Behiavoirally structured populations persist longer under harsh environmental conditions

Abstract
The factors and mechanisms that enhance population persistence in a fragmented habitat and/or under harsh environmental conditions are of significant current interest. We consider the dynamics of a population in an isolated habitat surrounded by an unfavourable environment subject to different behavioural responses between the individuals. We assume that there are two responses available: one of them is aggression in its extreme form, the other is its contrary when an individual takes flight in order to avoid any contact with its conspecific. We show that a behaviourally structured population consisting of individuals with fixed behavioural responses is intrinsically less prone to extinction under harsh environmental condition than a population where the individuals can ‘choose’ between the two given behaviours. We also show that, contrary to an intuitively expected negative impact of aggression on population persistence, the optimal conditions for population persistence are reached when a considerable proportion of the individuals exhibit aggressive behaviour.

Keywords
Aggression, behaviour, habitat fragmentation, harsh environmental conditions, population persistence.

INTRODUCTION
Population persistence under adverse environmental conditions arising from human activity or from natural hazards has become an issue of great importance in contemporary ecology (Lawton & May 1995). Such adverse or harsh conditions often result in habitat fragmentation (Saunders et al. 1991; Tilman et al. 1994; Klausmeier 1998, 2001) and/or lack of life-supporting resources. The impact of these detrimental processes apparently depends on their duration and the possibility of environmental rehabilitation. Whilst some processes may be virtually irreversible, e.g. forest fragmentation, others operate on a much smaller time-scale. For instance, lack of rainfall can cause the fragmentation of moisture-containing soil capable of supporting soil fauna; however, this period is usually well within one season and the normal soil properties are restored soon after the drought is over. Meanwhile, such short periods of harsh environmental conditions can cause a crash of ecological communities (White 1963; Milne et al. 1965; Blackshaw & Perry 1994). It is therefore an issue of considerable importance to identify factors that can moderate the negative impact of harsh conditions on a given population and prevent population extinction.

One of the factors which potentially adds plasticity to a population is the existence of different individual behaviours. Classical approaches to population dynamics are based on the assumption that all the individuals of a given population are identical and react in the same manner. Later developments have included consideration of population age or stage structure (Lefkovitch 1965; Cushing 1998) but still use the same assumption about the uniform (or ‘average’) behavioural response of individuals in the same group. However, this projection of uniform behavioural response onto individuals within a population is at variance with empirical evidence. It is readily accepted that distinctive behavioural repertoires are exhibited by individual mammals and that these can differentiate entities. Furthermore, there is now considerable evidence that individual behaviours can be considered as fixed (Budaev 1997; Reale et al. 2000; Iguchi et al. 2001) although they may be context-specific (Coleman & Wilson 1998). Work on octopuses (Mather & Anderson 1993) has revealed patterns of fixed distinctive behaviour exhibited in response to physical stimuli. These
have been described as 'passive, aggressive and paranoid' and were used to attribute 'personalities' to individuals. Studies on cheetahs (Wielebnowski 1999) also divided behaviour patterns into three components – 'tense-fearful, excitable-vocal, and aggressive'. Similar observations have been made on the larvae of the craneflies Tipula oleracea and T. paludosa, which, when stimulated with a mounted needle, either curled up, attacked or recoiled (R.P. Blackshaw, unpublished data). Studies such as these strongly suggest that behaviour and 'decisions' operating at the individual level may impact on ecological and evolutionary dynamics of populations (Maynard Smith & Price 1973; Houston et al. 1988; Clark 1993; Fryxell & Lundberg 1997). Interestingly, practically all the studies point out to the existence of, among other types of response, aggressive behaviour although the forms of aggression can be different; particularly, in invertebrate ecology it is often linked to cannibalism (Carter 1973).

