



## Evolutionary dynamics of fearfulness and boldness

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### ABSTRACT

A negative relationship between reproductive effort and survival is consistent with life-history. Evolutionary dynamics and evolutionarily stable strategy (ESS) for the trade-off between survival and reproduction are investigated using a simple model with two phenotypes, fearfulness and boldness. The dynamical stability of the pure strategy model and analysis of ESS conditions reveal that: (i) the simple coexistence of fearfulness and boldness is impossible; (ii) a small population size is favorable to fearfulness, but a large population size is favorable to boldness, i.e., neither fearfulness, nor boldness is always favored by natural selection; and (iii) the dynamics of population density is crucial for a proper understanding of the strategy dynamics.

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### 1. Introduction

A negative relationship between reproductive effort and survival is consistent with life-history (Hansen and Price, 1995; Kokko, 1998; Kokko et al., 2002). Recently, Siroto (2007) developed a simple evolutionary game model for the evolution of fearfulness in wild birds. Flightiness in birds can be affected by many environmental factors (Burger and Gochfeld, 1991; Gering and Blair, 1999), but it varies among species, and this variability remains difficult to explain (Ydenberg and Dill, 1986; Blumstein et al., 2003, 2005) (see also Siroto, 2007). However, as a reasonable explanation, this variability should partly originate in the evolutionary history of the different species or populations (Blumstein, 2006a, b). Siroto (2007) considered a bird population undergoing both predator attacks and non-lethal disturbing events, and assumed that when the population is disturbed, individuals display only two possible behavior traits, one is called the fearfulness, and the other the boldness, i.e., fearful individuals take flight immediately, but bold individuals are on the alert for some time and then take flight only if the threat proves to be a real predator attack. The basic idea behind Siroto's (2007) model is

that when the population is under predator attacks, (a) the fate of each individual not only depends on the way it reacts to danger, but also on the behavior of its companions, i.e., individual's expected survival probability is frequency-dependent and (b) a fearful individual has more chances for survival than a bold, but it also consumes more energy for escaping from the predator attacks, so its reproductive success is affected negatively, i.e., high levels of flightiness limit the risk of being killed by predators, but increase the amount of energy lost in flights during the season (Siroto, 2007). Thus, basically, Siroto's model concerns the evolution of trade-off between survival and reproduction.

For the importance of disturbance regimes in life-history evolution, Lytel (2001) developed a general disturbance model that combines the timing, frequency, severity, and predictability of disturbances with evolutionary life-history theory. Lytel (2001) thought that his disturbance model allows for the investigation of several questions: (a) How do disturbance regimes affect life-history attributes of organisms with complex life cycles, such as the size at and timing of maturity? (b) How frequently and predictably must disturbances recur to affect the evolution of these traits? (c) How does population structure influence the evolutionary response to disturbance? It is easy to see that the basic idea of Siroto's (2007) model is also similar to Lytel (2001), but Siroto more emphasized that the survival probability of each individual is frequency-dependent, i.e., the fate of each individual not only depends on the way it reacts to danger, but also on the behavior of its companions.

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In this paper, following Sirot (2007) we develop a simple model to investigate the evolutionary dynamics and evolutionarily stable strategy (ESS) for the trade-off between survival and reproduction in a population with asexual reproduction (Maynard Smith, 1982) and with non-overlapping generations. We focus our attention on the dynamical properties of the system and the evolutionary stability of a behavior trait compared to Sirot's (2007) results. Of course, there is no any prior reason to guarantee that our model is true in a real biological system, but it may provide some revelatory insights for us to understand the evolution of trade-off between survival and reproduction. The paper is organized as follows. In Section 2 we present a basic pure strategy model for the evolutionary dynamics of fearfulness and boldness, Section 3 gives the stability analysis of this model, Section 4 presents the ESS for the trade-off between survival and reproduction, and conclusions are presented in Section 5.

## 2. Basic model

Similar to the hawk–dove model developed by Maynard Smith (1982), let us construct a thought experiment for the evolution of fearfulness and boldness. Consider a population undergoing both predatory attacks and non-lethal disturbing events, where, for simplicity, we further assume that the reproduction is asexual (Maynard Smith, 1982) and that the generations are non-overlapping. Only two possible behavior traits can be exhibited when the population is disturbed, one is fearfulness (denoted by  $R_f$ ) and the other boldness (denoted by  $R_b$ ). The definitions of the phenotypes  $R_f$  and  $R_b$  are those of Sirot (2007), i.e., “when the population is disturbed, fearful individuals take escape immediately, but bold individuals are on the alert for some time and then take escape only if the threat proves to be a real predator attack.” However, for the evolution of behavior traits, a reasonable assumption is that when the population is under predator attacks, a fearful individual should have more chances for survival since it always leaves early, but this may be unfavorable for its reproductive success because of the energy lost (Cresswell et al., 2000; Sirot, 2007).

