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ON THE EVOLUTIONARY STABILITY OF MALE HARASSMENT IN A COERCIVE MATING GAME

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Abstract. In many animals, males employ coercive mating strategies to help them maximize their expected number of offspring. In such systems, selection will favor behavioral adaptations in females that help them mitigate harassment costs and maximize their reproductive fitness. Previously, Bokides et al. [1] presented a model showing how male harassment strategies can co-evolve with female habitat preferences in a mating game. Their results indicated that if females dispersed freely between habitats where males were present and where males were excluded, selection could favor males who strategically harassed at high (or low) levels, depending on the proximity of their phenotype to a threshold level h^*. This article is a continuation of that work addressing the questions of stability at equilibria where males harass at the threshold level (i.e., h^*). We show these states are both locally and globally asymptotically stable. Further, we argue based on these results that h^* is an evolutionary stable male harassment level at which females will be ideally distributed to match the resource quality and social environments of their alternative habitats.

1. Introduction

Sexual conflict is ubiquitous in animals—a consequence of the often divergent reproductive strategies of the sexes. This conflict can sometimes result in a co-evolutionary arms race where both males and females develop costly adaptations aimed at maximizing their reproductive fitness (to the detriment of the other). The emergence of mate coercion in systems where males cannot effectively control mating access to females, or contribute negligibly to the survival of their progeny is believed to be one such example of this phenomenon [2]. Mate coercion strategies like aggressive harassment can be fitness reducing to females especially if rejecting male advances allows them to mate with a genetically superior male or when ecological conditions are more suitable. In general, harassment is costly to both sexes (e.g., loss

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of feeding time, increased energy expenditure and predation risks, etc.) [2]. However, females can also suffer more direct fitness costs from mating superfluously (e.g., disease transmission and physical damage) [3, 4]. Consequently, they are expected develop a suite of morphological and behavioral counter-adaptations to mitigate male harassment. Dispersal behavior is one of several empirically noted examples of such adaptations [5, 6, 7].

In a predator-prey system, prey animals can increase their fitness by employing habitat use strategies that balance predation risk with expected foraging returns. Similarly, in a coercive mating system, females can increase their fitness by regulating their activity levels and availability in antagonistic (male-dominant) environments [7, 8]. When females can effectively disperse, the efficacy of male aggression strategies may become context-dependent. For instance, in a study of the common water strider Aquarius remigis, Eldakar et al. [7] showed that medially aggressive males had more successful copulations than highly aggressive males when females could move freely between several habitats. However, highly aggressive males were most successful when female movement was artificially restricted to a single habitat. This result is interesting because it suggest that a simple female behavioral rule (i.e., move away from overly aggressive males) can mediate population structure in ways that ultimately alter the fitness landscape for aggression in males.

Inspired by the mating conflict in A. remigis and similar systems [9, 10], Bokides et al. [1] modeled the dynamics of female patch use and male harassment as a habitat choice game with predator-prey style interactions. Their analysis revealed that selection always favored male strategies with harassment closest to a threshold level h^*. However, some questions remained. First, their analysis failed to predict evolutionary outcomes if males exactly adopted h^* in their strategy set. This question is critical to determine whether or not playing h^* is robust to the emergence of mutant strategies and/or stochastic perturbations in female patch use frequencies. Furthermore, their analysis failed to give any indication of whether non-equilibrium dynamics were possible in the model. A result like this would be unsurprising given that the fitness optima of both male and female strategies are asymmetrically coupled, and exhibit negative frequency-dependence.

Here, we address these questions in turn, ultimately showing that game equilibria in which males use the threshold harassment h^* in their strategy set corresponds to an attracting evolutionary stable state where females are optimally distributed between alternative habitats.

The rest of the article is structured as follows. In section 2, we briefly summarize the mating game model presented in Bokides et al. [1]. In section 3, we present our main results. We begin with a nonlinear analysis of the model under degeneracy condition, proving that all pure and mixed strategy equilibria are locally asymptotically stable whenever they exist [11].

Next, we rule out the existence of periodic solutions by applying Dulac's criterion [12]. Finally, using the results of Poincaré-Bendixson theorem [12], we show that these equilibria are globally stable. We conclude with a brief discussion our results, noting their biological implications in the context of evolutionary stable strategies (ESSs; Maynard Smith [13]) and ideal free distributions (IFDs; Fretwell & Lucas [14]) of fitness-optimizing animals in population games [15]. Proofs of our main analytical results are presented in the appendix.

2. A coercive mating game

For the reader's convenience, we briefly review and summarize main results of the Bokides et al. model [1]. The model is styled similar to classical habitat choice games [13] with a fixed population of females (N_f) and males (N_m) vying to maximize resource intake and mating benefits.

