $b = 0.05$  where the just settled squeezer waits for its neighbours demise. The comparison between the two scenarios is therefore not completely honest. An extra mortality cost for these fast growing squeezers (with  $b = 0.33$ ) could be introduced in later models to counter balance this high territorial benefit.

### *Winning*

Benefits seem to make a difference for the occurrence of squeezing. Surprisingly, the chance obtaining these benefits seems to have a much smaller impact. When the chance of winning a conflict was raised between simulations, the expected dramatic increase in squeezing frequency failed to occur. In fact, the difference between these simulations is strikingly small. Neighbours seem to resist a bit more often, when squeezers have a higher chance to win.

When raising the chance of winning a conflict, an individual has a higher probability of successfully squeezing in a territory, thereby increasing the expected benefits of squeezing. This should promote squeezing behaviour considerably, yet observed effects are small. Neighbours might increase their resistance to counterbalance against their lower chances of winning, keeping the total number of territory losses at bay.

But why the effects of winning are so small remains unclear. Doing more replicates might already give a clearer picture of what the effects are in the first place. A deeper analysis would give us more clues of what the processes are that make this win chance such an insignificant factor.

### *Mortality and population dynamics*

The choices fledglings make, revolve around competition for empty territories. The availability of empty territories and the strength of competition are both factors which are influenced by the mortality rates of the population. But mortality rates could also have direct influence on the frequency of squeezers. If one compares for instance the three situations where breeder mortality  $\mu_b = 0.1$  and floater mortality one of  $\mu_f = 0.1$ ,  $\mu_f = 0.3$  or  $\mu_f = 0.6$  (see figure 13) we see that floater mortality has a positive influence on the frequency of squeezing. Increased competition can not explain this; the number of floaters decreases with increased floater mortality. Instead, increased floater mortality will make the position of a breeder much more desirable. Squeezing provides a higher chance of getting a territory immediately. So even though the territory itself might not be useful, at least the individual is safe from the hazards that floating brings.

But this 'escape from death' hypothesis can not explain all phenomena. With increased breeder mortality waiting for a good territory to become available should be preferred over squeezing, as long as waiting provides a larger territory than squeezing. Yet, the simulation series [ $\mu_b = 0.1 \mu_f = 0.1$ ], [ $\mu_b = 0.1 \mu_f = 0.3$ ], [ $\mu_b = 0.1 \mu_f = 0.6$ ] (figure 13) show that in fact squeezing increases with breeder mortality. I can think of several arguments explaining this behaviour. The first is that even though the number of floaters decreases with breeder mortality, the number of breeders drops even more and with them the number of available territories, thereby increasing competition for empty territories. Taking a new piece of territory might therefore be an easier choice.

The second argument for preferring squeezing over squatting when breeder mortality is high, is because squeezing has become more profitable on its own accord. Due to the drop in breeders, the average size of the remaining territories is larger. Squeezers get therefore a larger amount of territory when winning a conflict. Squatters of

course also inherit a larger territory, but the relative increase in productivity is larger in smaller territories.

Furthermore, due to high mortality, the chances of squeezing next to an empty territory are much higher. Empty territories do not resist squeezing attempts. This higher frequency of empty territories also makes growing easier, so that small, just created territories, do not have to remain small for long.

The variable outcomes of the simulations are the result of all these dynamical processes. Identifying causal pathways from the data is sometimes quite difficult; for example, competition might have increased which promoted squeezing behaviour which levelled off the competition back its old level. The emergent stable states in the simulation [ $\mu_b = 0.3$   $\mu_f = 0.6$ ] show the interplay of resistance and squeezing frequency, but in order to understand this pattern further analysis is required.

### *Synthesis*

What factors in the end seem to contribute to the evolution of squeezing behaviour of fledglings? The habitat was always saturated in this model. I can not say if squeezing would also have evolved with free area still available. In this model that was impossible; at the end of every season floaters were assigned to every free territory left, so there were either no free territories, or otherwise no floaters who could squat. Other studies could not find an influence of competition for breeding sites (on delayed dispersal), yet still did not discard the influences of ecological constraints (Kokko & Ekman 2002). I do not doubt the importance of at least a certain degree of habitat saturation, especially in a qualitatively uniform habitat, for the evolution of budding or squeezing.