In order to investigate the evolutionary dynamics of fearfulness and boldness, we consider first a pure strategy model, i.e., we assume that all individuals are pure strategists. Let  $n_t$  and  $m_t$  denote the numbers of fearful and bold individuals at the start of generation  $t$ , respectively. The total population size is  $N_t = n_t + m_t$ , and  $p_t = n_t/N_t$  is the frequency of the phenotype  $R_f$ . In order to develop an evolutionary dynamics model, some definitions and assumptions are needed:

- (i) During one generation, the number of real predator attacks is assumed to be a constant, denoted by  $\psi_a$ , and, similarly, the number of simple disturbing events is denoted by  $\psi_d$ .
- (ii) Let the parameter  $\alpha \in (0, 1)$  represent the relative probability that a fearful individual is selected by the predators, compared with a bold individual. Clearly, if  $\alpha$  is near 0, then the fearful individuals are almost never attacked; conversely, if  $\alpha$  is near 1, then the risk is shared more equally by both fearful and bold individuals. The parameter  $\beta_f$  denotes the probability that a fearful individual is captured when selected by the predator, and, similarly,  $\beta_b$  the probability that a bold individual is captured when selected by the predator (see also Sirot, 2007). In this paper, without loss of generality, we assume  $\beta_f = \beta_b = \beta$ .
- (iii) During generation  $t$  the expected numbers of fearful and bold individuals after the  $i$ -th attack are denoted by  $n_t(i)$  and  $m_t(i)$ , respectively. For simplicity, in this paper we neglect stochastic effects, and assume that the population size is large (i.e.,

our analysis is based on the mean field). From (ii), the probability that a fearful individual is killed at the  $(i + 1)$ -th attack is

$$q_t(i) = \frac{\alpha\beta}{[\alpha p_t(i) + (1 - p_t(i))N_t(i)]}, \quad (1)$$

where  $N_t(i) = n_t(i) + m_t(i)$  and  $p_t(i) = n_t(i)/N_t(i)$ , and the probability that a bold individual is killed at the  $(i + 1)$ -th attack is

$$s_t(i) = \frac{\beta}{[\alpha p_t(i) + (1 - p_t(i))N_t(i)]}. \quad (2)$$

Thus, the numbers of fearful and bold individuals after the  $(i + 1)$ -th attack can be given by

$$\begin{aligned} n_t(i+1) &= n_t(i)(1 - q_t(i)), \\ m_t(i+1) &= m_t(i)(1 - s_t(i)), \end{aligned} \quad (3)$$

respectively, and the total population size is

$$N_t(i+1) = N_t(i) - \beta. \quad (4)$$

Let  $V_f$  and  $V_b$  denote the expected survival probabilities in generation  $t$ . Note that these probabilities actually depend on  $t$ . Then we have

$$\begin{aligned} V_f &= \prod_{i=0}^{\psi_a-1} (1 - q_t(i)) \\ &= \left(1 - \frac{\alpha\beta}{(\alpha p_t + (1 - p_t)N_t)}\right)^{\psi_a} \left(1 - \frac{\psi_a\beta}{N_t}\right) U(p_t), \\ V_b &= \prod_{i=0}^{\psi_a-1} (1 - s_t(i)) \\ &= \left(1 - \frac{\beta}{(\alpha p_t + (1 - p_t)N_t)}\right)^{\psi_a} \left(1 - \frac{\psi_a\beta}{N_t}\right) U(p_t), \end{aligned} \quad (5)$$

where

$$U(p_t) = \frac{1}{p_t(1 - q_t(0))^{\psi_a} + (1 - p_t)(1 - s_t(0))^{\psi_a}}, \quad (6)$$

i.e., the survival probabilities are frequency- and density-dependent (the derivation of Eq. (5) is given in Appendix A). Notice that if  $\alpha = 0$ , then we have

$$\begin{aligned} U(p_t) &= \frac{1}{p_t + (1 - p_t) \left(1 - \frac{\beta}{(1 - p_t)N_t}\right)^{\psi_a}} \\ &\approx \frac{1}{1 - \beta\psi_a/N_t} \end{aligned}$$

since

$$\begin{aligned} p_t + (1 - p_t) \left(1 - \frac{\beta}{(1 - p_t)N_t}\right)^{\psi_a} &= 1 - \frac{\beta\psi_a}{N_t} + O(1/N_t^2) \\ &\approx 1 - \frac{\beta\psi_a}{N_t}. \end{aligned}$$