The game unfolds over two interconnected patches: a communal habitat (patch 1) where males and females can interact, and a spatially isolated female refuge (patch 2) where males are excluded. The model assumes that there is intraspecific resource competition in each patch, but that sex ratio variation within the communal patch is strictly due to female movement to and from the refuge. Males are distinctly identifiable by their harassment phenotype h_r and h_i (respectively, low and high). The probabilities that a male uses each harassment type (or equivalently, the proportion of all males using each type) are represented by state variables m_r and m_i respectively. Similarly, the probabilities that a female uses the communal and refuge patches (or the proportion of all females using each patch) are represented by f_1 and f_2 respectively. Fitness is defined as lifetime reproductive success; it is calculated by multiplying the probability of survival ($1/\mu_f$ for females, and $1/\mu_m$ for males) with the value of reproduction. Reproductive success depends on resource intake for both males and females. However, for females, the model assumes that resource intake contributes more to lifetime reproductive fitness than mating alone. This can occur if females do not benefit from excessive mating, but suffer associated costs such as injury, predation risk, etc. [3, 16]. Conversely, for males, lifetime reproductive fitness is assumed to increase with mating frequency, which correlates with their harassment level (i.e., h_r or h_i). Moreover, males also pay an energetic cost (c) proportional to their aggression level. Because males behave like predators, acting to maximize food intake and mating interactions in patch 1, their fitness is calculated by multiplying together: (i) intake rate, (ii) the net benefit of using a harassment strategy relative to the total number of mating attempts per female, and (iii) survival probability.

$$W_{m_r} = \frac{v_1}{f_1 N_f + N_m} \cdot \frac{(f_1 N_f b - c) h_r}{(m_r h_r + m_i h_i) b N_m} \cdot \frac{1}{\mu_m} \tag{2.1a}$$

$$W_{m_i} = \frac{v_1}{f_1 N_f + N_m} \cdot \frac{(f_1 N_f b - c) h_i}{(m_r h_r + m_i h_i) b N_m} \cdot \frac{1}{\mu_m} \tag{2.1b}$$

On the other hand, because female survival in patch 1 is assumed to decrease with mating frequency, their fitness is calculated by multiplying together: (i) intake rate, (ii) the total number of mating attempts per female, and (iii) survival probability. Moreover, female fitness in patch 2 is only dependent on intake since males are excluded.

$$W_{f_1} = \frac{v_1}{f_1 N_f + N_m} \cdot \frac{1}{(m_r h_r + m_i h_i) N_m} \cdot \frac{1}{\mu_f} \tag{2.2a}$$

$$W_{f_2} = \frac{v_2}{f_2 N_f} \cdot \frac{1}{\mu_f} \tag{2.2b}$$

Since $f_1 + f_2 = 1$ and $m_r + m_i = 1$, the strategy dynamics of female patch use and male harassment can be modeled by a system of replicator equations [11]:

$$\begin{aligned} \dot{f}_1 &= f_1(1-f_1)[W_{f_1} - \bar{W}_f] \\ \dot{m}_r &= m_r(1-m_r)[W_{m_r} - \bar{W}_m] \end{aligned} \tag{2.3}$$

where:

$$\bar{W}_f = f_1 W_{f_1} + (1-f_1) W_{f_2} \tag{2.4a}$$

$$\bar{W}_m = m_r W_{m_r} + (1-m_r) W_{m_i} \tag{2.4b}$$

The dynamical system (2.3) is defined on the unit square: $\mathscr{S} = \{(f_1, m_r) : 0 \le f_1 \le 1, 0 \le m_r \le 1\}$ for non-negative initial conditions in $\mathscr{S}$. Moreover, it contains up to five equilibrium states, three of which females use the communal patch with non-zero probability (cf. Table 1). Bokides et al. [1] showed that the interior equilibrium where males use a probabilistic mix of low and high harassment (i.e., h_r and h_i) with females present was stable if and only if there existed intermediate harassment threshold:

$$h^* = \frac{v_1(bN_f - c)}{v_2(c + bN_m)N_m}, \qquad h_r < h^* < h_i \tag{2.5}$$

where $bN_f > c$. Moreover, in the limit when there is no harassment costs:

$$\lim_{c \to 0} h^* = \frac{v_1 N_f}{v_2 N_m^2}, \tag{2.6}$$

this threshold (2.5) depends on the relative resource quality of the communal and refuge habitats, as well as the population sex ratio. Since the communal patch sex ratio is driven by female dispersal, this suggests that selection would increasingly favor aggressive males whenever the local sex ratio (i.e., in the communal patch) became female-biased. Conversely, selection would favor non-aggressive males whenever the local sex ratio became male-biased.

