An Evolutionary Game Model of Sex-Dependent Antipredator Signaling

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Abstract: Various prey animals behave conspicuously to approaching predators. The conspicuous behavior is considered to be an antipredator signal, and the frequency of signaling individuals in a population differs between males and females in many species. We theoretically assessed the evolution of the inter- and intrasexual dimorphism in antipredator signaling by developing an evolutionary game model. We particularly focused on the Chinese grasshopper, Acrida cinerea, in which only a proportion of males and no females escape conspicuously. In our model, the antipredator signal was assumed to be costly and affect the probabilities of predation of both the signaling individual (individual effect) and the signaling or nonsignaling conspecifics around it (collective effect). The model indicates that (1) a positive individual effect is essential for the evolution of antipredator signaling; (2) sexual dimorphism in fecundity cost for signaling individuals or natural predation probability can produce intersexual dimorphism in the signaling where all individuals of one sex and no individuals of the other sex emit signal; and (3) a positive collective effect can explain the intrasexual dimorphism where only some individuals of one sex signal. This study provides the first model of intrasexual dimorphism in antipredator signaling and brings new testable predictions.

Keywords: crepitation, escape strategy, evolutionary dynamics, grasshopper, intrasexual dimorphism.

Introduction

Prey animals have evolved various escape strategies to avoid attacks by predators (Ruxton et al. 2004). Conspicuous behavior by prey animals in the face of an approaching predator is one such escape strategy (Ruxton et al. 2004; Caro 2005). For example, the Eurasian skylark, Alauda arvensis, sings loudly while escaping from the merlin, Falco columbarius, to deter the attack (Cresswell 1994), and the peacock butterfly, Inachis io, flicks its wings to turn away the predatory mice Apodemus flavicolis and A. sylvaticus (Olofsson et al. 2012). These conspicuous behaviors may signal the prey’s unprofitability (Vega-Redondo and Hasson 1993; Bergstrom and Lachmann 2001), startle the predator (Umbers et al. 2017), or confuse the predator by a sudden disappearance of the conspicuousness that highlighted the position of the prey animal originally (Loeffler-Henry et al. 2018). The conspicuous behaviors are thus considered to increase the survivorship of prey animals, although they may attract the predator’s attention. Note that kin selection may facilitate other types of conspicuous behaviors, such as altruistic alarm calls in group-living animals (Sherman 1977; Wheeler 2008), whereas the present study focuses on conspicuous behaviors that can evolve even in solitary animals.

The escape strategies of prey animals often differ between males and females. This may be caused by differential escape costs and predation risks between females and males. Females may invest fewer resources into escape strategies because of the higher resource demands females have for egg production (Queathem 1991), revealing a higher cost of escape than for males. Because male animals often move frequently to search for mates or show conspicuous displays to attract potential mates (Magnhagen 1991), they are more likely to draw attention from predators than females (Hernandez-Jimenez and Rios-Cardenas 2012). Such males may compensate for their high predation risk by behaving cautiously toward the predators (Hedrick 2000). Conversely, predators may prefer females over males because of their higher nutritional value (Ercit 2014). These differences
between sexes will affect the sex-dependent evolution of the escape strategies of prey animals (Stankowich and Blumstein 2005).

Several empirical studies show sexual dimorphism in the conspicuous signals used during escape attempts. The wall lizard, *Podarcis muralis*, shakes its foot more frequently in females than in males when it escapes from an approaching human (Font et al. 2012). Additionally, the female mountain katydid, *Acrípex reticulate*, escapes more conspicuously than the male (De Bona et al. 2020). In contrast, a male-biased frequency in the use of conspicuous escape is reported for the yellow-headed gecko, *Gonatodes albogularis*, which performs a tail-waving display against an approaching human (Bohórquez Alonso et al. 2010). An extreme example of sexual dimorphism in the conspicuous signals is found in the Chinese grasshopper, *Acrida cinerea* (Orthoptera: Acrididae). In this species, conspicuous sounds are produced only by males while they escape by flying (Takaie 1998), and females produce no conspicuous sounds even when they fly to escape (T. Kuga and E. Kasuya, unpublished data). A preliminary observation showed that the sound is not always produced during male flight (T. Kuga and E. Kasuya, unpublished data). To understand why these sexual dimorphisms in conspicuous escape have evolved, mathematical models that consider the evolutionary dynamics of signaling strategies in different sexes are useful. However, there has been no attempt to develop and analyze such models.

Previous theoretical studies of signaling during escape attempts have focused on models of pursuit deterrence where evolutionarily stable strategies for predator and prey animals are used, in which the prey signals and the predator receiving the signal does not attack (Zollman et al. 2013; Ramesh and Mitchell 2018). An evolutionarily stable strategy is defined as the strategy that gives the highest payoff to an individual when all of the other individuals follow it. To address sexual dimorphism in the frequencies of conspicuous signaling, we developed a new evolutionary game model by defining the differential cost of escape and predation risks between females and males. By examining the evolutionarily stable strategies of our model, we derived the condition that only a fraction of one sex produces the conspicuous escape signal observed in the Chinese grasshopper.

**Model**

*Defining the Cost and Benefits of Signaling*

We developed an evolutionary game model of the signaling strategies of a solitary prey population, such as the Chinese grasshopper, based on the framework of the bed net use model for malaria protection (Honjo et al. 2013; Honjo and Satake 2014). We found that the underlying mathematical structures of the bed net use model and the evolutionary game model of signaling are the same and extended the former to the latter. We assumed a prey population with an even sex ratio in which each individual adopts either of two strategies: signaling (S) or nonsignaling (N). Let \( x_s \) and \( x_n \) be the frequencies of signaling and nonsignaling females, and let \( y_s \) and \( y_n \) be the frequencies of signaling and nonsignaling males in the population. Because these variables indicate the frequency of each strategy, the relationship \( x_s + x_n = y_s + y_n = 1 \) is satisfied. Although we consider only the pure strategies of "always signal" and "never signal" in this study, we can directly apply the results below to the extended model that considers various mixed strategies of "signals with a certain probability." More specifically, we can show that the frequency of signaling individuals at an evolutionarily stable state in the present model is equal to the probability that an individual adopting an evolutionarily stable strategy emits signals in the extended model (supplemental PDF, available online).

Our model describes how the frequencies of signaling and nonsignaling strategies change over time depending on the fitness of each strategy. The fitness of each strategy is influenced by the benefit gained by a reduced probability of predation and signaling cost. Let \( P_s \) and \( P_n \) be the natural predation probabilities of females and males, respectively, when no individual emits signals (\( 0 < P_s, P_n \leq 1 \)). We assume that the probability of predation is decreased by both the individual effect and the collective effect of signaling. The individual effect of signaling is the reduction in probability of predation of the signaling prey, and it is denoted by \( \alpha_s \). The reduction in probability of predation is the result of three behaviors that are not mutually exclusive. The first behavior is deterring the predatory pursuit by honestly signaling the difficulty of capture. If the signaling prey has a high ability to escape (Vega-Redondo and Hasson 1993) or has detected the predator and is already prepared to escape (Bergstrom and Lachmann 2001), the predation of such prey will be difficult. The predator would then give up the pursuit of the signaling prey to enable optimal foraging. The second behavior is flash behavior: if the cryptic prey suddenly shows a conspicuous signal and hides the signal while escaping, the predator may lose the location of the prey (Loeffler-Henry et al. 2018). The third behavior is startling the predator with the sudden appearance of a conspicuous signal, which is called "deimatic behavior" (Umbers et al. 2017). Deimatic signals of prey animals can scare or startle predators or elicit other reflexive responses that delay or cease the attacks (Olofsson et al. 2012; Dookie et al. 2017). The probability of predation is reduced depending on the effectiveness of one, two, or all three of the behaviors. Through the individual effect of signaling, the probability of predation of signaling individuals is reduced and becomes \( \alpha_s P_n \) for females and \( \alpha_t P_s \) for males. The largest
individual effect results in a 100% success of escape, resulting in no predation (i.e., $\alpha_1 = 0$). In addition, we can further consider the case of the negative individual effect: the case that signaling increases the probability of predation (i.e., $\alpha_1 > 1$; e.g., Sherman 1985). Since the probabilities of predation of signaling individuals, $\alpha_1 P_x$ and $\alpha_1 P_y$, should be between 0 and 1, the range of $\alpha_1$ is limited within the following range:

$$0 < \alpha_1 < 1 / \max \{ P_x, P_y \}.$$  \hfill (1)