Thus,  $V_f = 1$  if  $\alpha = 0$ , i.e., if  $\alpha = 0$ , then the expected survival probability of fearful individuals is one.

- (iv) If a fearful individual survives to the time of reproduction, then the level of its energy reserves can be expressed simply as

$$\gamma_f = E - (\psi_a + \psi_d)\varepsilon, \quad (7)$$

where the parameter  $E$  represents the total energy gained during one generation for an individual, and  $\varepsilon$  is the energy lost per escape. Similarly, if a bold individual survives to the time of reproduction, then its energy reserves are given by

$$\gamma_b = E - \psi_a\varepsilon. \quad (8)$$

It is assumed that the reproductive success of an individual increases with the level of its energy reserves. Thus, the reproductive success of an individual with energy reserves  $\gamma$  at the time of reproduction can be measured by the function

$$\Phi(\gamma) = 1 - e^{-a\gamma}, \tag{9}$$

where  $a$  is a constant (Sirot, 2007), i.e., for both fearful and bold individuals, we have  $\Phi(\gamma_f) = 1 - \exp[-a(E - (\psi_a + \psi_a)\varepsilon)]$  and  $\Phi(\gamma_b) = 1 - \exp[-a(E - \psi_a\varepsilon)]$ , respectively. It is easy to see that the function  $\Phi(r)$  is concave since  $d^2\Phi/dr^2 > 0$ .

(v) In this model, we assume also that all individuals have the same background fitness, denoted by  $W(N_t)$  (Maynard Smith, 1982), which can be defined as

$$W(N_t) = \exp(r(1 - N_t/K)), \tag{10}$$

where  $r$  is the intrinsic growth rate, and  $K$  is called the carrying capacity. The background fitness measures individual's fitness if no disturbing event occurs during the generation.

In the above definitions and assumptions, (i)–(iv) are similar to Sirot (2007). According to these definitions and assumptions, the expected numbers of fearful and bold individuals at the start of generation  $t + 1$  can be written as

$$\begin{aligned} n_{t+1} &= n_t V_f \Phi(\gamma_f) W(N_t), \\ m_{t+1} &= m_t V_b \Phi(\gamma_b) W(N_t), \end{aligned} \tag{11}$$

where the term  $V_f \Phi(\gamma_f) W(N_t)$  represents the fitness of individuals with phenotype  $R_f$ , and the term  $V_b \Phi(\gamma_b) W(N_t)$  the fitness of individuals with phenotype  $R_b$ . For our main goal, we are more interested in the phenotypic frequency dynamics. Thus, the dynamics equation (11) can be equivalently expressed as

$$\begin{aligned} p_{t+1} &= \frac{p_t V_f \Phi(\gamma_f)}{p_t V_f \Phi(\gamma_f) + (1 - p_t) V_b \Phi(\gamma_b)}, \\ N_{t+1} &= N_t [p_t V_f \Phi(\gamma_f) + (1 - p_t) V_b \Phi(\gamma_b)] W(N_t), \end{aligned} \tag{12}$$

where the term  $[p_t V_f \Phi(\gamma_f) + (1 - p_t) V_b \Phi(\gamma_b)] W(N_t)$  is the mean fitness of the population. For simplicity, denote  $p' = p_{t+1}$ ,  $p = p_t$ ,  $N' = N_{t+1}$  and  $N = N_t$  in the rest of this paper.