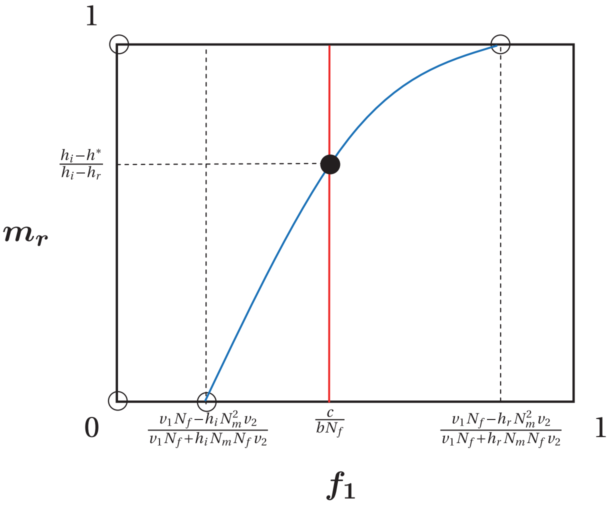

Figure 1: Phase portrait of model (2.3) when $h_r < h^* < h_i$. There is a unique stable mixed strategy interior equilibrium where G intersects the line $f_1 = c/bN_f$. All other equilibria are unstable.

3. Results

3.1. Degenerate case: $h_i = h^*$ $(h_r < h_i)$

When they exist, the mixed harassment equilibrium (E_1) as well as the pure high and low harassment equilibria (E_2 and E_3 respectively) are connected by a curve:

$$G(f_1; h_i) = \frac{h_i f_1 v_2 N_m N_f - v_1 N_f (1 - f_1) + h_i N_m^2 v_2)}{v_2 N_m (h_i - h_r)(f_1 N_f + N_m)} \tag{3.1}$$

which is strictly convex (i.e., $\frac{\partial G^2}{d f_1^2} < 0$) provided $h_r < h_i$. Biologically, G represents the *female equal-payoff curve* on which the expected value of using the communal and refuge patches are balanced for a given male harassment strategy. Under the condition $h_r \neq h_i$ and $h_r < h^* < h_i$, the phase portrait of (2.3) is partitioned into four distinct regions with a unique stable mixed strategy equilibrium, E_1 (Fig. 1). However, system (2.3) becomes degenerate if $h_i = h^*$ (or alternatively, $h_r = h^*$). In this paper, we will restrict our analysis to the former as these cases are symmetrical.

For instance, suppose that we take $h_i > h^*$ as a control parameter. Mathematically, we claim that system (2.3) undergoes a transcritical bifurcation at $h_i = h^*$, leading to a subsequent exchange of stability between the mixed strategy state (E_1) and the pure strategy state (E_2). To see this, we note that as h_i decreases towards h^*, $G(f_1)$ moves to the right, drawing E_1 and E_2 closer. When $h_i = h^*$, these points coalesce, destroying the mixed strategy. Moreover, when $h_i < h^*$, E_2 is the focal stable node. At the bifurcation point, a new equilibrium

Table 1: Equilibria and stability conditions for model (2.3) assuming $h_r < h_i$. Pure strategy equilibria where males harass close to the threshold level h^* are locally stable. Note that when E_1, E_2, or E_3 exist, they are the only stable points in the plane. However, E_4 and E_5 are not biologically realistic because in each case, females always use the refuge patch.

Equilibrium	Existence condition	Local stability
$E_1 = \left(\frac{c}{bN_f}, \frac{h_i - h^*}{h_i - h_r}\right)$	$h_r < h^* < h_i$	$h_r < h^* < h_i$
$E_2 = \left(\frac{v_1 N_f - h_i N_m^2 v_2}{v_1 N_f + h_i N_m N_f v_2}, 0\right)$	$v_1 N_f > h_i N_m^2 v_2$	$h_r < h_i < h^*$
$E_3 = \left(\frac{v_1 N_f - h_r N_m^2 v_2}{v_1 N_f + h_r N_m N_f v_2}, 1\right)$	$v_1 N_f > h_r N_m^2 v_2$	$h^* < h_r < h_i$
$E_4 = (0,1)$	Always	$h^* < h_r < h_i$, $v_1 N_f < h_r N_m^2 v_2$
$E_5 = (0,0)$	Always	Never

$E^* = (c/bN_f, 0)$ is formed where males use the harassment level h^* with unit probability. A straightforward linear analysis of (2.3) near E^* yields the following eigenvalues:

$$\lambda_1 = -\frac{(v_1 + h_i N_m v_2)(v_1 N_f - h_i N_m^2 v_2)}{h_i N_f N_m (N_f + N_m) v_1 \mu_f} < 0, \tag{3.2a}$$

$$\lambda_2 = \frac{(h_i - h_r)(h_i - h^*)(c + bN_m) v_2}{h_i b (N_f + N_m) \mu_m}. \tag{3.2b}$$

Clearly, λ_1 is strictly negative whenever E_2 exists (cf. Table 1). However, λ_2 is zero whenever $h_i = h^*$ (since we assume $h_r \neq h_i$). Thus, the linearization fails to predict local dynamics of (2.3) near E^*. Subsequent steps usually involve analysis of higher order terms in the Taylor series expansion, or using the Center Manifold Theorem as described in [11, 17]. Our approach here is subtler.