The concept of adaptive behaviours has become an important component of work on evolutionary biology (Yoshimura & Jansen 1996; Wilson 1998; Iguchi et al. 2001) and, increasingly, has led to genetic explanations of behaviour (Schwabl & Pillay 2001; Rankin 2002; Tandon & McGuffin 2002). The discovery of genetic mechanisms and emerging evidence for possible behavioural inheritance (Sinn et al. 2001) has focused attention on multigenerational population dynamics whereby consideration of individual behaviours has been mainly limited to enhanced reproductive success (Wilson 1998). In contrast to this, we specifically address the role of individual behaviours at the population level within a generation, being more concerned with survival than comparative fitness.

In this paper, we consider the population persistence under short-term harsh conditions taking into account different behavioural responses between the individuals which have been described as 'aggressive' and 'paranoid' (Mather & Anderson 1993). We show that, although the role of aggressive individuals may initially seem negative, populations with certain fractions of aggressive individuals have a higher probability of persistence through a period of harsh conditions.

THE MODEL

In order to provide an insight into possible ecological consequences of behavioural differences within a given population, we consider the following idealized situation. A population dwells in a spatially homogeneous environment at an approximately constant level of population density under favourable climatic conditions. At a certain moment, the climatic conditions become unfavourable, or even hazardous. This causes environment fragmentation so that the conditions are still favourable inside the fragmented habitats but essentially unfavourable in the rest of the environment which results in a much higher mortality rate. We then assume, for the sake of simplicity, that the distance between the different habitats is large enough so that they are not coupled with each other via migration of the individuals and focus our attention on the population dynamics inside one particular habitat. Population recruitment inside the given habitat is therefore limited to migration to the habitat of individuals from outside seeking a shelter from the harsh conditions (see Fig. 1a).

We assume that inside the habitat there is a direct agonistic interaction between the individuals. For example, each individual, when meeting another individual, chooses between the following two behaviours: either to fight (aggressive) or to run away and to take refuge from fighting outside of the habitat [paranoid; here we use the term 'paranoid' in the sense of Mather & Anderson (1993)]. We consider the aggressive behaviour in its extreme form so that fighting takes place if at least one of the individuals makes the 'decision' to fight and, as a result of fighting, one of the involved individuals die (Carter 1973; Foster 1996; Baker et al. 1999). We assume that the paranoid and aggressive behaviour occur with the probabilities β and (1 – β) correspondingly. Some of those individuals who have taken refuge outside the habitat in order to avoid fighting can return back after a certain time-lag τ. We use τ as an integrated measure of the harshness of environmental conditions: as harsher conditions will normally lead to a decrease in the habitat size, so that a refugee spends more time finding its way back.

A usual modelling approach to the system described above is based on the ideas of game theory when each individual is traced through all the events it encounters and the 'decisions' it makes (Maynard Smith & Price 1973; Houston et al. 1988; Clark 1993). However, as we are primarily concerned with the persistence of the population (c. Fryxell & Lundberg 1997), the individual-based approach seems to be excessive. To describe the population dynamics inside the favourable habitat, we apply the following single-species model:

\[
\frac{dU(t)}{dt} = kU_{ext}(t) - mU - \delta U^2 + \gamma \beta^2 U^2 (t - \tau)
\]

(assuming that the period of harsh environmental conditions falls within the generation so that the total population size does not increase). Here \(U\) is the population density inside the given habitat at time \(t\), \(U_{ext}\) is the population density outside the habitat, \(m\) is the per capita mortality rate due to 'natural' reasons (not taking into account agonistic interactions) and \(k\), \(\delta\) and \(\gamma\) are coefficients (\(\gamma\) is the fraction of the refugees coming back to the habitat after the...
time-lag \( \tau \)). Correspondingly, the first term in the right-hand side describes the flux into the habitat from the outside population, the second term accounts for the natural mortality, the third term describes the population decrease because of interindividual interactions, e.g. fighting or taking refuge outside the habitat (see also the next paragraph), and the fourth-term takes into account the proportion of the migrants that come back.