### 3. Stability analysis

In this section, the equilibrium structure of the dynamics given by Eq. (12) is considered. For convenience, use  $F_f$  and  $F_b$  to denote the fitnesses of fearful and bold individuals, respectively, i.e.,

$$\begin{aligned} F_f(p, N) &= V_f \Phi(\gamma_f) W(N), \\ F_b(p, N) &= V_b \Phi(\gamma_b) W(N). \end{aligned}$$

Notice that

$$\left(1 - \frac{\beta\psi_a}{N_t}\right) < p_t(1 - q_t(0))^{\psi_a} + (1 - p_t)(1 - s_t(0))^{\psi_a} < 1.$$

Thus, for large population size with  $\beta\psi_a \ll N$ ,  $F_f(p, N)$  and  $F_b(p, N)$  can be approximated as

$$\begin{aligned} F_f(p, N) &= \left(1 - \frac{\alpha\beta}{(\alpha p + (1 - p)N)}\right)^{\psi_a} \left(1 - \frac{\beta\psi_a}{N}\right) \Phi(\gamma_f) W(N), \\ F_b(p, N) &= \left(1 - \frac{\beta}{(\alpha p + (1 - p)N)}\right)^{\psi_a} \left(1 - \frac{\beta\psi_a}{N}\right) \Phi(\gamma_b) W(N). \end{aligned} \tag{13}$$

When the population consists only of individuals with phenotype  $R_f$ , in order to prevent the extinction of the population, we assume that

$$F_f(1, \psi_a) > 1. \tag{14}$$

Similarly, we assume also that

$$F_b(0, \psi_a) > 1. \tag{15}$$

#### 3.1. Boundary equilibria

The boundary corresponding to  $p = 0$  is denoted by  $(0, \hat{N})$  where  $\hat{N}$  is the solution to equation

$$F_b(0, N) = \left(1 - \frac{\beta}{N}\right)^{\psi_a} \left(1 - \frac{\beta\psi_a}{N}\right) \Phi(\gamma_b) W(N) = 1. \tag{16}$$

Notice that Eq. (16) can be equivalently expressed as

$$\psi_a \ln\left(1 - \frac{\beta}{N}\right) + \ln\left(1 - \frac{\beta\psi_a}{N}\right) + \ln \Phi(\gamma_b) + r\left(1 - \frac{N}{K}\right) = 0. \tag{17}$$

Thus, from Eq. (15), it is easy to see that  $\hat{N}$  must be unique. The Jacobian matrix of Eq. (12) about  $(0, \hat{N})$  is

$$J_{(0, \hat{N})} = \begin{pmatrix} F_f(0, \hat{N}) & 0 \\ \hat{N} \frac{\partial(pF_f + (1 - p)F_b)}{\partial p} \Big|_{(0, \hat{N})} & 1 + \hat{N} \frac{\partial F_b(p, N)}{\partial N} \Big|_{(0, \hat{N})} \end{pmatrix}, \tag{18}$$

where  $F_f(0, \hat{N}) = (1 - \alpha\beta/\hat{N})^{\psi_a} (1 - \psi_a\beta/\hat{N}) \Phi(\gamma_f) W(\hat{N})$ , and

$$\frac{\partial F_b(p, N)}{\partial N} \Big|_{(0, \hat{N})} = \frac{\psi_a\beta}{\hat{N}(\hat{N} - \beta)} + \frac{\psi_a\beta}{\hat{N}(\hat{N} - \psi_a\beta)} - \frac{r}{K}. \tag{19}$$

It is easy to see that the eigenvalues of the matrix  $J_{(0, \hat{N})}$  are  $F_f(0, \hat{N})$  and  $1 + \hat{N} \frac{\partial F_b(p, N)}{\partial N} \Big|_{(0, \hat{N})}$ , respectively. Thus, the boundary equilibrium  $(0, \hat{N})$  is locally asymptotically stable if the eigenvalues are less than 1 in absolute value, that is

$$\begin{aligned} \hat{N} &> \frac{\alpha\beta\Phi(\gamma_f)^{1/\psi_a} - \beta\Phi(\gamma_b)^{1/\psi_a}}{\Phi(\gamma_f)^{1/\psi_a} - \Phi(\gamma_b)^{1/\psi_a}}, \\ -2 &< \frac{\psi_a\beta}{\hat{N} - \beta} + \frac{\psi_a\beta}{\hat{N} - \psi_a\beta} - \frac{r\hat{N}}{K} < 0. \end{aligned} \tag{20}$$