The collective effect of signaling, denoted by $\alpha_c$, is the reduction of the probability of predation of prey individuals other than the signaling prey. When a prey animal signals to a predator, other prey animals around the signaling individual can notice the existence of the predator and change their behaviors to decrease their probability of predation. We assume that a prey individual can reduce its predation probability through the collective effect of signaling caused by other signaling individuals because once a predator considers the location of signaling prey to be less profitable than another patch, where there are no signaling prey animals, and leaves (Ramesh and Mitchell 2018). If the startled predator stops attacking temporarily or withdraws, prey individuals around the signaling individual can experience reduced predation risk through the signal. We assume that a prey individual can reduce its predation probability by $\alpha_1$ as a result of the collective effect from another signaling individual within the effective range of signaling. The effective range of signaling is defined as a circle expanding from the focal individual (fig. 1), and the expected number of the other conspecifics within the effective range of signaling is $n$. A higher population density indicates a higher value of $n$. When the distribution of signaling and nonsignaling individuals is random, the probability that $k$ individuals among $n$ emit signals, denoted as $p(k)$, is given by the binomial distribution as follows:

$$p(k) = \binom{n}{k} \left( \frac{x_1 + y_1}{2} \right)^k \left( 1 - \frac{x_1 + y_1}{2} \right)^{n-k},$$ \hfill (2)

where $(x_1 + y_1)/2$ is the probability that a signaling individual is chosen by random sampling under our assumption of an even sex ratio. Using equation (2), the expected collective benefit of signaling caused by other signaling individuals within the effective range of signaling (denoted by $\alpha_c$) can be written as

$$\alpha_c = \sum_{k=0}^{n} \alpha_1 p(k) = \cdots = \left[ 1 + (\alpha_1 - 1) \left( \frac{x_1 + y_1}{2} \right) \right]^n.$$ \hfill (3)

In addition, similarly to the above-mentioned negative individual effect, we can consider a negative collective effect (i.e., $\alpha_1 > 1$). When the conspicuous signal of a signaler attracts predatory or parasitic animals, its neighbors suffer an increase in predation or parasitism risk, called "collateral damage" (Trillo et al. 2019). We can choose the value of $\alpha_c$ from the following range:

$$0 < \alpha_c < \frac{1}{\max \{ 1, \alpha_1 \} \cdot \max \{ P_x, P_y \}^{1/n}},$$ \hfill (4)

where the upper limit is specified so that the probability of predation risk for an individual surrounded by $n$ signaling individuals—$\alpha_1 \alpha_1 P_x$, $\alpha_1 \alpha_1 P_y$, $\alpha_1 \alpha_1 P_x$, or $\alpha_1 \alpha_1 P_y$—is less than 1.

Nonsignaling individuals experience a reduced probability of predation only through the collective benefit of signaling by other signaling individuals because once a predator receives conspicuous signals from prey animals, its predation response is suppressed toward any prey animals regardless of whether they are signaling or nonsignaling individuals. In contrast, signaling individuals reduce the probability of predation for themselves and others. Taken together, the gross effect of signaling on predation is presented as the product of the individual and collective benefits of signaling, leading to the following:

preydation probability of signaling female: $\alpha_1 \alpha_c P_x$; \hfill (5-1)

preydation probability of signaling male: $\alpha_1 \alpha_c P_y$; \hfill (5-2)

preydation probability of nonsignaling female: $\alpha_1 P_x$; \hfill (5-3)

preydation probability of nonsignaling male: $\alpha_1 P_y$. \hfill (5-4)

The cost of signaling was built into the model by assuming that signaling females and males have lower fecundity than nonsignaling females and males, respectively. The signaling behavior during escape seems to require
additional movement that is unnecessary for the escape without signaling. Additionally, the organ for sound production or conspicuous body color for signaling may consume more energy for its development and/or its maintenance. We included these costs of signaling by assuming that the reproductive successes of nonsignaling females and males are $F_x$ and $F_y$, respectively, and that those of signaling females and males are $F_x/\beta_x$ and $F_y/\beta_y$, respectively ($\beta_x, \beta_y > 1$).

Given the benefit and cost of signaling, the fitness of signaling and nonsignaling strategies is defined as the product of the probability of survival and fecundity:

- fitness of signaling females: $\frac{(1 - \alpha_1 + \alpha_2 P_x) F_x}{\beta_x}$, (6-1)
- fitness of signaling males: $\frac{(1 - \alpha_1 + \alpha_2 P_x) F_y}{\beta_y}$, (6-2)
- fitness of nonsignaling females: $(1 - \alpha_2 P_x) F_x$, (6-3)
- fitness of nonsignaling males: $(1 - \alpha_2 P_y) F_y$. (6-4)

All parameters in the model are summarized in table 1.

**An Evolutionary Game Model for Escape Behavior in Solitary Prey Animals**

In evolutionary game theory, the fitness of each strategy depends on the frequency of different strategies, and frequency-dependent selection takes place between strategies. We model changes in frequencies of strategies over time using replicator dynamics (Nowak 2006). In the framework of evolutionary game theory, the evolutionary dynamics of signaling strategies in females and males are written as follows:

$$\frac{dx_t}{dt} = \left(\frac{(1 - \alpha_1 + \alpha_2 P_x) F_x}{\beta_x} - \phi_x\right)x_t,$$  \hspace{1cm} (7-1)

$$\frac{dy_t}{dt} = \left(\frac{(1 - \alpha_1 + \alpha_2 P_y) F_y}{\beta_y} - \phi_y\right)y_t,$$  \hspace{1cm} (7-2)

where $\phi_x$ and $\phi_y$ represent the average fitness of females and males, respectively, in a population. Using the relationship $x_N = 1 - x_s$ and $y_N = 1 - y_s$, they are given as

$$\phi_x = \frac{x_s(1 - \alpha_1 + \alpha_2 P_x) F_x}{\beta_x} + (1 - x_s)(1 - \alpha_2 P_x) F_x,$$  \hspace{1cm} (8-1)

$$\phi_y = \frac{y_s(1 - \alpha_1 + \alpha_2 P_y) F_y}{\beta_y} + (1 - y_s)(1 - \alpha_2 P_y) F_y.$$  \hspace{1cm} (8-2)

The total number of offspring from females must be equal to the total number of offspring from males, which is equivalent to $\phi_x = \phi_y$. Here we define $F_s$ as a function of $x_s$ and $y_s$, as follows:

$$F_s(x_s,y_s) = \frac{x_s(1 - \alpha_1 + \alpha_2 P_s) / \beta_x + (1 - x_s)(1 - \alpha_2 P_s)}{y_s(1 - \alpha_1 + \alpha_2 P_s) / \beta_y + (1 - y_s)(1 - \alpha_2 P_s)} F_s.$$  \hspace{1cm} (9)

Later in this article, we show that $F_s$ and $F_s$ never appear in the analytically obtained conditions for the evolution of signaling.

Note that our evolutionary game model formally describes the situation where there are female- and male-specific strategies that are inherited only by females and males, respectively. However, such a simple model usually generates the same conditions for evolutionary stability of each genetic equilibrium as a genetic model assuming that (1) the female and male strategies are coded on two distinct autosomal loci, (2) an individual inherits two strategies regardless of its sex and expresses one depending on its sex, and (3) mating occurs randomly among genotypes (e.g., compare Wakano and Ihara [2005] and Seki et al. [2007], model 1). Equations (7) describe the frequency-dependent evolutionary dynamics. Each strategy increases (or decreases) if the fitness is higher (or lower) than the average. In the following, we analyze the evolution of signaling strategies by examining the equilibria and the stability of the equilibria of equations (7).

**Results**

**Monomorphic and Inter- and Intrasexually Dimorphic Equilibria Derived from the Evolutionary Dynamics of Signaling Strategies**

We derived the eight equilibria of equations (7), $(x_s^*, y_s^*)$, by setting $dx_t/dt = dy_t/dt = 0$ (table 2; app. A). Two equilibria are monomorphic, nonsignaling $(0, 0)$ or signaling $(1, 1)$.
Table 2: Summary of equilibrium type and condition for a valid evolutionarily stable state (ESS) for each of the eight equilibria \((x'_i, y'_j)\)

| \((x', y')\) | Type of equilibria | Condition for valid ESS | Requirement for ESS condition |
|-------------|-----------------|------------------------|-----------------------------|
| \((0, 0)\)  | Monomorphic     | \(\max\{Q_x, Q_y\} < 1\) | …                           |
| \((1, 1)\)  | Monomorphic     | \(\min\{Q_x, Q_y\} > \left(\frac{1}{\alpha_2}\right)^*\) | …                           |
| \((0, 1)\)  | Intersexually dimorphic\(^a\) | \(Q_x < \left(\frac{2}{1 + \alpha_2}\right)^*\) \(< Q_y\) | \(Q_x < Q_y\) |
| \((1, 0)\)  | Intersexually dimorphic\(^a\) | \(Q_y < \left(\frac{2}{1 + \alpha_2}\right)^*\) \(< Q_x\) | \(Q_y > Q_x\) |
| \((0, y)\)  | Intrasexually dimorphic\(^a\) | \(\max\{1, Q_x\} < Q_y < \left(\frac{2}{1 + \alpha_2}\right)^*\) | \(\alpha_2 < 1, Q_y < Q_x\) |
| \((x', 1)\) | Intrasexually dimorphic\(^a\) | \(\left(\frac{2}{1 + \alpha_2}\right)^*\) \(< Q_y < \min\left\{\left(\frac{1}{\alpha_2}\right)^*, Q_y\right\}\) | \(\alpha_2 < 1, Q_y < Q_x\) |
| \((x', 0)\) | Intrasexually dimorphic\(^a\) | \(\max\{1, Q_y\} < Q_x < \left(\frac{2}{1 + \alpha_2}\right)^*\) | \(\alpha_2 < 1, Q_y > Q_x\) |
| \((1, y)\)  | Intrasexually dimorphic\(^a\) | \(\left(\frac{2}{1 + \alpha_2}\right)^*\) \(< Q_y < \min\left\{\left(\frac{1}{\alpha_2}\right)^*, Q_x\right\}\) | \(\alpha_2 < 1, Q_y > Q_x\) |

\(^a\) Dimorphic equilibria can also be called free-riding equilibria when \(\alpha_2 < 1\).