3.2. Non-linear stability analysis of E^*

To determine whether (2.3) is stable against perturbations once at the new pure strategy state $E^* = (c/bN_f, 0)$, we analyzed its nonlinear dynamics near E^*. Figure 2 shows the phase portrait of (2.3). The nullclines of $\dot{f}_1$ are the lines $f_1 = 0$ and $f_1 = 1$. There is also an interior nullcline defined by:

$$G(f_1; h^*) = \frac{(1 - f_1)(c + bN_m) v_1 N_f - (f_1 N_f + N_m)(bN_f - c) v_1}{(f_1 N_f + N_m)((c + bN_m) h_r N_m v_2 - (bN_f - c) v_1)} \tag{3.3}$$

which connects equilibriums E^* and E_3 when $h_i = h^*$. The nullclines of $\dot{m}_r$ are the lines $m_r = 0$, $m_r = 1$. There is also an interior nullcline defined by:

$$f_1 = \frac{c}{bN_f} \tag{3.4}$$

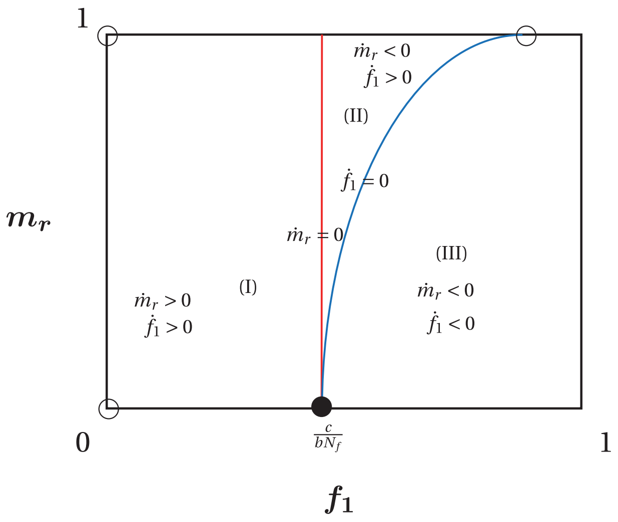

Figure 2: Phase portrait of (2.3) when $h_i = h^*$. The interior nullclines of m_r (red) and f_1 (blue) partition the strategy space into distinct regions (I), (II) & (III). We conjecture that the given sufficient time, all initial conditions converge to $(f_1^*, m_r^*) = c/bN_f, 0)$.

on which the fitness of male using alternative strategies are identically zero. Thus, (3.4) represents the *male equal-payoff curve.*

Starting in region (I), trajectories tend away from E^* (Fig. 2). This is because when there are few available females, the costs of harassing to males are much greater than the expected benefits (i.e., $bf_1N_f < c$). As such, males can increase their fitness by using the less aggressive strategy. This dynamic, in turn, improves the social environment of the communal patch, and drives females to use with it increasing frequency especially if intake rates are lower in the refuge. However, as more females become available, there is weak selection for aggressive males who will get a slightly greater share of mating by harassing more than others. Moreover, the communal patch will remain favorable for females until average fitness in both patches are balanced (i.e., on the equal payoff curve G). Consequently, in region (III), all trajectories tend towards E^*.

We conjectured that an invariant region exists inside $\mathscr{S}$, which traps local trajectories and forces them toward E^* asymptotically. We proved this by first showing that (2.3) is bounded in the strip $\Omega \subset \mathscr{S}$:

$$\Omega = \left\{ (f_1, m_r) : \frac{c}{2bN_f} \le f_1 \le \frac{c}{bN_f},\ 0 \le m_r \le 1 \right\}. \tag{3.5}$$

In particular, we claim the following lemmas.