Note that in our model a meeting between any two individuals results in a decrease in the population size inside the habitat. As we are particularly interested in ecological consequences of aggression, we assume that not only a meeting between two individuals with aggressive behaviour leads to the death of one of them but also an interaction ‘aggressive plus paranoid’ leads to the death of the paranoid. Regarding the interparanoid interactions, we assume that paranoids strongly tend to avoid any contact with their conspecifics so that a meeting of two paranoids leads to a retreat of one of them taking refuge outside the habitat.

It must be mentioned that there can be somewhat different types of interaction between the inside and outside populations. For very primitive organisms, they can be expected to ‘forget’ about the favourable habitat immediately after leaving it and in that sense become indistinguishable from the individuals of the outside population. Organisms of higher biological organization, however, are more likely to remember about the favourable habitat where they have just been. They would probably try to return to it in order to avoid the harsh environmental conditions outside. That may result in a more effective searching strategy. In this paper, as we are concerned with ecological consequences of different behaviours which, by definition, implies a sufficiently high biological organization, the latter approach seems to be more appropriate for our purposes. Thus, it looks biologically reasonable to describe the fluxes from the true outside population and the migrants from the habitat by different terms, \( c \), the first and the last terms in the right-hand side of eqn 1.

We neglect the fragmentation time and assume that the dynamics of the population is described by eqn 1 for \( t > 0 \) and \( U = U_0 \) for \( t \leq 0 \). Outside the habitat, we assume that the high mortality because of the impact of the harsh conditions predominates over other factors. Thus it is described by the following equation:

\[
\frac{dU_{\text{ext}}(t)}{dt} = -\alpha U_{\text{ext}} \quad \text{so that} \quad U_{\text{ext}}(t) = U_0 e^{-\alpha t} \tag{2}
\]

where \( U_0 \) is the initial density and \( \alpha \) is the \textit{per capita} mortality rate outside the habitat, \( \alpha \gg m \).

As the individuals leaving the habitat are immediately exposed to the harsh environmental conditions, the period they spend outside their number also decreases with time.
exponentially with the same rate $\tau$. Thus, $\gamma$ and the time-lag $\tau$ are related as follows:

$$\gamma = \gamma_0 e^{-\alpha \tau}$$  \hspace{1cm} (3)

where $\gamma_0$ is a coefficient. Note that we can re-scale the population density to $U_0$ and time to $1/\alpha$. Thus, below, we let $U_0 = 1$ and $\alpha = 1$ without any loss of generality. The corresponding choice of the dimensionless variables and parameters is rather obvious and we do not introduce them explicitly here for the sake of brevity.

As we have assumed that there are no off-spring during the period of harsh conditions, the only source of ‘new’ individuals inside the favourable habitat is associated with the population outside (i.e. the first term in eqn 1), the density of which decreases exponentially. Thus, over a sufficiently large period of time the density of the population inside the habitat will also decay to small values. This is in agreement with reality. When the population density reaches very small values, its extinction becomes probable because of stochastic environmental perturbations (Goel & Richter-Dyn 1974; Lande 1993). However, as we are concerned with short-term harsh conditions, the longer it takes the population density to fall below the ‘extinction threshold’, the higher are its chances of local persistence.

It is, therefore, the rate of population decay which is of particular interest in assessing the impact of different factors on population persistence under these circumstances. Fig. 1b gives the population density vs. time calculated numerically from eqn 1 with 2 and 3 for $\beta = 1$ and for different values of $\tau$: curves from top to bottom correspond to $\tau = 0$, 1, 2 and 5, respectively. For the values of $\tau > 5$, the corresponding curves (not shown here) are practically indistinguishable from each other. As expected, the larger $\tau$ (i.e. the harsher the conditions), the shorter is the time taken by the population to fall below the extinction threshold. For smaller values of $\beta$ the curves corresponding to different $\tau$ values lie closer to each other and for $\beta = 0$ all the curves coincide (approximately with the lowest one in Fig. 1b). Thus, models (1–3) leads to the intuitively expected result that the rate of population decay increases with an increase in the probability of the aggressive behaviour.