In equilibria in which both females and males adopt the non-signaling or signaling strategy, respectively. The other six equilibria are dimorphic equilibria. At a dimorphic equilibrium, nonsignaling individuals can enjoy the collective benefit from signaling individuals without paying any cost when signaling gives a positive collective effect (i.e., when \(\alpha_2 < 1\)). The dimorphic equilibria can be classified into two types depending on whether dimorphism appears between the sexes or within the same sex. Intersexually dimorphic equilibria are \((0, 1)\) and \((1, 0)\), in which only all males or all females adopt a signaling strategy, respectively. There are four intrasexually dimorphic equilibria, \((0, y)\), \((1, y)\), \((x', 1)\), and \((x', 0)\), where \(x'_i, x'_j, y'_i\), and \(y'_j\) are given in appendix A. In the first equilibrium, \((0, y)\), a fraction \(y'_i\) of males emit signal and the rest of the males and all females do not emit signal, as in the case of *Acrida cinerea*. The other three intrasexually dimorphic equilibria also show such within-sex dimorphism in either females or males. In addition, a closed set of equilibria in which both sexes show dimorphism are found when female- and male-relevant parameters satisfy a special relationship (app. A).

We assessed the evolutionary stability of the eight equilibria with the sign of eigenvalues of the Jacobian of the system in equations (7) (app. A). By examining the conditions that both eigenvalues are negative, we derived the conditions when each equilibrium becomes locally stable. Under replicator dynamics, frequencies of strategies gradually approach the state corresponding to the locally stable equilibrium, and thus we call such a state an “evolutionarily stable state” (ESS). Depending on the magnitudes of the direct individual effect of signaling (\(\alpha_1\)) and the indirect collective effect of signaling (\(\alpha_2\)), a set of equilibria that can be evolutionarily stable varies.

**Positive Individual Effect Is Essential for the Evolution of Signaling**

When signaling has no or a negative individual effect (i.e., when \(\alpha_1 \geq 1\)), the nonsignaling equilibrium \((0, 0)\) is the single ESS regardless of the other parameter values, including the collective effect (app. A). The other monomorphic equilibrium, \((1, 1)\), and the two intrasexually dimorphic equilibria, \((0, 1)\) and \((1, 0)\), are unstable, and no intrasexually dimorphic equilibria exist. This indicates that a positive individual effect (i.e., \(\alpha_1 < 1\)) is the necessary condition for the evolution of signaling. Hereafter, we consider only the case of a positive individual effect.

**Monomorphism or Sexual Dimorphism Is Expected without a Collective Effect**

In the absence of any collective effect (i.e., when \(\alpha_2 = 1\)), exactly one of the four monomorphic or intersexually dimorphic equilibria—\((0, 0), (0, 1), (1, 0)\), and \((1, 1)\)—satisfies
the conditions for an ESS (fig. 2A; app. A), and none of the intrasexually dimorphic equilibria can be an ESS. A population gradually approaches the single ESS determined by the parameter values regardless of the initial frequencies of signaling and nonsignaling strategies (fig. 2B–2E).

To simply describe and interpret the analytical results presented below, we introduced two quantities, $Q_s$ and $Q_y$, that represent the canonical net individual benefit of signaling in females and males, respectively. In the absence of a collective effect, all females evolve to adopt nonsignaling and signaling strategies when $Q_s < 1$ and $Q_s > 1$, respectively, where

$$Q_s = \frac{\beta_x - \alpha_1}{\beta_x - 1} P_x. \tag{10}$$

Likewise, all males come to adopt nonsignaling and signaling strategies when $Q_s < 1$ and $Q_s > 1$, respectively, where

$$Q_y = \frac{\beta_y - \alpha_1}{\beta_y - 1} P_y. \tag{11}$$

The quantities $Q_s$ and $Q_y$ depend positively on the natural predation probability ($P_x$ and $P_y$) and the magnitude of the positive individual effect (i.e., smallness of $\alpha_1$), depend negatively on the fecundity cost for signaling ($\beta_x$ and $\beta_y$), and are independent of the magnitude of the collective effect ($\alpha_2$) or the number of neighboring conspecifics ($n$). Overall, $Q_s$ and $Q_y$ can be regarded as net individual benefit-to-cost ratios of signaling: signaling evolves in each sex if the net individual benefit-to-cost ratio is greater than a threshold, which is unity when there is no collective effect (app. A).

**A Positive Collective Effect Enables the Evolutionary Stability of Intrasexual Dimorphism**

In the presence of a positive collective effect (i.e., when $\alpha_2 < 1$), exactly one equilibrium satisfies the conditions for an ESS (fig. 3A; app. A). Unlike the case of $\alpha_2 = 1$, for a given parameter set at most two intrasexually dimorphic equilibria exist. An existing intrasexually dimorphic equilibrium can be a stable fixed point (fig. 3B, 3D) or a
saddle point (fig. 3D, 3E). Under the positive collective effect, inter- and intrasexually dimorphic equilibria contain nonsignaling individuals that, without paying any fecundity cost, enjoy the benefit of a positive collective effect provided from signaling individuals. Such an individual is called a "free rider" in the literature of game theory, and we call the six inter- and intrasexually dimorphic equilibria "free-riding equilibria" when $\alpha_2 < 1$.

The intrasexually dimorphic equilibrium $(0,y'_1)$ exists when the net individual benefit-to-cost ratio for males is sufficiently but not overly large ($1 < Q_x < [2/(1 + \alpha_2)]^2$; fig. 3A, 3B; app. A). Within this range of $Q_x$, signaling males always have greater fitness than nonsignaling males when all males do not signal (represented by equilibrium $(0,0)$) but lower fitness than nonsignaling males when all males do signal (represented by equilibrium $(0,1)$; app. B). The equilibrium $(0,y'_1)$ is a balancing point at which signaling and nonsignaling males share the same fitness value (app. B). It is an ESS when $Q_x < Q_*$ (app. A), which means that the net individual benefit-to-cost ratio of signaling is greater in males than in females. A detailed analysis revealed that the inequality $Q_x < Q_*$ also means that nonsignaling females have higher fitness than signaling females when all females do not signal and the fraction of signaling males is $y'_1$ (represented by equilibrium $(0,y'_1)$; app. B). This inequality is achieved when males have a higher natural predation probability than females ($P_x > P_y$) and/or have a lower signaling cost than females ($\beta_x > \beta_y$). When the opposite condition, $Q_x > Q_*$, is satisfied, the equilibrium $(0,y'_1)$ is unstable because it is a saddle point, and the population evolves to another equilibrium state including some or all signaling females and no signaling males, $(x'_1,0)$ or $(1,0)$ (fig. 3D, 3E). Note that the focal condition $Q_x > Q_*$ implies that nonsignaling males gain higher fitness than signaling males at the ESS (either $(x'_1,0)$ or $(1,0)$), leading to the male monomorphism. Using similar arguments, we can interpret existence and stability conditions for the other three intrasexually dimorphic (i.e., intrasexually free-riding) equilibria (app. B). In addition, the special case of $Q_1 = Q_*$ yields $x'_1 = y'_1 = 1 + x'_2 = 1 + y_2$ and a set of
ininitely many equilibria on the line connecting \((0, y_1^*)\) and \((x_1^*, 0)\) or \((1, y_1^*)\) and \((x_1^*, 0)\). Each of the equilibria shows the same total frequency of signaling individuals of \(x_1^*/2\) (=\(y_1^*/2\)), and a population approaches one of the equilibria depending on the initial frequencies of signaling females and males (fig. 3C). Therefore, dimorphism can be maintained simultaneously in both sexes if \(Q_x = Q_y\).

