A model of sexual selection and female use of refuge in a coercive mating system

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In many non-monogamous systems, males invest less in progeny than do females. This leaves males with higher potential rates of reproduction, and a likelihood of sexual conflict, including, in some systems, coercive matings. If coercive matings are costly, the best female strategy may be to avoid male interaction. We present a model that demonstrates female movement in response to male harassment as a mechanism to lower the costs associated with male coercion, and the effect that female movement has on selection in males for male harassment. We found that, when females can move from a habitat patch to a refuge to which males do not have access, there may be a selection for either high, or low harassment male phenotype, or both, depending on the relationship between the harassment level of male types in the population and a threshold level of male harassment. This threshold harassment level depends on the relative number of males and females in the population, and the relative resource values of the habitat; the threshold increases as the sex ratio favours females, and decreases with the value of the refugee patch or total population. Our model predicts that selection will favour the harassment level that lies closest to this threshold level of harassment, and differing harassment levels will coexist within the population only if they lie on the opposite sides of the threshold harassment. Our model is consistent with empirical results suggesting that an intermediate harassment level provides maximum reproductive fitness to males when females are mobile.

Keywords: coercive mating system; female refuge; harassment; selection; sexual conflict

1. INTRODUCTION

Sexual conflict arises when male and female evolutionary interests diverge [1]. In the absence of parental care, males typically invest less in progeny than do females [2], and consequently, males have a higher potential rate of reproduction. In species where sperm production is the only contribution provided by males, it is unlikely that female fitness increases in direct proportion to increased matings (but see [3,4], for possible female advantages to multiple copulations). Additionally, mating behaviour of males may be detrimental to female fitness. Females can suffer direct costs owing to unnecessary multiple matings and harassment (e.g. reduced foraging, predation risk, disease transmission and physical damage) [5–8]. Sexual coercion is increasingly acknowledged as another form of sexual selection, distinct from intrasexual competition (competition between males) and intersexual mate choice (males display for female selection) [9].

If each mating event is costly, there may be selection for female strategies that lessen these costs. For example, the best female strategy may be to obtain a low number of copulations with high-quality males to guarantee fertilization. Conversely, there may be selection for males to obtain copulations aggressively when females do not choose them. The evolution of coercive mating and that of female resistance are potential outcomes of these conflicting strategies to maximize reproductive fitness [9].

Coevolutionary arms-races can develop between female defences against coercive mating and male counter-adaptions [10]. Females present a wide range of defences, many of which are morphological. Well-known examples for such defences are female water striders (Gerridae gracilicornis), which have their gonadal area shielded by the ovipositor and vulva so that males cannot obtain matings unless the female is persuaded to allow male access [11], and female diving beetles, whose dense punctures in the dorsal shell or setose furrows impede male grasping during the mating process [12].

Morphological defences are not universal in species with coercive mating systems. Some mosquitofish, Gambusia spp., and water striders, Aquarius spp., have well-studied coercive mating systems, and no morphology to provide female defence, despite the fact that coercive mating appears to be costly in these systems. In Aquarius remigis female motility is reduced during copulation (where she carries the male on her back), putting her at an increased predation risk [5]. Male Gambusia holbrooki attempt to copulate about once a minute [13]; yet, sperm storage leaves females with a need to mate infrequently with a preferred mate [14]. The excessive male harassment greatly reduces the female foraging efficiency [15] and attracts attention from predators [16]. The risk that males impose upon themselves with female harassment is lessened by the benefit of a successful mating; however, female benefit is outweighed by the costs of male harassment [15].

For females lacking morphological defences, alternative behavioural mechanisms to avoid costly matings include moving away from harassing males. Eldakar et al. [17] found that the relationship between harassment and reproductive success in A. remigis depends on mobility. When confined to one pool, male harassment level
and mating success were positively correlated, but when dispersal within a multi-pool environment was allowed, males of an intermediate harassment level obtained the most matings [18]. Females appear to respond to local harassment by moving away, and that patterns of female movement can favour males of a low-harassment level. In this paper, we present a general model to investigate how female dispersal, in response to male harassment, influences both observed female distribution and selection on male harassment, and to predict under what conditions female movement will lead to selection for reduced or intermediate male harassment.