### THE IMPACT OF BEHAVIOURAL STRUCTURE

The model based on eqn 1 does not yet distinguish between different individuals because each of them can choose between the same available behaviours (e.g. Maynard Smith & Price 1973; Houston et al. 1988; Clark 1993), i.e. either fight or run away. Now, if we assume, based on the recent findings (Budaev 1997; Coleman & Wilson 1998; Reale et al. 2000; Iguchi et al. 2001) that different behavioural responses are fixed to different individuals, and thus the existence of subpopulations, an immediate consequence is that the factors controlling the population dynamics are not distributed equally among the subpopulations. Specifically, the fraction of the population taking refuge and then coming back is associated with paranoids. Instead of eqn 1 we now have a system of two equations:

$$\frac{dA(t)}{dt} = \beta_A k U_0 e^{-\beta \tau} - m A - \delta A^2$$  \hspace{1cm} (4)

$$\frac{dP(t)}{dt} = \beta_P k U_0 e^{-\beta \tau} - m P - \delta P^2 - \delta PA + \delta \gamma_0 e^{-\alpha \tau} P^2 (t - \tau)$$  \hspace{1cm} (5)

where $A$ and $P$ are the densities of the aggressive and paranoid subpopulations, respectively. $\beta_A$ and $\beta_P$ give the fraction of aggressive and paranoid subpopulations in the population outside the habitat; so that $\beta_A + \beta_P = 1$. As we neglect the interindividual interactions outside the habitat, i.e. eqn 2, both types of subpopulations in the population outside decrease in the same manner and thus $\beta_A$ and $\beta_P$ can be regarded as constant coefficients. Here $A + P = V$ is the density of the structured population; in general, $V \neq U$ where $U$ is the density of the unstructured population given by eqn 1. (Note that in the two limiting cases corresponding to the absence of behavioural structure, i.e. $\beta_A = 1$ and $\beta_A = 0$, only one of eqns 4 and 5 remains and it then coincides with eqn 1.) At the beginning of the process, the ratio between the two sub-populations inside the habitat is assumed to be the same as outside, i.e. $A(0) = \beta_A$ and $P(0) = \beta_P$. In the course of time, however, the aggressive and paranoid fractions can change because of the interactions between the individuals.

We emphasize that there exists an apparent asymmetry in the inter-subpopulation interaction: a meeting between a paranoid and an aggressive results in the decrease in the number of paranoids but not in the number of aggressives. The decrease in the density of paranoids because of their killing by aggressives is taken into account by the term $(-\delta PA)$ in eqn 5. However, as the aggressives are not affected by paranoids, a similar term is absent in eqn 4. An immediate consequence is that, if we sum up both eqns 4 and 5 and compare the result with eqn 1 [where $\beta U(t - \tau)$ can be interpreted as $P(t - \tau)$], the press of the agonistic inter-individual interactions will appear stronger in the unstructured population than in the structured. Thus, one can expect that the rate of decay of the structured population will be lower than that for the unstructured population.

Figure 1c shows a typical time-dependence in the density of both subpopulations, $A$ and $P$, and the total densities in the structured and unstructured cases, i.e. $V$ and $U$ respectively, assuming that the fraction of aggressive
individuals in the population outside is 20% of total population size, i.e. $\beta_A = 0.2$, $\beta_P = 0.8$. As above, we let $\alpha = 1$ and $U_0 = 1$ in eqn 4 and 5 which means that the population densities are rescaled to $U_0$ and time is rescaled to $1/\alpha$. In order to make possible the comparison between structured and unstructured models, we let $\beta = \beta_P$ in eqn 1. Remarkably, the density of the behaviourally structured population (shown by thick solid line) decreases more slowly than that of the unstructured population (dashed-and-dotted line). Thus it takes a longer time for the density of the structured population to reach the very small values where it becomes prone to extinction. For the particular case shown in Fig. 1c, if we assume that the ‘extinction threshold’ $\varepsilon$ is 1% of the initial population density (i.e. the dotted line), this time $T_e$, which we will call the ‘estimated time of population persistence’, appears to be about 40 and 35 for the structured and unstructured populations, respectively. Thus, the behaviourally structured population has an intrinsically higher probability of persistence through harsh environmental conditions. In the course of population dynamics inside the habitat, the aggressive fraction $A(t)/(A(t) + P(t))$ increases (curve 3 in Fig. 1c) approaching a constant value $\omega_A$ in the large-time limit.