Comparing figure 2A and figure 3A, we can see that the positive collective effect does not expand the parameter region in which signaling can evolve. Alternatively, the positive collective effect allows nonsignaling individuals to coexist with signaling individuals in some parameter regions in which the nonsignaling individuals would become extinct without the positive collective effect. Specifically, \((0, y_1^*)\) and \((x_1^*, 0)\) are ESSs in the part of the parameter regions in which \((0, 1)\) and \((1, 0)\), respectively, are stable without the collective effect. The intersexually dimorphic equilibria \((1, 0)\) and \((1, 0)\) are, on the other hand, ESSs in some regions in which \((1, 1)\) is an ESS without the collective effect. The above-mentioned changes from figure 2A (\(\alpha_2 = 1\)) to figure 3A (\(\alpha_2 < 1\)) were accompanied by separation of the thresholds that depend on \(\alpha_2\) \([2/(1 + \alpha_2)]^+\) and \(\frac{1}{\alpha_2} \frac{1}{\alpha_2}^+\) from the constant threshold (1). Note that the threshold values \(1, \frac{2}{(1 + \alpha_2)}\), and \(\frac{1}{\alpha_2}\) are equal to the inverse numbers of \(\alpha_2\) (the expected magnitude of the collective effect on an individual) at the monomorphic nonsignaling equilibrium \((0, 0)\), at the intersexually dimorphic equilibria \((0, 1)\) and \((1, 0)\), and at the monomorphic signaling equilibrium \((1, 1)\), respectively. The region for the free-riding equilibrium is expanded (i.e., threshold values \([2/(1 + \alpha_2)]^+\) and \(\frac{1}{\alpha_2} \frac{1}{\alpha_2}^+\) are increased; the corresponding four border lines shown in fig. 3A move upward or rightward) as the magnitude of the positive collective effect increases (i.e., \(\alpha_2\) decreases) and/or population density \((n)\) increases. The absence of conspecifics within the effective range (i.e., \(n = 0\)), consistent with intuition, brings exactly the same results as the case of the absence of a collective effect (i.e., \(\alpha_2 = 1\)); intrasexually dimorphic equilibria cannot be an ESS, and one of \((0, 0)\), \((0, 1)\), \((1, 0)\), and \((1, 1)\) is stable.

**A Negative Collective Effect Can Lead to Multiple ESSs**

In the presence of a negative collective effect (i.e., when \(\alpha_2 > 1\)), a population evolves to either one of the four monomorphic or intersexually dimorphic equilibria—\((0, 0)\), \((0, 1)\), \((1, 0)\), and \((1, 1)\)—similarly to the case of no collective effect \((\alpha_2 = 1)\). The unique outcome from the negative collective effect is that two or three equilibria simultaneously satisfy conditions for an ESS (fig. 4A). When there is more than one ESS, a population approaches one of those ESSs depending on the initial population density of each signaling strategy (filled circles in fig. 4B–4E). Such bi- or tristable dynamics are accompanied by one or two intrasexually dimorphic equilibria. For example, \((0, y_1^*)\) exists whenever \((0, 0)\) and \((0, 1)\) are simultaneously stable (fig. 4C).

In the absence of signaling females, the population reaches to \((0, 0)\) and \((0, 1)\) when the initial density of signaling males are less and more, respectively, than \(y_1^*\). Therefore, \((0, y_1^*)\) is an evolutionary bifurcation point that determines the critical density for the evolution of a specific strategy set. Under a negative collective effect of signaling, all of the intrasexually dimorphic equilibria are always unstable (open circles in fig. 4B–4E). The bi- or tristable dynamics can occur among seven combinations of equilibria: \{\((0, 0), (0, 1)\}\), \{\((0, 0), (1, 0)\}\), \{\((0, 0), (1, 1)\}\} (fig. 4D, 4E), \{\((0, 1), (1, 1)\)\} (fig. 4B), \{\((1, 0), (1, 1)\)\}, \{\((0, 0), (0, 1), (1, 1)\)\} (fig. 4C), and \{\((0, 0), (1, 0), (1, 1)\)\}. Note that these are all of the possible combinations that do not simultaneously include \((0, 1)\) and \((1, 0)\), which have mutually incompatible ESS conditions (app. A).

The simultaneous existence of more than one ESS is observed in a marginal parameter region in which the net individual benefit-to-cost ratio of signaling, \(Q_x\), and/or \(Q_y\), takes intermediate values compared with the magnitude of the negative collective effect (i.e., \((1/\alpha_2)^+ < Q_x, Q_y < 1;\) fig. 4A; app. A). When the net individual benefit-to-cost ratio is below and beyond the intermediate range, the nonsignaling and signaling strategies, respectively, are better than the other strategy regardless of the behavior of other individuals.

Comparison of figure 2A and figure 4A indicates that the negative collective effect does and does not expand parameter regions in which signaling and nonsignaling individuals, respectively, can exist. Signaling is more favored for a stronger negative collective effect (i.e., larger \(\alpha_2\)) and a greater population density \((n)\) because threshold values \((1/\alpha_2)^+\) and \([2/(1 + \alpha_2)]^+\) are decreased, and the corresponding four border lines in figure 4A move downward or leftward. Notably, the region in which the monomorphic signaling equilibrium \((1, 1)\) is the single ESS is expanded by a negative collective effect.

**Negative and Positive Feedback between Frequency of Signaling Individuals and Efficiency of Signaling**

Stable intrasexual dimorphism in the signaling behavior, which occurs only when there is a positive collective effect of signaling \((\alpha_2 < 1)\), is driven by a negative feedback between the relative fitness of signaling individuals compared with nonsignaling ones and the frequency of signaling individuals, as explained below. To intuitively understand the negative feedback, consider an extreme case of \(P_1 = 1\) and \(\alpha_2 < 1\) and then the two marginal situations in which a female is surrounded by no and \(n\) signaling individuals. If the focal female does not emit signals, predation probabilities are calculated as \(\alpha_2^2 P_1 = 1\) and \(\alpha_2^2 P_1 \approx 0\) in the former and latter situations, respectively. If the focal female emits
signals at a cost of reduced fertility, predation risk is further suppressed by the individual effect $\alpha_1$ (e.g., $\alpha_1 = 0.5$). In the former situation, the predation risk is significantly reduced (from 100% to 50%). In the latter situation, on the other hand, the reduction is negligible because the predation risk is low enough as a result of the collective effect only. Therefore, the signaling strategy is favored when there is a low frequency of signaling individuals, while the nonsignaling strategy is favored when many other individuals emit signals. In general, the relative fitness of the signaling strategy to that of the nonsignaling strategy is a decreasing function of the frequency of signaling individuals if $\alpha_1 < 1$ and $\alpha_2 < 1$ (app. A). Therefore, an increase in the frequency of signaling individuals due to the fitness advantage of the signaling strategy gradually reduces the degree of advantage, which is called “negative feedback.” Under negative feedback, there may be a stable balancing point at which signaling and nonsignaling females have the same fitness.

The mechanism resulting in the bi- or tristable dynamics, which are found when there is a negative collective effect of signaling ($\alpha_1 > 1$), is a positive feedback between the relative fitness of signaling individuals and the frequency of signaling individuals. It may be a better choice for an individual to emit a costly signal than not to only when the focal individual is surrounded by signaling individuals, which impose a high risk of predation on the focal individual because of the negative collective effect. Formal analysis revealed that the relative fitness of the signaling strategy to that of the nonsignaling strategy is an increasing function of the frequency of signaling individuals under $\alpha_1 < 1$ and $\alpha_2 > 1$ (app. A). There may be a balancing point, that is, as opposed to the case of $\alpha_1 < 1$, an unstable bifurcation point.