Lemma 3.2.1. *Suppose that* $h_r < h_i = h^*$. *Then, there exists some positive constant* C_1 *such* *that*

$$\dot{f}_1 \geq C_1 \left(\frac{c}{bN_f} - f_1 \right), \quad \forall\, (f_1, m_r) \in \Omega.$$

Lemma 3.2.2. *Suppose that* $h_r < h_i = h^*$*. Then, there exists some positive constant* C_2 *such that*

$$\dot{m}_r \leq C_2 m_r \left(\frac{c}{bN_f} - f_1 \right), \quad \forall\, (f_1, m_r) \in \Omega.$$

Lemma 3.2.3. *Suppose that* $h_r < h_i = h^*$*. There exists some positive constant* C_3 *such that*

$$\frac{\dot{m}_r}{\dot{f}_1} \leq C_3 m_r, \quad \forall\, (f_1, m_r) \in \Omega.$$

We direct the reader to appendix A for detailed proofs of these results. Next, we showed that for some sufficiently small $\varepsilon > 0$, the ratio $\frac{\dot{m}_r}{\dot{f}_1} = \frac{dm_r}{df_1} < 1$ holds on a line segment $\mathscr{L}$ in the (f_1, m_r) plane (Fig. 3). Specifically, $\mathscr{L}$ is given by:

$$\mathscr{L} = \left\{ (f_1, m_r) : \; m_r = f_1 - \left(\frac{c}{bN_f} - \varepsilon \right), \quad \frac{c}{bN_f} - \varepsilon \leq f_1 \leq \frac{c}{bN_f} \right\}, \tag{3.6}$$

which connects the points $(\frac{c}{bN_f} - \varepsilon, 0)$ and $(\frac{c}{bN_f}, \varepsilon)$ and forms a right triangle with the lines $m_r = 0$ and $f_1 = \frac{c}{bN_f}$ in region (I) (Fig. 3). This result is summarized in the following lemma (a proof of which is also given in appendix A).

Lemma 3.2.4. *Suppose that* $h_r < h_i = h^*$*. For any* $0 < \varepsilon \leq \min\left\{ \frac{c}{2bN_f}, \frac{1}{2C_3} \right\}$,

$$\frac{\dot{m}_r}{\dot{f}_1} \leq \frac{1}{2}, \quad \forall\, (f_1, m_r) \in \mathscr{L}.$$

To complete the argument, it sufficed to construct a square of dimensions $l = w = \varepsilon$, which together with $\mathscr{L}$ forms a trapezoid ABCD enclosing E^*. All together, Lemmas 3.2.1–3.2.4 show that the region contained with trapezoid ABCD is invariant under the flow of system (2.3). Moreover, since ε can be chosen to be arbitrarily small, E^* is locally asymptotically stable.

3.3. Ruling out closed orbits

Periodic solutions are not uncommon in asymmetric fitness games with co-evolving strategies (e.g., predator-prey games [15]). Like predator-prey conflicts, mating conflicts between males and females may also generate a co-evolutionary cycling especially if the value of adaptations exhibits negative frequency-dependence (i.e., rare strategies have higher fitness than common types). However, we claim that the system (2.3) cannot have periodic solutions as

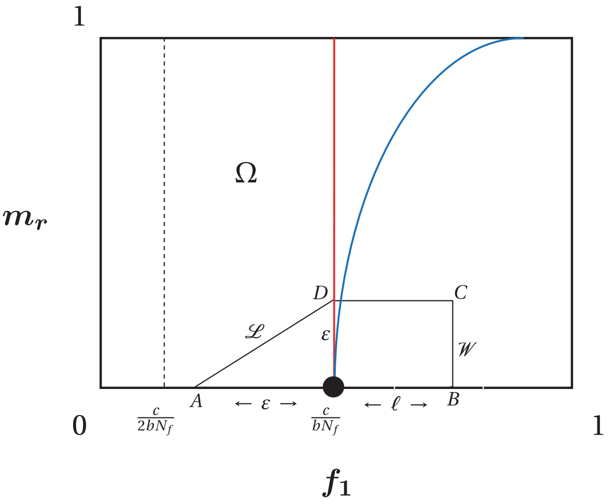

Figure 3: Trapping region. The trapezoid $ABCD$ defines an invariant region within which trajectories approach $E^* = (c/bN_f, 0)$ asymptotically. Note also that Ω always contains $\mathscr{L}$ because $\varepsilon \leq \frac{c}{2bN_f}$. Also, since ε can be chosen arbitrarily small, the construction always exists.

a consequence of the Bendixson-Dulac theorem. A proof of this theorem can be found in Strogatz [12]. In appendix B, we show that:

$$\beta(f_1, m_r) = \left[\frac{(f_1 N_f + N_m)((h_r - h_i)m_r + h_i)}{f_1(1-f_1)(1-m_r)m_r}\right] \tag{3.7}$$

is a Dulac function for system (2.3), which necessarily excludes the possibility of closed orbit solutions lying entirely in $\mathscr{S}$.

3.4. Global stability

By excluding periodic orbits from system (2.3), our analysis also suggest that all locally stable equilibria (even in the degenerate case $h_i = h^*$) are in fact globally asymptotically stable whenever they exist. This result is a directly corollary of the Poincaré-Bendixson theorem — a proof of which can also be found in Strogatz [12].