A point of interest is to understand how $T_e$ and the dynamically emerging value of aggressive fraction $\omega_A$ depends on the initial ratio between the fractions. Fig. 2a–d shows $T_e$ calculated for different values of aggressive fraction $\beta_A$ and for different values of the time-lag $\tau$. For any given value of $\beta_A$ the expected time of population persistence is larger for the structured population than for the unstructured population. Note that, while the positive impact of paranoid behaviour on the population persistence is intuitively clear (as the paranoids try to avoid fighting and tend to return to the habitat after taking refuge outside), the

![Figure 2](https://example.com/figure2.png)

**Figure 2** (a)–(d) Estimated time $T_e$ of the population persistence (solid curve; dimensionless) calculated for the population consisting of aggressive and paranoid individuals for different values of the aggressive fraction $\beta_A$ and for different value of the time-lag: (a) for $\tau = 0$, (b) for $\tau = 1$, (c) for $\tau = 2$, (d) for $\tau = 5$. Dashed-and-dotted curve shows $T_e$ for the corresponding unstructured population, i.e. eqn 1 with $\beta = \beta_P$. Other parameters are: $\alpha = 1$, $\mu = 0.05$, $\delta = 1$, $\gamma_0 = 0.25$, $k = 0.1$, $U_0 = 1$, $\varepsilon = 0.01$, (e)–(f) the aggressive fraction inside the habitat emerging in the course of population dynamics vs. the aggressive fraction outside the habitat, curves from bottom to top correspond to $\tau = 0, 1, 2$ and 5 respectively, (e) for $\gamma_0 = 0.25$, (f) for $\gamma_0 = 0.5$, other parameters are the same as above.
role of the aggressive behaviour may seem, at first sight, negative. Surprisingly, however, a population with a certain fraction of aggressive individuals appears to have higher chances to persist than the population consisting of paranoid individuals only: the hump in the dependence \( T_e \) on \( b_A \) gives the value of \( T_e \) which is larger than the persistence time of the all-paranoid population (given by the left-hand end of the dashed-and-dotted curve). Moreover, an increase in \( \tau \) corresponding to harsher environmental conditions even leads to an increase in the initial fraction of aggressives optimal for the population persistence: it is about 8% for \( \tau = 0 \) (Fig. 2a) and nearly 20% for \( \tau = 5 \) (Fig. 2d). The dynamically emerging aggressive fraction \( \omega_A \) appears to be even larger (see Fig. 2c); except for the small values \( \beta_A < 0.1 \), more than one half of the population inside the habitat consists of individuals with aggressive behaviour. The results of computer simulations show that this conclusion is remarkably robust to parameter variation. In particular, Fig. 2f shows \( \omega_A \) vs. \( \beta_A \) for the value of \( \gamma_0 \) two times larger than in Fig. 2e. Variation of other parameters has even smaller impact.

Note that in the large-\( \tau \) limit, when the number of migrants coming back to the habitat becomes negligible and the last term in eqn 5 can be omitted, and in the absence of behavioural structure, i.e. for \( \beta_A = 1 \) or \( \beta_P = 1 \), both eqn 4 and 5 coincide with each other. That accounts for the fact that the left-hand and right-hand ends of the curves in Fig. 2d are at approximately the same level.