2. THE MODEL

The model is based on predator–prey habitat selection games [18]. In our case, females are analogous to prey, and coercive males are analogous to predators because male harassment always decreases female fitness, while male fitness increases in the presence of females. The model system consists of two patches. The strategy set for females is the choice of which of the two patches to reside in, while the strategy set for males is the possible levels of harassment. For simplicity, we assume that males can choose between a ‘high’ harassment (h) and a ‘low’ harassment strategy (h'). The proportion of males of type h and h' are given by m and m', respectively, and the total number of males is given by Nm. We assume that female patch-use decisions are ideal-free, ‘ideal’ meaning they have perfect knowledge of the quality (resource value and harassment level) in each patch and ‘free’ meaning they can freely move between patches [19]. All males in the population are confined to patch 1 and variation between patches is strictly due to the movement of females. The proportion of females in patches 1 and 2 is represented by f1 and f2, respectively, and the total number of females is given by Nf. Patch 2 can be thought of as a refuge for females, where males are excluded because of high risk [20] or an inability to access this site owing to a larger size [21,22]. Figure 1 shows the distribution of males and females in each patch and the movement between patches.

We constructed female and male fitness functions in patches 1 and 2 and find evolutionarily stable distributions of male harassment and female patch use. Fitness is defined as an individual’s lifetime reproductive success and is the product of the expected lifetime of an individual (modelled as 1/mortality rate, ut and ut, for female and male mortality rate, respectively), and the rate of reproductive success. Reproductive success for both males and females depends on the rate of net resource intake. For males, it also depends on the mating rate. We assume that females mate once and gain no further benefit from multiple matings, so that female reproductive success depends only on resource intake. However, female survival decreases as a function of mating attempt frequency. The intake component depends upon the resource value of the patch, v1 or v2, which is divided by the resident density to give the rate of individual energy intake. We assume that males and females are equally competitive for the resource, giving the same intake component for males and females in patch 1. The resource intake rates for residents of patch 1 and 2, respectively, are I1 given in equation (2.1a), and I2 given in equation (2.1b):

\[ I_1 = \frac{v_1}{f_1 N_f + m N_m} \]  

(2.1a)

and

\[ I_2 = \frac{v_2}{f_2 N_f} \]  

(2.1b)

The rate of mating attempts is dependent upon the number of encounters between males and females, which depends in part on male harassment level, h or h'. The total rate of mating attempts per female is given by equation (2.2):

\[ A_1 = (m h_i + m_i h) N_m. \]  

(2.2)

We assume that females store sperm and gain no other benefit from multiple matings. For example, species of Gambusia affinis can store viable sperm for months after insemination [14] and A. remigis can store sperm for approximately three weeks [23]. We assume that most females, even those primarily located in patch 2, gain at least one successful mating in their lifetime. If the probability of gaining one successful mating is equal for females in patch 1 and 2 (for example, if they mate before moving to these patches), female mating success will have no effect on the model. The fitness functions for females in patches 1 and 2 are given by equations (2.3a,b):

\[ W_f = \frac{I_1}{A_1 \mu_t} \]  

(2.3a)

and

\[ W_f = \frac{I_2}{\mu_t} \]  

(2.3b)

The mating component of male fitness is directly proportional to the rate of mating attempts. We assume that males produce an excess of sperm; therefore, male reproductive success is entirely dependent upon access to females. The total number of mating attempts is given by male harassment level multiplied by the number of females present. We also assume that males have no depletion of sperm throughout the breeding season. Under these conditions, there is no direct cost of mating to males, instead they receive some benefit, b,
Because if there is a cost, c, associated with harassment level. This cost is the instantaneous rate of offspring lost, which is proportional to the individual’s level of harassment relative to the harassment level of the population. Relatively, more aggressive individuals are more likely to receive this cost; if the entire population has the same harassment level, (i.e. \( h_i = h_h \)), then the cost is simply c, whereas if they differ, the cost for \( h_i \) is \( h_i c/(h_h m_i + h_m) N_m \). This cost is owing to energy expenditure, conspecific behavioural response to harassment, mortality risk or other factors that reduce the fitness of harassing males. This cost is imposed whether males are successful at mating or not. We assume that males compete with each other for access to females, this is described by dividing the benefit from mating by the total number of mating attempts per female, G gives the male net benefit of mating:

\[
G_i = \frac{h_i(f_i N_i(b - c))}{A_i}.
\]

(2.4)

G_i is similarly defined.