Life history traits are important factors determining the success of fighting for a territory. The exact relations are of yet not clear, but societies with higher mortalities do show a higher chance of squeezing behaviour. From this the prediction follows that long lived species will display less aggressive-territorial behaviour. These long lived species show on the other hand more delayed dispersal (Pen & Weissing 2000b), though these two behaviours are not mutually exclusive and exist side-by-side (Komdeur & Edelaar 2001)

If a phylogenetic study will be performed on territorial squeezing, it is important to measure not only the average survival; this study showed that the survival discrepancy of the different life stages of an individual can be more important than mere average survival for the evolution of squeezing. These findings did not always support the benefits-of-a-territory hypothesis, since also higher breeder mortality promoted squeezing. Kokko and Ekman (2002) did find this effect for delaying dispersal and dubbed it the 'safe-haven' mechanism. The possibility of other benefits for a territory owner have not been explored in this model, although one could argue that any benefit can in the end be expressed in a survival advantage (apart from reproduction, which has been separate in this model as well).

In species or populations where territory owners are weak defenders and fledglings could steal a larger part of the owner's territory, a higher frequency of squeezing behaviour is expected. Although resistance will also increase, so breeders will most likely evolve to better defenders of their territory. A high defensive effort has consequences for the population at large; less breeding spots will be created and therefore

the population will grow smaller. Similar results have been found in a model where fledgling choices did not evolve and territory sizes were averaged (Lopez-Sepulcre & Kokko 2005).

When a population is large and keeping track of a large amount of territories is relatively cheap (by say for instances, just flying over them), less territories are expected to be squeezed in. This prediction is mostly a consequence of the fact that territory growth can only be accomplished by incorporating neighbouring empty territories. Since in real life there are more ways of expanding one's territory, I expect squeezing to be more prevalent in large populations than this model predicts.

Comparing the philopatric model with the random territory squeezer showed that resistance by territory owners reduced the number of breeders in a population. For the population it would therefore have been better if all breeders refrain from defending, yet this is most likely not an evolutionary stable strategy. Breeders allow a loss of territory only when either this loss of territory is low, or when the chance that own offspring will receive this territory is high. Apparently only in these cases are the costs made by resisting (costs of fighting, thwarting own offspring in their breeding attempt) higher than the territory and thereby the reproduction that is lost.

#### *Methods*

This computer model is a simplified version of reality. The more 'realism' one adds to a model, the more explanatory power it loses. For example the mortality of breeders could have been dependent on floater intrusion and the size of their own territory. But if I would have done this, I would have completely lost track of the influence of breeder mortality itself. The dynamic processes are so intertwined that the exact influence of a certain parameter is lost in its dependence on number of territories available, competition with other floaters and the at that time prevailing squeezing frequency. The question remains whether these add-ons will influence the outcome of the program.

One possible future add-on which I would like to do is change the options for territory growth. I expect that the conclusion of the influence of larger territories will show not to be robust if territories can also 'nibble' parts from neighbouring occupied territories.

The problem with the current mechanism is that the processes behind the parameter  $b$  differed per value. With  $b = 0.05$ , the reward for fighting is actually quite small. The benefits for the squeezer lie in the fact that it owns a territory and can now increase it by slowly expanding its border into neighbouring territories. The choice of a fledgling would be the choice between immediately getting a small and useless territory but with potential, or wait for a productive territory to become available with the risk of dying without offspring.

'Slowly expanding its border into neighbouring territories' has proven hard to program without losing simplicity. The only mechanism for these small territories to grow is to 'outlast' its neighbours and then incorporate those now vacant territories. That is why I also investigated the second scenario with  $b = 0.33$ . Here it is assumed that the 'slow expansion' has already occurred that first season until the average size of the neighbouring territories is reached. But both are not ideal.

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