**Discussion**

We have addressed why prey animals show inter- and intrasexual dimorphism in their signaling strategy during escape by developing and analyzing the evolutionary dynamics of signaling and nonsignaling strategies in the prey population. The model, which assumes that a conspicuous

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**Figure 4:** Phase diagrams for evolutionary consequences under negative collective effect of signaling (i.e., $\alpha_2 > 1$). A. Division of the parameter space according to the evolutionarily stable equilibria. The horizontal and vertical axes represent the net individual benefit-to-cost ratios of signaling for females, $Q_x = (\beta_x - \alpha_1)P_x/(\beta_x - 1)$, and males, $Q_y = (\beta_y - \alpha_2)P_y/(\beta_y - 1)$, respectively. The general algebraic forms of thresholds are shown on the phase diagram using parameter values $\alpha_x = 1.2$ and $n = 2$. Open circles mark the sets of parameter values used to obtain B–E. B–E, Sample trajectories of evolutionary dynamics plotted on the phase plane in which the horizontal and vertical axes are the frequencies of signaling females ($x_s$) and males ($y_s$), respectively. Red and blue lines indicate nullclines satisfying $dx_s/dt = 0$ (no change in the frequencies of female strategies) and $dy_s/dt = 0$ (no change in the frequencies of male strategies), respectively. Filled and open circles indicate stable and unstable equilibria, respectively. Parameter values are as follows: $\alpha_1 = 1.2$, $n = 2$, $\beta_x = 1.4$, $\beta_y = 1.3$, and $P_x = 0.5$; B, $\alpha_1 = 0.78$ and $P_y = 0.6$, with which (0, 1) and (1, 1) are stable; C, $\alpha_1 = 0.78$ and $P_y = 0.5$ ($= P_x$), with which (0, 0), (0, 1), and (1, 1) are stable; D, $\alpha_1 = 0.78$ and $P_y = 0.46$, with which (0, 0) and (1, 1) are stable; and E, $\alpha_1 = 0.72$ and $P_y = 0.5$ ($= P_x$), with which (0, 0) and (1, 1) are stable.
signal may positively or negatively affect survivorship of the signaler itself (individual effect) and survivorship of neighboring individuals (collective effect), indicated that signaling can evolve only when the signal has a positive individual effect. Under a positive individual effect, different magnitudes of the collective effect yield different types of evolutionarily stable equilibrium states. The state in which all individuals in each sex take either the signaling strategy or the non-signaling strategy can be evolutionarily stable without a collective effect. Signalers and nonsignalers can coexist within one sex when the signal decreases the predation risk of individuals around the signaler, that is, when signaling has a positive collective effect. Coexistence occurs when a nonsignerer (which does not gain a positive individual effect of signaling, unlike a signaler) enjoys a sufficiently greater benefit of the positive collective effect than a signaler (app. B).

In addition to the individual and collective effects, the net individual benefit-to-cost ratio of signaling affects the types of signal usage in males and females. The antipredator signal can evolve more easily in the sex whose net individual benefit-to-cost ratio of signaling is higher than that of the other sex. Males are usually the sex that explores their mates and thus suffer a higher predation risk (Magnhagen 1991). Females will suffer a higher signaling cost if the body movement for signaling requires higher energy because of the heavy eggs they hold. Thus, the net individual benefit-to-cost ratio of signaling is considered to be larger in males, and the evolution of signaling will be easier in males. A recent literature survey on the defensive sounds of insects by Low, Naranjo, and Yack (2021) suggested that males are usually the ones that use antipredator signals when only one sex in a species signals. Part of our findings is consistent with those of previous studies of sexual dimorphism demonstrating that the intrinsic differences between sexes brings dimorphic niches of traits, leading to the evolution of sexual dimorphism (Lande 1980; Rice 1984; Slatkin 1984). Our model, unlike previous models focusing on sexual dimorphism, also predicts dimorphism in one sex and monomorphism in the other by considering a collective effect that may be induced by the antipredator signal.

The density of the conspecifics can also affect the evolution of signaling. If the signaling provides a positive collective effect to conspecifics, an increase in the population density promotes the invasion of free-riding, nonsignaling individuals. On the other hand, when the density is so low that no conspecifics interact with each other, neither state in which only a part of the male or female population emits signal is evolutionarily stable. Our model predicts differences in the proportion of signaling males and females between populations with different population densities. The Chinese grasshopper, Acrida cinerea, seems to be suitable for testing this prediction because its population density is likely to vary in Japan depending on habitat size, which ranges from large city parks to small school grounds (Enju 2017).

Our model provides insight into the function of conspicuous sound produced by flying grasshoppers during escape from predators. Grasshoppers in Acridinae, Gomphocerinae, and Oedipodinae often emit conspicuous sounds while flying, which is called “crepitation” (Otto 1984). Crepitation is also observed during flights for escaping (Willey and Willey 1969; Capinera et al. 2001). The conspicuous escape of grasshoppers has been considered beneficial for avoiding predatory attacks (Edmunds 1974), although empirical evidence has been insufficient. In A. cinerea, about 70% of males escape conspicuously from an approach by a human observer, whereas females always escape inconspicuously (T. Kuga and E. Kasuya, unpublished data). This type of sexual dimorphism in signaling frequency requires a higher cost of signaling and/or a lower natural predation probability in females relative to males in the model as well as both a positive individual effect and a positive collective effect of signaling. In general, the body size of female grasshoppers is larger than that of males (Whitman 2008), which holds true for A. cinerea (Murai and Ito 2011). Because additional movement will be necessary to make conspicuous sounds during flight (Lorier et al. 2002), the larger body size in females should require more energy sources for signaling, resulting in a higher cost of signaling. Further studies are needed to clarify the biological process underlying the decrease in the probability of predation, modeled as the individual and collective benefits of signaling. We note that the same results are obtained in the extended model, which allows the use of mixed strategies: the males escape conspicuously with certain probabilities, and females always escape inconspicuously (supplemental PDF). This is more realistic in the case of A. cinerea because an individual male often shows both a conspicuous escape and an inconspicuous escape when it is approached repeatedly (T. Kuga and E. Kasuya, unpublished data).

Our model also indicates that dimorphism in both females and males, which has been reported for lizards (Bohórquez Alonso et al. 2010; Font et al. 2012) and mountain katydids (De Bona et al. 2020), can be evolutionarily stable when signaling has a positive collective effect. However, the stable dimorphism in both sexes requires a special condition that signaling provide the same net individual benefit-to-cost ratio to a signaling individual regardless of its sex. When this ecologically feasible yet special condition is not satisfied, the present model predicts that dimorphism is maintained only in one sex.

Our models can explain the sex differences in defensive signals by solitary animals other than the grasshopper, katydid, and lizard, as described above. For example, the distress call of Neotropical anuran species was observed in only some males, only some females, or some males and females
The observation indicated that the distress call may also be observed in all females and some males or in all females and males in the Neotropical anuran species. Our model could also provide a new insight into the evolution of plant-plant interaction by airborne signals. Volatile organic compounds (VOCs), which are released from damaged plants by herbivores or pathogens, can trigger specific defensive responses in neighboring plants of various species (Heil and Karban 2010). The evolution of VOC signaling could be explained by the relative importance of individual interactions and the collective effects of the VOC signaling. Note that we have considered intersex differences and intrasex homogeneity in the net individual benefit-to-cost ratio of signaling. The present model outcomes suggest the existence of a general rule that dimorphism in antipredator signaling occurs between two classes having different net individual benefit-to-cost ratios of signaling. The two classes were sexes in this model, but they could be two genotypes, each of which consists of both females and males. In that case, fixation of antipredator signal in one genotype will be accompanied by dimorphism in both sexes. Further studies are required to clarify this point.

We note that predators are not incorporated as players into the present evolutionary game model, and thus prey animals receive a fixed reaction from predators throughout generations. Assuming a fixed reaction of predators to the evolution of signaling modeled here might be feasible in the case of A. cinerea. In general, grasshoppers have various species of predators (Belovsky et al. 1990), and interactions between a specific pair of a grasshopper individual and a predator species seem to be not very frequent. That may mean that the grasshopper has few chances to alter its behavior depending on the reaction of predators. However, two extensions are possible to treat predators as players.

First, the effectiveness of signaling may relate to the learning or habituation of predators. Conspicuous antipredatory signals may act effectively after predators learn the relationship between the signal and the unprofitability of the signaler (Mappes et al. 2014; Cyriac and Kodandaramaiah 2019) or act ineffectively after predators habituate to the conspicuousness of signaling (Umbers et al. 2019). Thus, the values of the individual and collective effects of signaling may change depending on the frequency of signaling individuals because a high frequency of signalers can accelerate learning and habituation. Additionally, the frequency of the signaler may change the relative fitness of attacking and nonattacking strategies of predators and thus may change the effectiveness of signaling.

Second, the number of predators may affect the evolution of signaling. Predator-prey dynamics are affected by the coevolution of predator and prey traits and vice versa (van Velzen and Gaedke 2017; Govaert et al. 2019). Our study emphasizes the importance of prey-prey interactions in signaling strategies, which are often neglected in the co-evolution model (e.g., Cortez and Weitz 2014; van Velzen and Gaedke 2017). Additionally, the density of prey population may change over time through predator-prey dynamics, which could be affected by the frequency of signaling individuals in each generation. For example, consider the case where signaling has a positive collective effect and a high frequency of signaling individuals has positive effects on the growth of the prey population. A small population with many signaling individuals can increase, which may allow invasion of free-riding, nonsignaling individuals because of the increased population density (see above). That may, in turn, lead to population decline, and it is of great interest to consider which one of the two possible goals—extinction of the free riders and extinction of the prey population—will be achieved. Such complex eco-evolutionary dynamics should be analyzed in future studies.