While Fig. 2a–d gives the comparison between the dynamics of structured and unstructured populations, Fig. 3 gives a full account of the dependence of \( T_e \) for the structured population on \( \beta_A \) and \( \tau \). Thus, \( T_e \) exhibits apparent scaling behaviour for \( \tau > 5 \). This is an intuitively clear result: for large values of the time-delay, the number of the paranoids who survived and returned to the habitat becomes negligible so that neither \( \gamma_0 \) nor \( \tau \) affects the rate of the population decay any more.

**CONCLUDING REMARKS**

The model we have presented is rooted in current understanding of invertebrate ecology (White 1963; Milne et al. 1965; Carter 1973; Blackshaw & Perry 1994; Foster 1996; Baker et al. 1999) but is expected to be applicable in a much more general context. Recent studies revealed many indications of a behavioural structure of populations of various species through different behavioural responses fixed to different individuals (Mather & Anderson 1993; Budaev 1997; Coleman & Wilson 1998; Wielebnowski 1999; Reale et al. 2000; Iguchi et al. 2001). The ecological implications of these findings have remained obscure, though. Our analysis provides an insight into the problem and leads to the following two essentially new conclusions. Firstly, we have shown that the existence of subpopulations of individual behaviours can be of vital importance to the local spatial persistence of a population and to environmental adaptation. We draw no conclusions about whether these behaviours arise genetically or environmentally but do note the increasing evidence for a genetic influence (Schwaibold & Pillay 2001; Rankin 2002; Tandon & McGuffin 2002). Secondly, the conditions optimal for the population persistence under harsh environmental conditions are shown to arise when a significant number of the individuals exhibit aggressive behaviour. We believe that this is a strong indication that, in adverse circumstances leading to an increased competition for space and/or resource, aggression may become an essential component of species persistence operating more on the population level rather than between individuals.

It should be mentioned that, if considered in a wider ecological perspective, a population of individuals with fixed different behaviours may be regarded as hierarchically structured. For the model considered in this paper, the hierarchy would consist of two ranks: high (aggressive) and low (paranoid), where the low ranks have no chance of...
staying when they encounter high ranks. This interpretation, however, should be used with care because it could be misleading in certain ecological circumstances; although high ranks affect low ranks they also affect each other through encounter-driven mortality. Low ranks are affected by high ranks but their effect on themselves can vary significantly depending on environmental conditions. Under very harsh conditions practically none of the paranoids leaving the habitat would ever come back, c. eqn 5 for large values of τ. Under these conditions, the paranoids affect each other as much as the aggressives, i.e. every meeting between them results, albeit indirectly, in the death of one of them. In this case, the population can be considered as hierarchically structured.

The situation, however, becomes essentially different under less harsh conditions. In this case, a large part of the migrants returns to the habitat, c. eqn 5 for τ = 0. Thus it means that the paranoids affect each other much less than the aggressives affect each other. An immediate consequence is that the all-paranoid population appears intrinsically more persistent than the all-aggressive population (c. Fig. 2a–c where the left-hand end of the curves lays higher than the right-hand end). In a situation like that, the simple concept of two-rank hierarchy would be ambiguous, if appropriate at all. It should be mentioned that the situation when the origin of interspecies or intergroup interaction, within the same community can change depending on the impact of various environmental factors, is in full agreement with the contemporary ecological knowledge (Thompson 1988; Hochberg et al. 2000).

In this paper, our intention was more to provide an insight into possible ecological consequences of a population behavioural structure rather than to consider this fertile issue in all detail. Thus, our study leaves a number of open questions. First of all, a point of significant interest is to check whether our conclusion that a behavioural structure with distinct aggressive component can enhance population persistence stays true on a larger time scale when the change of generations and population multiplication are taken into account. To address this issue properly, one would have to use more specific information about possible mechanisms of the behavioural traits transfer between generations. Another challenging problem could be to investigate the impact on the population dynamics of other types of behaviour, e.g. neutral. Finally, a question of interest is how the existence of behavioural structure can modify interspecies relations, e.g. prey–predator interactions. These and other issues may outline future research in this field.

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