Male fitness functions are given in equations (2.5a,b):

\[
W_m = \frac{G_i I_i}{\mu_m}.
\]

(2.5a)

and

\[
W_m = \frac{G_i I_i}{\mu_m}.
\]

(2.5b)

Because \( f_2 = 1 - f_1 \) and \( m_i = 1 - m_i \) we only consider the differential equations for \( f_1 \) and \( m_i \). Using replicator dynamics (see appendices, equations (A 1) and (A 2) for derivation), the following system of ordinary differential equations is obtained:

\[
\dot{f}_1 = f_1(1 - f_1) \left( \frac{I_1}{A_1 \mu_l} - \frac{I_2}{\mu_1} \right),
\]

(2.6a)

and

\[
m_i = m_i(1 - m_i) \left( \frac{G_i I_i}{\mu_m} - \frac{G_j I_j}{\mu_m} \right).
\]

(2.6b)

Equilibrium points \((f_1^*, m_i^*)\), occur either with monomorphic populations \((m_i = 0 \text{ or } m_i = 1, \text{ and } f_1 = 0)\), or when the relative benefits of the two patches \((W_{f_1} = W_{f_2})\) or strategies \((W_m = W_m)\) are equal. We do not consider \( f_1 = 1 \) as an equilibrium \((W_{f_1} \text{ is undefined, and } \dot{f}_1 < 0 \text{ when } f_1 \text{ is close to 1})\). There are five possible equilibrium points: two monomorphic solutions \((0,0)\) and \((0,1)\), two with females polymorphic and males monomorphic \((f_1^*, 0)\) and \((f_1^*, 1)\), and an interior equilibrium where both males and females use mixed strategies \((f_1^*, m_i^*)\). Existence and stability depend on female behaviour, male harassment and the values of patches 1 and 2. For simplicity, we will consider \( h_i \) to always be greater than \( h_h \) (an equal but opposite outcome will result by setting \( h_h \) greater than \( h_i \)).

(a) Selection on male harassment when all females are in patch 1

Consider first the reduced model where all females are restricted to patch 1. We only consider the dynamics of males. We find that there are two equilibrium points for male harassment, at \( m_i = 0 \) and \( m_i = 1 \). Per equation (2.6b), the rate of change in \( m_i \) is negatively proportional to \((b f_i N_i - c)\). Thus, if

\[
b f_i N_i > c,
\]

(3.1)

then \( m_i = 0 \) is stable and there is selection for higher harassment, \( h_i \). If inequality (equation (3.1)) fails, then \( m_i = 1 \) is stable and there is selection is for lower harassment, \( h_i \). Hereafter, we assume that inequality (equation (3.1)) will always hold true because we are considering a large female population and we expect that there will always be a substantial benefit from mating.

(b) Selection on male harassment when females occupy patches 1 and 2

As stated previously, when females are able to move between the habitat and refuge, there are up to five possible equilibrium points to the system. These points are presented in figure 2. Not all of these equilibria exist for all combinations of parameters. By considering the conditions under which the polymorphic equilibrium exists, we can define a threshold harassment level, \( h_t^* \), defined as equation (4.1) (see appendices, equations (B 1) and (B 2)).

\[
h_t^* = \frac{(b N_i - c) v_1}{N_m(c + b N_m) v_2}.
\]

(4.1)

The stability of each equilibrium point will be analysed in terms of \( h_t^* \). The interior equilibrium (I), if it exists, is located at \((c/b N_i) (h_t^* - h_h)/(h_i - h_h)\).

Equilibrium I is the single point at which high- and low-harassment levels stably coexist in the population (figure 2). For equilibrium I to exist at biologically reasonable values (i.e. \([0,1] \times [0,1]\)), \( h_t^* \) must lie between \( h_h \) and \( h_i \). If it exists, it is always stable (see appendices, equations (C 2)–(C 5) for stability analysis). Thus, if \( h_t^* \) is intermediate between the two harassment levels displayed by males, then males of different levels of harassment can coexist in the population.