In appendix C, we remark that (2.3) satisfies the hypothesis of the Poincaré-Bendixson theorem specifically because it is continuously differentiable and bounded in the unit square $\mathscr{S}$, which is a closed subset of $\mathbb{R}^2$. Moreover, because (2.3) never exhibits multstability (i.e., simultaneously contain two or more locally stable equilibria; c.f. Table 1), Poincaré-Bendixson theorem allows us to conclude that any existing locally stable equilibrium of (2.3) must also be globally asymptotically stable.

In biological terms, this result suggests that any initial combination of female patch use frequency and male aggression lead to one of two outcomes: (i) fixation of a pure male harassment strategy with female patch use at a low or high frequencies or (ii) fixation of mixed male harassment strategy with female patch use at an intermediate frequency. In either case, the average frequency at which females use the communal patch at equilibrium will balance the costs of male harassment.

4. Discussion

We analyzed the replicator equations (2.3) of a mating game between females who modulate the proportion of time spent in a refuge patch where they are not available to mate, and males who employ one of two costly harassment tactics (h_r or h_i) to mate with available females. Specifically, we focused on the stability of system (2.3) at a degenerate equilibrium $E^* = (c/bN_f, 0)$ where females use the communal patch with frequency $f^* = c/bN_f$ and aggressive males always use the threshold harassment (i.e., $h_i = h^*$) (see equation (2.5)). Our analysis revealed that E^* is globally asymptotically stable, suggesting that the implied equilibrium strategies are evolutionarily optimal. We will argue this claim using analogous principles from evolutionary game theory [13] and ideal free distribution theory [14].

In evolutionary game theory, a strategy is called evolutionary stable (i.e., an ESS) if the strategy cannot be invaded by an initially rare mutant once it is being used by majority of individuals in a population [13, 18]. Generally speaking, there is a tight correspondence between ESSs and asymptotically stable equilibria of replicator equations [11]. This is because the replicator dynamics provide a trajectory of the expected fitness of any strategy. Hence, by proving that E^* is both locally and globally convergent, we have also shown that in a monomorphic population, any female (or male) deviating from the equilibrium strategy will have a lower average fitness relative to others. Consequently, these variants will ultimately be purged from the population. More generally, our results also hold in non-degenerate cases $h_i \neq h^*$ for any existing pure or mixed equilibrium strategies (cf. Table 1).

Our results also argue that f^* is an optimal patch use frequency for females in the context of an ideal free distribution (IFD). IFD theory [14] provides a framework to understand how animals should be distributed in patchy environments, assuming they can move freely and have a complete knowledge about the quality of each habitat. Previously, Cressman et al. [15] showed that IFD strategies in a general two-patch predator-prey game always correspond to locally asymptotically stable equilibria of the replicator equation if intraspecific prey competition was allowed.

In the mating game modeled by (2.3), males act like predators altering their harassment strategy, while females act like prey freely moving between a communal and refuge habitat. Moreover both sexes compete for resources which contribute to their fitness. The *female equal-payoff curve* (3.1) describes the set of male harassment strategies that equalize fitness between habitats. Similarly, the *male equal-payoff curve* (3.4) describes the set of patch use frequencies at which males are indifferent to harassing at high or low levels. Therefore, points on either curve correspond to fitness matching Nash equilibria. However, these equilibria are only evolutionarily stable when they coincide (Fig. 1). As we have shown, a female strategy that uses the communal patch with probability $f^* = c/bN_f$ when males use h^* with unit probability satisfies these Nash conditions, and is convergent (Fig. 2-3). Thus, they correspond to IFD strategies for the mating game.

Our global stability results strengthen those reported in Bokides et al. [1] by predicting one of two evolutionary outcomes at the population scale: (i) fixation of males who always harass at high (or low) levels with female patch use at a low (or high) frequencies or (ii) fixation of males who use mixed harassment strategy depending on h^* with female patch use at an intermediate frequency (cf. Table 1). Some recent experiments [20, 21] provide evidence for evolutionarily stable moderate aggression phenotype in artificially structured populations of *A. remigis*. In these studies, the overall mating activity of groups declined with the proportion of hyper-aggressive males they contained. Consequently, groups with less aggressive males produced more offspring than those with hyper-aggressive males [20].

In reality, female dispersal reduces the fitness of nearby males regardless of their aggression level. Thus, non-aggressive males may respond in kind by dispersing away from overly aggressive individuals (i.e., to improve their mating prospects) [6, 20, 21]. We can capture this dynamic in (2.3) by allowing males to access the refuge patch, but with additional mortality associated with their harassment strategy. This is plausible if males face predation risk tradeoffs while mating/foraging in the refuge [19]. Clearly, in this scenario, the equilibrium IFD female strategies will depend both on the sex ratio and the distribution of male harassment strategies between patches. Thus, we may find the emergence of different kinds of asymptotic behavior driven by coexisting ESSs and/or limit cycles, as is the norm for similarly styled predator-prey games (cf. [15]).