There is also room for prey-prey interactions in future studies. Although one outcome of the present model was that a purely altruistic signal (i.e., a signal that shows a negative individual effect and a positive collective effect) never evolves, some group-living animals are thought to emit altruistic alarm calls (Caro 2005). The theory of kin selection predicts that such altruistic signaling can evolve if a prey emits the signal only when it is surrounded by its relatives (Hamilton 1964). Altruistic alarm calls may also evolve if they are coupled with the mechanism of reciprocal altruism (Trivers 1971; Krams et al. 2008). The green beard effect, which refers to the situation where an individual behaves altruistically only to individuals of a certain phenotype (such as those with a green beard) and is now studied within the general framework of indirect genetic effects (Wolf et al. 1998; McGlothlin et al. 2010), can also lead to the evolution of altruistic alarm calls. In any of these mechanisms, the free-rider problem should be more severe than in the present study, and it is of great interest to investigate whether polymorphism in altruistic signaling can be maintained.

Another possible extension is to consider the effect of the sex ratio of the prey population on the evolution of polymorphism in signaling behavior. Although we have focused on prey with an even sex ratio in this study, various species show a biased sex ratio (West et al. 2002). Moreover, sex differences in predation risk might directly lead to a change in the sex ratio until the reproductive season. Future theoretical studies are required to examine whether the dimorphic states can be evolutionarily stable even after incorporating the sex ratio as an additional factor.

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Statement of Authorship
A.S. and M.S. initiated the development of the model. T.K. and E.K. provided significant input to improve the model from a biological viewpoint. A.S. and M.S. analyzed the model. M.S. and T.K. visualized the results. T.K. and M.S. brought biological interpretations to the results with the help of A.S. and E.K. All authors contributed to writing and revising the manuscript.

APPENDIX A

Local Stability Conditions for Equilibria

Using $Q_s$ and $Q_p$, defined by equations (10) and (11), respectively, equations (7) describing the replicator dynamics in the present model are further transformed to

$$\frac{dx_i}{dt} = F_i(\beta_i - 1)\alpha_{i}, x_i (1 - x_i) \left( Q_s - \frac{1}{\alpha_s} \right),$$  \hspace{1cm} (A1-1)

$$\frac{dy_i}{dt} = F_i(\beta_i - 1)\alpha_{i}, y_i (1 - y_i) \left( Q_p - \frac{1}{\alpha_p} \right).$$  \hspace{1cm} (A1-2)

Equation (A1-1) shows that the frequency of signaling females increases and decreases when $1/\alpha_s$, a function ranging from 1 (when $x_s = y_s = 0$; see eq. (3)) to $(1/\alpha_s)^*$ (when $x_s = y_s = 1$), is smaller and greater, respectively, than the parameter-dependent constant $Q_s$, defined by equation (10). The quantity $1/\alpha_s$ is constant if $\alpha_s = 1$, a monotonically increasing function of $x_s + y_s$ if $\alpha_s < 1$, or a monotonically decreasing function of $x_s + y_s$ if $\alpha_s > 1$. Equation (A1-2) is the male version of the above and is similarly interpreted. The system has the following three nullclines for $x_s$ on which $dx_s/dt = 0$ holds and thus no change in $x_s$ occurs: $x_s = 0, x_s = 1$, and a line satisfying

$$Q_s - \frac{1}{\alpha_s(x_s, y_s)} = 0 \Leftrightarrow x_s + y_s = \frac{2}{1 - \frac{1}{\sqrt{Q_s}}}. \hspace{1cm} (A2)$$

where the double arrow means “if and only if.” Similarly, the system has the three nullclines for $y_s$: $y_s = 0, y_s = 1$, and a line satisfying

$$x_s + y_s = \frac{2}{1 - \frac{1}{\sqrt{Q_s}}}. \hspace{1cm} (A3)$$

The two lines (A2) and (A3) are identical if $Q_s = Q_p$ and are parallel otherwise (i.e., if $Q_s \neq Q_p$). Below in this appendix, we mainly describe the case of $Q_s \neq Q_p$ and mention the special case of $Q_s = Q_p$ in the last part.

An equilibrium of the replicator dynamics, $(x'_i, y'_i)$, is a point satisfying $dx_i/dt = dy_i/dt = 0$ and thus is an intersection of a nullcline for $x_i$ and one for $y_i$. We obtained the following eight single-point equilibria:

$$(x'_s, y'_s) = \{(0, 0), (0, 1), (1, 0), (1, 1), (0, y'_1), (1, y'_1), (x'_s, 0), (x'_s, 1)\}, \hspace{1cm} (A4-1)$$

where

$$y'_1 = \frac{2}{1 - \alpha_2} \left( 1 - \frac{1}{\sqrt{Q_p}} \right), \hspace{1cm} (A4-2)$$

$$y'_2 = \frac{2}{1 - \alpha_2} \left( \frac{1 + \alpha_2}{2} - \frac{1}{\sqrt{Q_p}} \right), \hspace{1cm} (A4-3)$$

$$x'_1 = \frac{2}{1 - \alpha_2} \left( 1 - \frac{1}{\sqrt{Q_p}} \right), \hspace{1cm} (A4-4)$$

$$x'_2 = \frac{2}{1 - \alpha_2} \left( \frac{1 + \alpha_2}{2} - \frac{1}{\sqrt{Q_p}} \right). \hspace{1cm} (A4-5)$$

The above equilibrium frequencies of signaling females and males are greater for greater values of $Q_s$ and $Q_p$, respectively. Note that $y'_1 = 1 + y'_2$, which means that the two within-male dimorphic equilibria $(0, y'_1)$ and $(1, y'_2)$ share the same total frequency of signaling individuals. The identity $y'_1 = 1 + y'_2$ also implies that $0 < y'_1 < 1$ and $0 < y'_2 < 1$ do not simultaneously hold, and thus these equilibria cannot simultaneously exist within the biologically feasible range. A similar relationship is found for the two within-female dimorphic equilibria: $x'_1 = 1 + x'_2$. The first four of (A4-1) always exist regardless of the parameter values. Local stability conditions of these equilibria, which are evaluated with the sign of eigenvalues of the Jacobian of the system in equations (7) (tables A1, A2), are summarized as follows:

$$(0, 0): \max\{Q_s, Q_p\} < 1, \hspace{1cm} (A5-1)$$

$$(0, 1): \quad Q_s < \left( \frac{2}{1 + \alpha_2} \right)^* < Q_p, \hspace{1cm} (A5-2)$$

$$(1, 0): \quad Q_p < \left( \frac{2}{1 + \alpha_2} \right)^* < Q_s, \hspace{1cm} (A5-3)$$

$$(1, 1): \min\{Q_s, Q_p\} > \left( \frac{1}{\alpha_2} \right)^*. \hspace{1cm} (A5-4)$$

Note that the conditions (A5-2) and (A5-3) are mutually incompatible, and thus the two intersex free-riding equilibria
which is satisfied in case 2. The second condition is

\[(0, y'_1) \text{ and } (x'_1, 1): Q_s < Q_y, \quad (A8-1)\]

\[(1, y'_1) \text{ and } (x'_1, 0): Q_s > Q_y, \quad (A8-2)\]

Simultaneously considering (A5), (A6), and (A8), we find that exactly one equilibrium is stable for a given parameter set when \(\alpha_s < 1\), as summarized in figure 3A. Note that when an unstable intrasexually dimorphic equilibrium exists, the corresponding Jacobian has positive and negative eigenvalues (table A1). The equilibrium is thus a saddle point: attracting within one sex while repelling if considering both sexes.

Case 3. In the presence of a negative collective effect (i.e., when \(\alpha_s > 1\)), \((1/(\alpha_s) - 2/(1 + \alpha_s)) < 1\) holds. The four intrasexually dimorphic equilibria exist if the following conditions are satisfied:

\[(0, y'_1): \left(\frac{2}{1 + \alpha_s}\right)^n < Q_s < 1, \quad (A9-1)\]

\[(1, y'_1): \left(\frac{1}{\alpha_s}\right)^n < Q_s < \left(\frac{2}{1 + \alpha_s}\right)^n, \quad (A9-2)\]

\[(x'_1, 0): \left(\frac{2}{1 + \alpha_s}\right)^n < Q_s < 1, \quad (A9-3)\]

\[(x'_1, 1): \left(\frac{1}{\alpha_s}\right)^n < Q_s < \left(\frac{2}{1 + \alpha_s}\right)^n. \quad (A9-4)\]

Note that the conditions (A9-1) and (A9-2), as well as the conditions (A9-3) and (A9-4), are mutually incompatible. In this case, an intrasexually dimorphic equilibrium exists as an unstable evolutionary bifurcation point because one stability condition, (A7), is not satisfied. Evaluating (A5) under the condition \(\alpha_s > 1\), we find that more than one of the always-existing equilibria can be simultaneously stable. The two intersexually dimorphic equilibria, \((0, 1)\) and \((1, 0)\), cannot be simultaneously stable, as shown above, and all of the other pairs and two trios of equilibria, \{\((0, 0), (0, 1), (1, 1)\}\} and \{\((0, 0), (1, 0), (1, 1)\}\}, can be simultaneously stable.