(c) Homogenous systems

Equilibria II \((f_1^*, 0)\), and III \((f_1^*, 1)\), represent populations in which all males are of one type and females are distributed in both patches 1 and 2. These equilibrium points exist when either the value of patch 1 and the total number of females is sufficiently large:

\[
v_1 N_i > v_2 h_i N_m^2.
\]

(5.1)

where \( h_i \) represents the harassment level of the prevailing male type (i.e. \( h_i \) or \( h_h \)). If inequality (equation (5.1)) holds, either equilibrium II or III will exist, and stability is dependent upon the threshold harassment level, \( h_t^* \), relative to the harassment levels of the two male phenotypes.

Consider equilibrium II \((f_1^*, 0)\). When equilibrium II exists, inequality (equation (5.1)) holds and males of harassment \( h_i \) prevail. The eigenvalues of the Jacobian of the system at equilibrium II (see appendix, equations (C 7a,b))

\[
\lambda_1 = \frac{(v_1 + h_i N_m v_2)(-N v_1 + h_i N_m^2 v_2)}{h_i N_i(N_i + N_m) v_1 m}
\]

and

\[
\lambda_2 = \frac{(h_i - h_h)(v_1 - h_i)(c + b N_m) v_2}{h_i b(N_i + N_m) m}
\]
This system always has exactly one stable equilibrium. If equilibrium II exists, all males have harassment level \( h_i \), is stable if \( h_i > h_* \), where \( h_* \) is negative. \( \lambda_2 \) is negative when

\[
hr < h_* < h'.
\]

We see that stability depends only on the relationship between \( h_0, h_* \) and \( h' \). In general, equilibrium II, where all males have harassment level \( h_0 \), is stable if \( h_0 \) is closer to \( h' \) than \( h_* \) is. A similar but reciprocal result occurs for the stability of equilibrium III \( (f_1^*, 1) \), where all males have harassment level \( h_* \). Because we assume \( h_0 > h_* \), equilibrium III becomes stable when both \( h_0 \) and \( h_* \) are greater than \( h' \), leaving \( h_* \) closer to \( h' \) than is \( h_0 \) (table 1).

**Varying stability as threshold harassment changes**

In table 1, we summarize the stability of the equilibrium points to the system under different parameter values. This system always has exactly one stable equilibrium and any of the five equilibria except \((0,0)\) can be the attractor. Equilibrium points \( IV (0,1), \) and \( V (0,0), \) always exist, but their stability varies with the value of the patches, the costs and benefits of patch use for females, and harassment level. The existence of equilibria II \( (f_1^*=0), \) and III \( (f_1^*, 1), \) depends on inequality (equation (5.1)) for \( h_0 = h_* \) and \( h_0 = h_0 \), respectively. Equilibrium I only exists when \( h_* \) is intermediate between the harassment levels existing in the population. However, when it exists, it is the only stable equilibrium, and coexistence of males with high- and low-harassment levels is stable.

Table 1 shows that as long as females are distributed in both patches at equilibrium, selection can act to favour either high or low harassment. If both \( h_0 \) and \( h_* \) are less than \( h_0 \), and inequality (equation (5.1)) holds for both levels of harassment, then equilibrium II is stable. All males exhibit high harassment level, \( h_* \); If \( h_0 > h_* \) but \( h_0 \) and \( h_* \) are both greater than \( h_0 \), equilibrium II is unstable, while equilibrium III is stable and all males exhibit low harassment, \( h_* \).

Finally, at equilibria IV and V, females do not use habitat patch 1 at equilibrium. If inequality (equation (5.1)) fails for both \( h_0 = h_* \) and \( h_0 = h_0 \), equilibrium II and III cease to exist and equilibrium IV will gain stability.

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**Table 1.** Varying existence and stability conditions of the five possible equilibrium points as the relationship between harassment levels in the population and threshold aggression varies. (It is assumed that \( h_0 > h_* \) and \( bN_1 > c \).)