Furthermore, because population structure can emerge from females (and males) dispersing away from low quality social/resource environments and assorting in high quality ones [22], multi-level selection may favor the evolution of tapered male aggression [6, 20, 21]. Thus, expanding the current model to multiple patches of varying accessibility may yield insights on the evolutionary trajectory of male aggression in a realistic population.

In summary, we showed that the Bokides et al. [1] model only exhibits equilibrium behavior. We also proved that any existing equilibrium strategy would be globally asymptotically stable, improving on their results. Finally, we concluded that due to the asymptotic convergence of these equilibria (even in degenerate cases), the implied male harassment and female patch use strategies would be evolutionarily stable. Future work on this model should incorporate male movement within the current framework. This work might provide further insights into how conditional dispersal and assortment can influence selection for costly mate coercion strategies in a realistic population.

Appendix

A: Constructing a Locally Invariant Region

Consider the following region:

$$\Omega = \left\{ (f_1, m_r) : \frac{c}{2bN_f} \le f_1 \le \frac{c}{bN_f},\ 0 \le m_r \le 1 \right\}. \tag{3.8}$$

Note that $\Omega \subset \mathscr{S}$ and contains the degenerate monomorphic equilibrium:

$$E^* = (f_1^*, m_r^*) = \left(\frac{c}{bN_f}, 0 \right) \tag{3.9}$$

where males use an intermediate harassment level

$$h^* = \frac{(bN_f - c)v_1}{v_2(c + bN_m)N_m}.$$

Proof of the Lemma 3.2.1. Since $h_r < h_i = h^*$, from (2.3) we have

$$\dot{f}_1 = \frac{df_1}{dt} = f_1(1 - f_1)\left[\frac{v_1}{(f_1 N_f + N_m)h^* N_m \mu_f} - \frac{v_2}{(1 - f_1)N_f \mu_f} \right] \tag{3.10}$$

After some direct calculations, we obtain

$$\begin{aligned} \frac{df_1}{dt} &\ge \frac{f_1}{\mu_f} \cdot \left[\frac{v_1(1 - f_1)}{(f_1 N_f + N_m)h^* N_m} - \frac{(bN_f - c)v_1}{(c + bN_m)h^* N_m N_f} \right] \\ &= \frac{f_1}{f_1 N_f + N_m} \cdot \frac{v_1(N_f + N_m)}{h^* N_m \mu_f (c + bN_m)} \cdot \left(\frac{c}{bN_f} - f_1 \right). \end{aligned} \tag{3.11}$$

Since $\frac{c}{2bN_f} < f_1 < \frac{c}{bN_f}$, we have

$$\frac{f_1}{f_1 N_f + N_m} \ge \frac{c}{2N_f(c + bN_m)}.$$

Therefore, we conclude that:

$$\frac{df_1}{dt} \ge \frac{c}{2N_f(c + bN_m)} \cdot \frac{v_1(N_f + N_m)}{h^* N_m \mu_f (c + bN_m)} \cdot \left(\frac{c}{bN_f} - f_1 \right) = C_1 \left(\frac{c}{bN_f} - f_1 \right), \tag{3.12}$$

where C_1 is a positive constant independent of $(f_1, m_r) \in \Omega$. ☐

Proof of the Lemma 3.2.2. From (2.3), we have

$$\dot{m}_r = \frac{dm_r}{dt} = m_r\left(\frac{c}{bN_f} - f_1\right)\frac{(1-m_r)(h^* - h_r)\nu_1 N_f}{(f_1 N_f + N_m)[(h_r - h^*)m_r + h^*]N_m\mu_m}. \tag{3.13}$$

Since $(f_1, m_r) \in \Omega$, we obtain

$$0 < 1 - m_r < 1, \quad f_1 N_f + N_m \geq \frac{c}{2b} + N_m, \quad (h_r - h^*)m_r + h^* \geq h_r.$$

Hence,

$$\frac{dm_r}{dt} \leq m_r\left(\frac{c}{bN_f} - f_1\right)\frac{(h^* - h_r)\nu_1 N_f}{[c/(2b) + N_m]h_r N_m \mu_m} := C_2 m_r\left(\frac{c}{bN_f} - f_1\right),$$

where C_2 is a positive constant independent of $(f_1, m_r) \in \Omega$. □

Proof of the Lemma 3.2.3. This result follows from Lemmas 3.2.1–3.2.2 immediately since $C_3 = \frac{C_2}{C_1}$ which is independent of $(f_1, m_r) \in \Omega$. □