In any of the above-described cases, a positive individual effect (\(\alpha_s < 1\)) is necessary for the stable existence of signaling individuals. Otherwise (i.e., if \(\alpha_s \geq 1\)), we can show that no intrasexually dimorphic equilibria exist and the monomorphic nonsignaling equilibrium \((0, 0)\) is the exclusive ESS. The negative individual effect \(\alpha_s \geq 1\) yields \(Q_s \leq P_s < 1\) and \(Q_s \leq P_s < 1\), and thus \((0, 0)\) is stable. Under a negative collective effect (i.e., \(\alpha_s > 1\); case 3), in which signaling without a positive individual effect (i.e., \(\alpha_s \geq 1\)) is regarded as a costly harassment to other conspecifics, we need an additional condition of \(\max\{Q_s, Q_y\} < (1/\alpha_s)^n\) to show that

(0, 1) and (1, 0) cannot be stable simultaneously. It is necessary that males rather than females gain greater net individual benefit by signaling (i.e., \(Q_s < Q_y\)) for the female-nonsignaling–male-signaling equilibrium \((0, 1)\) to be stable. On the other hand, \(Q_s > Q_y\) is necessary for the female-signaling–male-nonsignaling equilibrium \((1, 0)\) to be stable.

For the second four of (A4-1), intrasexually dimorphic equilibria, to be biologically feasible states, equilibrium values for the frequency of signaling females and males, \(x_s^*\) and \(y_s^*\), have to be between 0 and 1. The conditions for existence of these intrasexually dimorphic equilibria are described as inequalities including \(Q_s\) or \(Q_y\) and the three threshold values of \((1/\alpha_s)^n\), \([2/(1 + \alpha_s)]^n\), and 1, which appeared in (A5). Below we consider the three cases according to the value of \(\alpha_s\), which determines whether \((1/\alpha_s)^n\) is equal to, smaller than, or greater than 1.

Case 1. In the absence of a positive or negative collective effect (i.e., when \(\alpha_s = 1\)), \([2/(1 + \alpha_s)]^n = (1/\alpha_s)^n = 1\) holds. None of the four intrasex free-riding equilibria exist (observe that the denominators of \(y_s^*, y_s^*, x_s^*, x_s^*\) in (A4) become zero when \(\alpha_s = 1\)), and only one of \((0, 0), (0, 1), (1, 0),\) and \((1, 1)\) is stable for a given parameter set. Female and male signaling strategies are stable if \(Q_s > 1\) and \(Q_s > 1\), respectively, and female and male nonsignaling strategies are stable if \(Q_s < 1\) and \(Q_s < 1\), respectively.

Case 2. In the presence of a positive collective effect (i.e., when \(\alpha_s < 1\)), \(1 < [2/(1 + \alpha_s)]^n < (1/\alpha_s)^n\) holds. The following inequalities need to be satisfied for the existence of the four intrasexually dimorphic equilibria:

\[(0, y'_1): 1 < Q_s < \left(\frac{2}{1 + \alpha_s}\right)^n, \quad (A6-1)\]

\[(1, y'_1): \left(\frac{2}{1 + \alpha_s}\right)^n < Q_s < \left(\frac{1}{\alpha_s}\right)^n, \quad (A6-2)\]

\[(x'_1, 0): 1 < Q_s < \left(\frac{2}{1 + \alpha_s}\right)^n, \quad (A6-3)\]

\[(x'_1, 1): \left(\frac{2}{1 + \alpha_s}\right)^n < Q_s < \left(\frac{1}{\alpha_s}\right)^n. \quad (A6-4)\]

Note that (A6-1) and (A6-2) are mutually incompatible, and so are (A6-3) and (A6-4). When (A6-1) holds and \((0, y'_1)\) exists, we can show from (A5-1) and (A5-2) that \((0, 0)\) and \((0, 1)\) are unstable. The other three conditions also mean that one monomorphic equilibrium and one intersexually dimorphic equilibrium are unstable. An existing intrasex free-riding equilibrium is stable if two additional conditions are satisfied (table A2). The first condition is

\[\alpha_s < 1, \quad (A7)\]
the other equilibria cannot be ESSs. The model restrictions on predation probabilities, \( \alpha_1\alpha_2 P_x < 1 \) and \( \alpha_1\alpha_2 P_y < 1 \), yields

\[
Q_x = \frac{\beta_x - \alpha_1}{\beta_x - 1} \cdot P_x < \frac{\beta_x - \alpha_1}{\beta_x - 1} \cdot \frac{1}{\alpha_1\alpha_2} = \frac{\beta_x - \alpha_1}{\alpha_x(\beta_x - 1)} \cdot \left( \frac{1}{\alpha_x} \right)^n \leq \left( \frac{1}{\alpha_x} \right)^n
\]

(A10)

and \( Q < (1/\alpha_2)^n \), respectively. Overall, regardless of the values of \( \alpha_x \), the monomorphic nonsignaling equilibrium \((0, 0)\) is the exclusively stable state if \( \alpha_1 \geq 1 \). Existence and behavior of intrasex equilibria in each of the three cases are summarized in table A3.

In the end, consider the special case of \( Q_x = Q_y = Q \). We find a closed set, \( S \), of infinitely many equilibria, \((\hat{x}, \hat{y}) \in S\), on the overlapped nullcline of (A2) and (A3). A part of them exist within the biologically feasible range of \( 0 < x_1 < 1 \) and \( 0 < y_1 < 1 \) if \( 0 < (\hat{x} + \hat{y})/2 < 1 \), yielding

\[
\left\{ \begin{array}{l}
1 < Q < \left( \frac{1}{\alpha_2} \right)^n \quad \text{for } \alpha_1 < 1, \\
\left( \frac{1}{\alpha_2} \right)^n < Q < 1 \quad \text{for } \alpha_1 > 1.
\end{array} \right.
\]

(A11)

Both ends of the segment \( S \) are \((0, y_1')\) and \((x_1', 0)\) if \( Q \) is between 1 and \([2/(1 + \alpha_2)]^n\) and are \((1, y_1')\) and \((x_1', 1)\) if \( Q \) is between \([2/(1 + \alpha_2)]^n\) and \((1/\alpha_2)^n\). Nullcline analyses reveal that an existing \( S \) is, as a set, stable if \( \alpha_1 < 1 \) and unstable if \( \alpha_1 > 1 \). In the latter case, the two monomorphic equilibria, \((0, 0)\) and \((1, 1)\), are simultaneously stable.

| \((x_1', y_1')\) | \(\lambda_1\) | \(\lambda_2\) |
|-----------------|-------------|-------------|
| \((0, 0)\)     | \(- (\beta_x - 1) + (\beta_x - \alpha_1)P_x / \beta_x\) | \(- (\beta_x - 1) + (\beta_x - \alpha_1)P_x / \beta_x\) |
| \((0, 1)\)     | \(- (\beta_x - 1) + \left( \frac{1 + \alpha_2}{2} \right)^n (\beta_x - \alpha_1)P_x / \beta_x\) | \(\left( \frac{\beta_x - 1}{1 + \alpha_2} \right)^n (\beta_x - \alpha_1)P_x / \beta_x\) |
| \((1, 0)\)     | \(\left( \frac{\beta_x - 1}{1 + \alpha_2} \right)^n (\beta_x - \alpha_1)P_x / \beta_x\) | \(- (\beta_x - 1) + \left( \frac{1 + \alpha_2}{2} \right)^n (\beta_x - \alpha_1)P_x / \beta_x\) |
| \((1, 1)\)     | \(\left( \frac{\beta_x - 1}{1 + \alpha_2} \right)^n (\beta_x - \alpha_1)P_x / \beta_x\) | \(\left( \frac{\beta_x - 1}{1 + \alpha_2} \right)^n (\beta_x - \alpha_1)P_x / \beta_x\) |
| \((0, y_1')\)  | \(- (\beta_x - 1) + (\beta_x - \alpha_1)P_x / (\beta_x - \alpha_1)P_y / \beta_x\) | \(- 1/2 y'_1(1 - y'_1)(1 - \alpha_2) \cdot \left( \frac{\beta_x - \alpha_1}{\beta_x - 1} \right) / \beta_x\) |
| \((1, y_1')\)  | \(\left( \frac{\beta_x - 1}{1 + \alpha_2} \right)^n (\beta_x - \alpha_1)P_x / (\beta_x - \alpha_1)P_y / \beta_x\) | \(- 1/2 y'_1(1 - y'_1)(1 - \alpha_2) \cdot \left( \frac{\beta_x - \alpha_1}{\beta_x - 1} \right) / \beta_x\) |
| \((x_1', 0)\)  | \(- 1/2 x'_1(1 - x'_1)(1 - \alpha_2) \cdot \left( \frac{\beta_x - \alpha_1}{\beta_x - 1} \right) / \beta_x\) | \(- (\beta_x - 1)(\beta_x - \alpha_1)P_x / (\beta_x - \alpha_1)P_x - (\beta_x - 1) / \beta_x\) |
| \((x_1', 1)\)  | \(- 1/2 x'_1(1 - x'_1)(1 - \alpha_2) \cdot \left( \frac{\beta_x - \alpha_1}{\beta_x - 1} \right) / \beta_x\) | \(- (\beta_x - 1)(\beta_x - \alpha_1)P_x / (\beta_x - \alpha_1)P_x + (\beta_x - 1) / \beta_x\) |
In this appendix, we give biological interpretations of the conditions obtained above. We first define $R_s$ and $R_c$ as the ratios of the fitness of signaling females and males to those of nonsignaling ones, respectively:

$$ R_s = \frac{1 - \alpha_s \bar{P}_s}{(1 - \bar{P}_s)\bar{P}_s}, \quad (B1-1) $$

$$ R_c = \frac{1 - \alpha_c \bar{P}_c}{(1 - \bar{P}_c)\bar{P}_c}, \quad (B1-2) $$

where the double arrows mean “if and only if.” The quantities $Q_s$ and $Q_c$ consist of parameters relevant to the individual effect of signaling ($\alpha_s$, $\beta_s$, $P_s$, and $P_c$) and, as mentioned in the main text, are interpreted as the benefit-to-cost ratios of the individual effect for females and males, respectively. The variable $\bar{\alpha}_s$ includes the other parameters representing the collective effect of signaling ($\bar{\alpha}_s$ and $n$) and equals 1 when there is no collective effect (i.e., when $\alpha_s = 1$, $n = 0$, or $x_s = y_s = 0$).

Equation (3) gives the value of $\bar{\alpha}_s$ at each equilibrium state as follows:

$$ (0, 0): \quad \frac{1}{\alpha_s} = 1, \quad (B3-1) $$

$$ (0, 1) \text{ and } (1, 0): \quad \frac{1}{\alpha_s} = \left(\frac{2}{1 + \alpha_s}\right)^{\pi}, \quad (B3-2) $$

**APPENDIX B**

**Biological Interpretation of the Mathematically Obtained Conditions and Negative and Positive Feedback Mechanisms**

Table A2: Lists of conditions when two eigenvalues of the system ($\lambda_1$ and $\lambda_2$) are negative for each of the eight equilibria $(x_i^*, y_i^*)$

| $(x_i^*, y_i^*)$ | $\lambda_1 < 0$ | $\lambda_2 < 0$ | $Q_s < Q_c$ | $Q_s > Q_c$ |
|------------------|----------------|----------------|------------|------------|
| $(0, 0)$         | $Q_s < 1$      | $Q_s < 1$      | $Q_s < 1$  | $Q_s < 1$  |
| $(0, 1)$         | $Q_s < \left(\frac{2}{1 + \alpha_s}\right)^{\pi}$ | $Q_s > \left(\frac{2}{1 + \alpha_s}\right)^{\pi}$ | $\left\{ Q_s < \left(\frac{2}{1 + \alpha_s}\right)^{\pi}, \quad \left\} Q_s > \left(\frac{2}{1 + \alpha_s}\right)^{\pi} \right.$ | Unstable |
| $(1, 0)$         | $Q_s > \left(\frac{2}{1 + \alpha_s}\right)^{\pi}$ | $Q_s < \left(\frac{2}{1 + \alpha_s}\right)^{\pi}$ | Unstable | \left\{ Q_s > \left(\frac{2}{1 + \alpha_s}\right)^{\pi}, \quad \left\} Q_s < \left(\frac{2}{1 + \alpha_s}\right)^{\pi} \right.$ |
| $(1, 1)$         | $Q_s > \left(\frac{1}{\alpha_s}\right)^{\pi}$ | $Q_s > \left(\frac{1}{\alpha_s}\right)^{\pi}$ | $Q_s > \left(\frac{1}{\alpha_s}\right)^{\pi}$ | $Q_s > \left(\frac{1}{\alpha_s}\right)^{\pi}$ |

| $(0, y_1^*)$     | $Q_s < Q_c^*$ | $\alpha_s < 1$ when $0 < y_1^* < 1$ | $\alpha_s < 1$ when $(0, y_1^*)$ exists | Unstable |
| $(1, y_1^*)$     | $Q_s > Q_c^*$ | $\alpha_s < 1$ when $0 < y_1^* < 1$ | $\alpha_s < 1$ when $(1, y_1^*)$ exists | $\alpha_s < 1$ when $(1, 0)$ exists |
| $(x_2^*, 0)$     | $\alpha_s < 1$ when $0 < x_2^* < 1$ | $Q_s > Q_c$ | Unstable | $\alpha_s < 1$ when $(x_2^*, 0)$ exists |
| $(x_2^*, 1)$     | $\alpha_s < 1$ when $0 < x_2^* < 1$ | $Q_s < Q_c$ | $\alpha_s < 1$ when $(x_2^*, 1)$ exists | Unstable |

$^*$ An existing intrasexually dimorphic equilibrium is always attracting within the focal sex.

$^a$ An intrasexually dimorphic equilibrium is always repelling within the focal sex.

In this appendix, we give biological interpretations of the conditions obtained above. We first define $R_s$ and $R_c$ as the ratios of the fitness of signaling females and males to those of nonsignaling ones, respectively:
Equations (B2) and (B3-1) show that the ESS condition for the monomorphic nonsignaling equilibrium \((x_0, y_0) = (0, 0)\) in (A5-1), \(Q_1 < 1\) and \(Q_2 < 1\), is equivalent to \(R_1 < 1\) and \(R_2 < 1\) at \((0, 0)\), which means that signaling females and males gain lower fitness than nonsignaling females and males, respectively, at the monomorphic nonsignaling equilibrium. We can understand the other conditions in (A5) in the same way. At the intrasex dimorphic equilibrium \((x_i, y_i) = (0, y_i')\), the equality in (B2-2) holds (i.e., \(R_1 = 1\) from \(B3-4\)), and thus nonsignaling and signaling males share the same fitness value at \((0, y_i')\). In addition, inequality (A8-1) is equivalent to \(R_2 < 1\), which we can show using equations (B2-1) and (B3-4), and thus nonsignaling females have higher fitness than signaling females at \((0, y_i')\). Condition (A8-2) can be interpreted in a similar way.

Using ratios (B1), we can also obtain the conditions for negative and positive feedbacks to occur. By substituting the far right-hand side of equation (3), a function of the frequency of signaling individuals \((x_1 + y_1)/2\) (hereafter denoted as \(z_0\)), into \(\alpha_2\) in the right-hand sides of (B1) and differentiating them by \(z_0\), we obtain

\[
\frac{d}{dz_1} R_1 = -(\alpha_1 - 1)(\alpha_2 - 1) \frac{n p_1 (1 - z_1) + \alpha_1 z_1}{\beta_1 (1 - (1 - z_1) + \alpha_1 z_1) P_1} \cdot
\]

(B3-4)

These conditions indicate that (i) \(R_1\) and \(R_2\) are independent of \(z_1\) (i.e., \(dR_1/dz_1 = dR_2/dz_1 = 0\)) if either the individual effect or the collective effect does not exist (i.e., if \(\alpha_1 = 1\) or \(\alpha_2 = 1\)), (ii) \(R_1\) and \(R_2\) are decreasing functions of \(z_1\) (i.e., \(dR_1/dz_1 < 0\) and \(dR_2/dz_1 < 0\)) when individual and collective effects of signaling are both positive or both negative (i.e., if \(\alpha_1 < 1\) and \(\alpha_2 < 1\), or if \(\alpha_1 > 1\) and \(\alpha_2 > 1\)), and (iii) \(R_1\) and \(R_2\) are increasing functions of \(z_1\) (i.e., \(dR_1/dz_1 > 0\) and \(dR_2/dz_1 > 0\)) when the two effects are in opposite directions (i.e., if \(\alpha_1 < 1\) and \(\alpha_2 > 1\) or if \(\alpha_1 > 1\) and \(\alpha_2 < 1\)). In the cases of ii and iii, there are negative and positive feedbacks, respectively, between the fitness ratio and the frequency of signaling individuals. Condition (A7) means that the negative feedback is required for the stable intrasex dimorphism.
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