<table>
<thead>
<tr>
<th>equilibrium point ((f_1^<em>, m_1^</em>))</th>
<th>existence</th>
<th>stability</th>
</tr>
</thead>
<tbody>
<tr>
<td>I ( (c, h_1 - h^*)/bN_1 - h_1) )</td>
<td>( h_1 &lt; h^* &lt; h_* )</td>
<td>( h_1 &lt; h^* &lt; h_* )</td>
</tr>
<tr>
<td>II ( (c, v_1N_1 + v_2h_1N_m^2)/v_2h_1N_mN_1 + v_1h_1, 0) )</td>
<td>( v_1N_1 &gt; v_2h_1N_m^2 )</td>
<td>( h_1 &lt; h_1 &lt; h_* )</td>
</tr>
<tr>
<td>III ( (c, v_1N_1 - v_2h_1N_m^2)/v_2h_1N_mN_1 + v_1h_1, 1) )</td>
<td>( v_1N_1 &gt; v_2h_1N_m^2 )</td>
<td>( h_1 &lt; h_1 &lt; h_* )</td>
</tr>
<tr>
<td>IV ( (0,1) )</td>
<td>always</td>
<td>( v_1N_1 &lt; v_2h_1N_m^2 )</td>
</tr>
<tr>
<td>V ( (0,0) )</td>
<td>always</td>
<td>never</td>
</tr>
</tbody>
</table>
(table 1). This means that all males are of harassment \( h_L \) (by definition, low harassment) and females are all in patch 2. At this point, males, which are confined to patch 1, have no reproductive fitness. Although these equilibrium points are biologically unrealistic, they conform to our previous results; i.e. selection is in favour of low harassment, \( h_L \), because it is closer to \( h^* \) than \( h_H \).

3. DISCUSSION

This paper analyses a two-patch system where males are confined to one patch but females have free movement between them. In our model, females trade off the benefits of living in highly productive environments with the cost of receiving harassment from males. The presence of high-harassing males results in more females using lower quality habitats that are unavailable to males, thus reducing the fitness of all males regardless of their harassment level. This is a form of environmental feedback where a trait (harassment level) affects the quality of the environment and individuals are likely to live in low-quality (high-harassment) environments and remain in high-quality (intermediate harassment) environments [24]. Males displaying greater harassment gain a larger share of matings available, but they also pay a higher direct cost from this act. Our model demonstrates that female movement in response to male harassment can be a mechanism to lower costs associated with male coercion and that it can influence selection on male harassment.

By constructing a female population with access to a refuge patch and comparing the results with a single patch model, we can examine the influence of female movement on selection for male harassment. Consider when females are restricted to a single patch shared with males, selection favours males that display greater harassment, provided that the female population is sufficiently large and males receive a considerable benefit from mating (i.e. inequality (3.1) is satisfied). However, when females have access to a refuge from which males are absent, we found that selection leads to intermediate harassment levels. If males are restricted to two distinct levels of harassment, selection for high or low harassment varies with the relationship of the threshold harassment level, \( h^* \), to these phenotypic values. If \( h^* \) is intermediate between high and low harassment, then individuals with both high and low-harassment levels remain in the population. If both harassment levels are greater or lesser than \( h^* \), the harassment level that lies closer to \( h^* \) is favoured by selection, and thus remains in the population (i.e. male population becomes monomorphic).

Our model identifies the parameters upon which this threshold harassment level is dependent. By letting the cost of harassment approach zero, we can deduce the parameters that influence \( h^* \):

\[
\lim_{c \to 0} h^* = \frac{N_f v_1}{N_m v_2}
\]

Threshold harassment depends upon the ratios of female to male population sizes and relative patch values. \( h^* \) decreases if: (i) the sex ratio changes to favour males, (ii) the value of the refuge patch increases, or (iii) the male population size increases. Assuming that male population size is proportional to total population size (i.e. \( N_f / N_m \) does not change with total population size), then this also implies that \( h^* \) decreases with increasing population size. As use of patch 2 becomes less costly for females, a larger proportion of females use this safe patch and become unavailable to males.