Proof of the Lemma 3.2.4. Given any $\varepsilon > 0$, consider the following line segment in (f_1, m_r) plane, denoted by $\mathscr{L}$, which is given by

$$\mathscr{L} = \left\{(f_1, m_r) : \; m_r = f_1 - \left(\frac{c}{bN_f} - \varepsilon\right), \quad \frac{c}{bN_f} - \varepsilon \leq f_1 \leq \frac{c}{bN_f}\right\}.$$

Note that the slope of $\mathscr{L}$ is equal to 1, and $\mathscr{L}$ connects points $(c/(bN_f) - \varepsilon, 0)$ with $(c/(bN_f), \varepsilon)$.

Without loss of generality, we choose $\varepsilon \leq \min\left\{\frac{c}{2bN_f}, \frac{1}{2C_3}\right\}$. Note that $\mathscr{L}$ is contained in Ω since $\varepsilon \leq \frac{c}{2bN_f}$. Also note that $0 \leq m_r \leq \varepsilon$ for any $(f_1, m_r) \in \mathscr{L}$. Then by Lemma 3.2.3, for any $(f_1, m_r) \in \mathscr{L}$,

$$\frac{\frac{dm_r}{dt}}{\frac{df_1}{dt}} \leq C_3 m_r \leq C_3 \varepsilon \leq \frac{1}{2}, \tag{3.14}$$

where the last inequality follows form our choice of ε. □

B: Ruling out Closed Orbits

Bendixson-Dulac Criterion

Let $\dot{\mathbf{x}} = f(\mathbf{x})$ *be a continuously differentiable vector field defined on a simply connected subset* $\mathbf{R}$ *of the plane. If there exists a continuously differentiable, real-valued function* $\beta(\mathbf{x})$ *such that* $\nabla \cdot \beta(\dot{\mathbf{x}})$ *has only one sign throughout* $\mathbf{R}$*, then there are no closed orbits lying entirely in* $\mathbf{R}$.

A proof of this result is given in on p. 202 in Strogatz [15]. It is easy to see that system (2.3) satisfies the hypothesis of the Bendixson-Dulac theorem since it is continuously differentiable in the interior of the unit square $\mathscr{S}$:

$$\mathscr{S} = \{(f_1, m_r) : 0 \leq f_1 \leq 1, 0 \leq m_r \leq 1\}.$$

We will now show for system (2.3) that:

$$\beta(f_1, m_r) = \left[\frac{(f_1 N_f + N_m)((h_r - h_i)m_r + h_i)N_m\mu_m}{f_1(1-f_1)(1-m_r)m_r}\right]$$

satisfies the Bendixson-Dulac theorem. First, we define the following functions over interior of $\mathscr{S}$:

$$\begin{aligned} K_1(m_r) &= \frac{v_1}{m_r(1-m_r)N_m\mu_f} \\ K_2(m_r) &= \frac{v_2((h_r - h_i)m_r + h_i)}{m_r(1-m_r)N_f\mu_f} \\ K_3(f_1) &= \frac{v_1(bN_f - c)(h_r - h_i)}{f_1(1-f_1)N_m\mu_m}. \end{aligned} \tag{3.15}$$

Then,

$$\triangledown\cdot\beta(\dot{\mathbf{x}}) = \frac{\partial}{df_1}(\beta\cdot\dot{f}_1) + \frac{\partial}{df_1}(\beta\cdot\dot{m}_r) = -\left(\frac{N_f + N_m}{(1-f_1)^2}\right)\cdot K_2 < 0. \tag{3.16}$$

Since $\triangledown\cdot\beta(\dot{\mathbf{x}})$ holds $\forall\ (f_1, m_r) \in \mathring{\mathscr{S}}$, we conclude that there are no closed orbits lying entirely in $\mathscr{S}$.

C: Globally stable

Poincare-Bendixson Theorem

Let **R** *be a closed, bounded subset of the plane and let* $\dot{\mathbf{x}} = f(\mathbf{x})$ *be a continuously differentiable vector field defined on an open set containing* **R**. *If* **R** *does not contain any fixed points; and there exists a trajectory C that remains confined in* **R** *for all time, then either C is a closed orbit or it spirals toward a closed orbit as* $t \to \infty$.

A proof of this result is given in on p. 203 in Strogatz [15]. Again, system (2.3) satisfies the hypothesis of the Poincare-Bendixson theorem since it is continuously differentiable and bounded in the unit square S. Moreover, because there can be no closed orbit solution lying entirely in S, any equilibrium of (2.3) that exists uniquely in $\mathscr{S}$ and is locally asymptotically stable must also be globally stable.

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