Support for the role of movement influencing selection on male harassment has been found in the water strider, A. remigis. Both male and female water striders are generally less active in the presence of predators [25]. Excess matings are costly because they put females at an increased predation risk, and owing to females’ ability to store viable sperm for up to 24 days [23], few copulations are necessary to guarantee fertilization. Females use inactivity, by moving to the waters edge or completely out of the water, as a defence mechanism in the presence of males [26]. Active males will jump on any other adult, males or females; however, some males will attack other males and females more aggressively; these males have been termed ‘hyper-aggressive’ by Sih & Watters [27]. Males with higher activity have more encounters with females, and thus more mating opportunities than less active males [28]; therefore, hyper-aggressive males are also hyper-harassing males. Consistent with the predictions of our model, Sih & Watters [27] observed that the presence of ‘hyper-aggressive’ (or hyper-harassing) males decreases overall group mating activity by decreasing female activity. Similarly, Eldakar et al. [17] showed that an intermediate harassment level was optimal in a multi-group population. This is because ‘hyper-aggressive’ males cause females to be inactive, and hypo-aggressive males do not have frequent encounters with females.

The observation that aggressive males reduce the overall success of all males, both in nature and in our model, suggests that, when extended to a multi-group scale, feedback resulting from female movement may influence selection on male harassment. The effects of environmental feedback on selection for male harassment could be considered by extending our model to allow male movement in response to surrounding male harassment in a multipatch environment where there exist multiple highly productive patches for males and females to choose from (i.e. patch 1) and multiple low-quality patches where males are excluded (i.e. patch 2). Other extensions of our model regarding assortment could consider the effect of male mate preference and female response (i.e. higher quality females may spend more time in a refuge patch, leaving lower quality females more readily available for mating). It is unlikely that males will be completely excluded from a patch. However, patches may differ in their costs and benefits to males and females, even if males are not strictly prevented from using a patch. In Gambusia spp. and Atherina spp., males are smaller than females and may be at a higher predation risk than females. Differences in risk of predation should be considered in future models.

Females are able to reduce the cost of male coercion by simply moving away from local harassment. We show that incorporating female spatial distribution into a model of sexual conflict results in selection for high harassment, low harassment or stabilizing selection for an intermediate harassment level, depending on the relationship between the harassment of males in the population and the threshold harassment level, \( h^* \). Although there are male reproductive benefits to high harassment (i.e. increased female interaction), it also carries with it a cost to the fitness of the individual,
owing to the high cost of harassment, as well as the availability of mates to all males in the group [26]. Yet, low-harassment results in fewer female interactions and thus lower reproductive fitness. If threshold harassment is an intermediate to the male harassment levels that exist in the population, then both male phenotypes can coexist, but if harassment levels of male types in the population are both either greater or lesser than threshold harassment, our model predicts that selection will favour the harassment level closest to the threshold harassment. When either $h_1$ or $h_2$ is equal to 0, linear stability analysis is not possible; nonlinear analysis of the system under these conditions will be included in forthcoming works. Our model is consistent with empirical results that suggest that an intermediate harassment level is favoured when females are mobile [17]. Furthermore, the effects of female movement on overall male fitness suggest that between-patch variation in female distribution, arising from variation in harassment, may contribute to selection against high levels of harassment, depending on the patterns of male and female movement between patches.

**APPENDIX A. DERIVATION OF REPLICATOR DYNAMICS**

The temporal dynamics of the frequency of females using patch 1 and males using the ‘low’ harassment strategy are described by $f_1$ and $m_r$, respectively. Recall that $f_2 = 1 - f_1$ and $m_l = 1 - m_r$. Replicator dynamics gives the following ordinary differential equations (ODEs), which we use to find evolutionary stable distributions of male harassment and female patch use:

$$
\dot{f}_1 = f_1(W_{f1} - W_f) = f_1(1 - f_1)(W_{f1} - W_f)
$$

(A 1)

and

$$
\dot{m}_r = m_r(W_{mr} - W_m) = m_r(1 - m_r)(W_{mr} - W_m).
$$

(A 2)

Substituting fitness equations into (A 1) and (A 2) gives ODEs (2.6a,b).

**APPENDIX B. THE CONDITION FOR AN INTERIOR EQUILIBRIUM**

Here we consider the conditions where the polymorphic female and male equilibria are biologically viable (i.e. both types of females and both types of males can exist in the population at equilibria, so that $f_1^*$ and $m_r^*$ are between 0 and 1). Per assumptions on the model (i.e. inequality (equation (3.1)) holds true) interior equilibrium point, $f^k = c/bN_2$, is already between 0 and 1. Now we are interested in the condition when $0 < m_r^* < 1$, that is, when both male types can exist in the population. Substituting for $m_r^*$, we get equation (B 1)

$$
0 < \frac{(bN_r - c)v_1/N_m(c + bN_m)v_2 - h_i}{h_i - h} < 1.
$$

(B 1)

Simplifying equation (B 1), we get equation (B 2)

$$
h_r < \frac{(bN_r - c)v_1}{N_m(c + bN_m)v_2} < h_i.
$$

(B 2)

The threshold harassment level is given by the interior value and will be referred to as $h^*$.

**APPENDIX C. EXISTENCE AND STABILITY CRITERIA FOR EQUILIBRIA**

Stability of the equilibrium points is determined by linearization of the system about the fixed points. The Jacobian matrix, $J$, is the linearization of the system. A fixed point is stable under the constraints that cause negative eigenvalues:

$$
J = \begin{pmatrix}
\frac{(-f_1^2N_1 - 2f_1N_m + N_m)v_1}{(f_1N_1 + N_m)(m_rh_i + (1 - m_r)h_1)N_mu_1} & v_2 \\
\frac{v_1(h_i - h_1)N_1(c + bN_m)}{bN_mu_1(m_rh_i + (1 - m_r)h_1)(f_1N_1 + N_m)} & \frac{-f_1(1 - f_1)v_1(h_i - h_1)}{(f_1N_1 + N_m)(m_rh_i + (1 - m_r)h_1)^2} \\
\frac{m_r(1 - m_r)}{bN_mu_1(m_rh_i + (1 - m_r)h_1)(f_1N_1 + N_m)} & \frac{(m_r((h_i - h_1)m_r - 2h_1 + h_1)h_i - h_1)(b_2N_r - c)}{(m_rh_i + (1 - m_r)h_1)^2bN_mu_1(f_1N_1 + N_m)}
\end{pmatrix}
$$

(C 1)

Consider the existence and stability of the five equilibrium points and isolation of females in patch 1 with respect to $h^*$.

First consider equilibrium I, $(c/bN_1, (h_i - h^*)/(h_i - h_1))$. The Jacobian matrix analysed at equilibrium I is given by equation (C 2):

$$
J = \begin{pmatrix}
\frac{bc(N_1 + N_m)v_2}{(h_i - h^*)(h_i - h_1)} & c(bN_r - c)v_1(h_i - h_1) \\
\frac{bc(N_1 + N_m)v_2}{(h_i - h^*)(h_i - h_1)} & \frac{c(bN_r - c)v_1(h_i - h_1)}{bN_mu_1(c + bN_m)N_m(a^*)} \\
\frac{(h_i - h^*)(h_i - h_1)}{bN_mu_1(c + bN_m)} & \frac{c(bN_r - c)v_1(h_i - h_1)}{bN_mu_1(c + bN_m)N_m(a^*)} & 0
\end{pmatrix}
$$

(C 2)

The trace is given in equation (C 3):

$$
\tau = \frac{bc(N_1 + N_m)v_2}{N_1(c - bN_1)(c + bN_m)} < 0.
$$

(C 3)
The trace is always negative when equilibrium I exists owing to the constraints on \( f_i^+ \) and the term \((c - bN_f)\). The determinant is given in equation (C 4):

\[
\Delta = \frac{c(bN_f - c)v_1(h^* - h_1)(h_2 - h^*)v_1N_f(N_m b + c)}{b^2N_f^2u(\epsilon + bN_mN_hh^*u_m(c/b + N_m^2))}.
\]  

All factors are positive constants except for differences in harassment levels; so it is helpful to consider the determinant with only terms involving harassment:

\[
\Delta = \frac{(h^* - h_1)(h_2 - h^*)}{h^*} > 0.
\]

The determinant will always be positive when equilibrium I exists because of the constraints on \( m^\circ \). Since \( \text{tr} < 0 \) and \( \text{det} > 0 \), the equilibrium is stable. Therefore, the same criterion \((h_i < h^* < h_0)\) establishes both existence and stability of the equilibrium.

(a) Female polymorphisms couples with monomorphic males

Now consider equilibria II \((f_i^+, 0)\), and III \((f_i^+, 1)\); female polymorphisms with monomorphic male populations. The Jacobian matrix analysed at equilibrium II \( ((v_1N_f - v_2h_1N_m^2)/(v_2h_1N_mN_f + v_1N_f), 0)\), is given by equation (C 6):

\[
\mathcal{J} = \begin{pmatrix}
\frac{(v_1 + h_bN_m^2v_2)(-N_fv_1 + h_bN_m^2v_2)}{h_fN_fN_m(N_f + N_m)v_1u_i} & \frac{(-h_1v_2(-N_fv_1 + h_bN_m^2v_2))}{h_fN_m^2u(v_1 + h_bN_m^2v_2)} \\
0 & \frac{(h_1 - h_2)(h_2 - h^*)(c + bN_m)N_f}{h_b(N_f + N_m)u_m}
\end{pmatrix}
\]

Because the Jacobian at equilibrium II is upper triangular, the eigenvalues are the diagonal elements

\[
\lambda_1 = \frac{(v_1 + h_bN_m^2v_2)(-N_fv_1 + h_bN_m^2v_2)}{h_fN_fN_m(N_f + N_m)v_1u_i}
\]

(C 7a)

and

\[
\lambda_2 = \frac{(h_1 - h_2)(h_2 - h^*)(c + bN_m)N_f}{h_b(N_f + N_m)u_m}.
\]

(C 7b)

Equilibrium II exists if equation (C 8) holds,

\[
v_1N_f > v_2h_1N_m^2;
\]

(C 8)

this condition also implies that \(\lambda_1 < 0\). \(\lambda_2\) is negative under the condition that

\[
h_1 < h < h^*.
\]

(C 9)

In general, if equilibrium II exists and \( h^* \) exceeds the highest harassment level, it is stable.

Similarly, equilibrium III \(((v_1N_f - v_2h_1N_m^2)/(v_2h_2N_mN_f + v_1N_f), 1)\), exists if equation (C 10) holds, and it is stable if equation (C 11) holds:

\[
v_1N_f > v_2h_2N_m^2
\]

(C 10)

and

\[
h^* < h < h_1
\]

(C 11)

Note that the existence of equilibrium II implies the existence of equilibrium III (i.e. \(h_i < h_0\)). In general, equilibrium III is stable when \(h^*\) is lesser than the lowest harassment level.

(b) Strictly monomorphic populations

Consider equilibria IV \((0, 1)\) and V \((0, 0)\); monomorphic male and female populations. The Jacobian matrix analysed at the point \((0, 1)\) gives a diagonal matrix with eigenvalues given by equations (C 12a, b):

\[
\lambda_1 = \frac{v_1}{N_m^2h_fu_i} - \frac{v_2}{N_fu_f}
\]

(C 12a)

and

\[
\lambda_2 = \frac{cv_1(h_2 - h_1)}{h_bN_m^2u_m} < 0.
\]

(C 12b)

Equilibrium IV \((0, 1)\), is stable under the condition that (C 13) holds. Note the stability condition is opposite to the existence condition of equilibrium III:

\[
v_1N_f < v_2h_2N_m^2.
\]

(C 13)
In like manner, the point \((0,0)\) is always an equilibrium solution and has a diagonal Jacobian with eigenvalues given by equations (C 14a,b):

\[
\lambda_1 = \frac{v_1}{N_m h u_l} - \frac{v_2}{N_l u_l}
\]

and

\[
\lambda_2 = -\frac{c r_1 (h_l - h_i)}{h_l b N_m u_m} < 0.
\]

Under model assumptions, \((h_l < h_i), \lambda_2 > 0\) and thus the point can never be stable.

REFERENCES


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