Similar to  $(0, \hat{N})$ , for the boundary corresponding to  $p = 1$ , denoted by  $(1, \tilde{N})$ ,  $\tilde{N}$  must be also a unique solution to equation  $F_f(1, \tilde{N}) = 1$ , and  $(1, \tilde{N})$  is locally asymptotically stable if

$$\begin{aligned} \tilde{N} &< \frac{1}{\alpha} \cdot \frac{\alpha\beta\Phi(\gamma_f)^{1/\psi_a} - \beta\Phi(\gamma_b)^{1/\psi_a}}{\Phi(\gamma_f)^{1/\psi_a} - \Phi(\gamma_b)^{1/\psi_a}}, \\ -2 &< \frac{\psi_a\beta}{\tilde{N} - \beta} + \frac{\psi_a\beta}{\tilde{N} - \psi_a\beta} - \frac{r\tilde{N}}{K} < 0. \end{aligned} \tag{21}$$

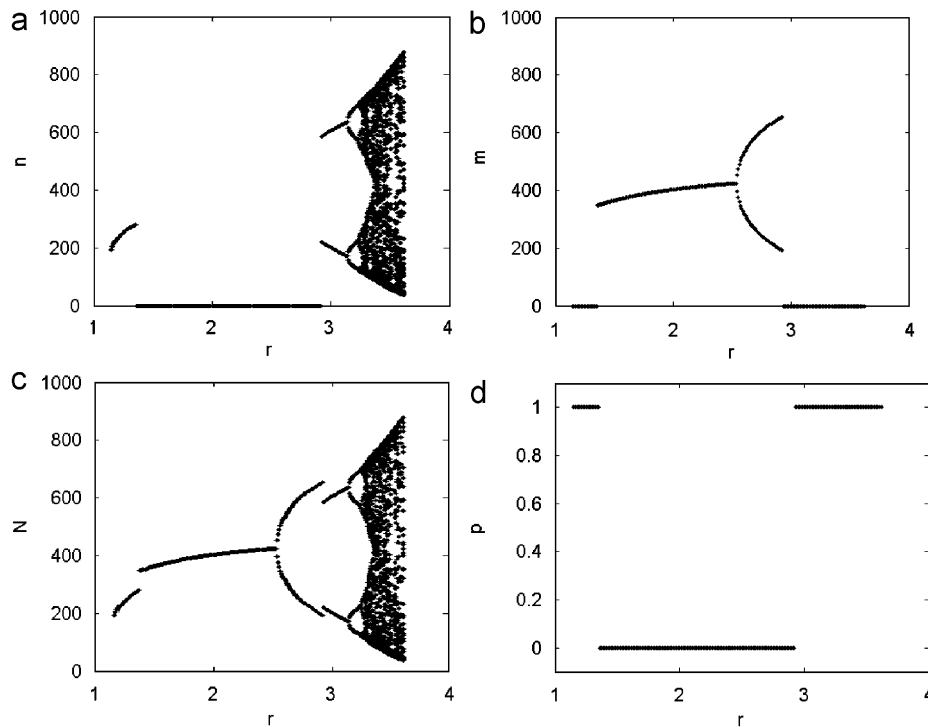
Thus, Eqs. (20) and (21) show that it is possible to have, at both evolutionary and population dynamics equilibria, populations with only fearful individuals, and populations with only bold individuals. Eqs. (20) and (21) imply also that the fearful population is stable on the population size if its equilibrium size is small, and that the bold population is stable on the population size if its equilibrium size is large. However, for both fearful and bold populations, if the intrinsic growth rate  $r$  does not satisfy

$$-2 > \frac{\psi_a\beta}{N - B} + \frac{\psi_a\beta}{N - \psi_a\beta} - \frac{rN}{K} > 0$$

there will be a periodic or chaotic attractor about population size (see Fig. 1).

#### 3.2. Interior equilibrium

Let  $(p^*, N^*)$  denote the interior equilibrium of Eq. (12), i.e.,  $(p^*, N^*)$  is the solution to equation  $F_f(p, N) = F_b(p, N) = 1$ . It is easy



**Fig. 1.** The effects of parameter  $r$  on the equilibrium structure of Eq. (12). The parameters are taken as  $\alpha = 0.2$ ,  $\beta = 0.8$ ,  $\psi_a = 40$ ,  $\psi_b = 40$ ,  $K = 500$ ,  $a = 0.1$ ,  $E = 20$ , and  $\varepsilon = 0.1$ . The dynamical behaviors of  $n$ ,  $m$ ,  $N$ , and  $p$  with the increase in parameter  $r$  are plotted in (a), (b), (c), and (d), respectively. These numerical solutions show clearly that (i) the simple coexistence of fearfulness and boldness is impossible; (ii) if  $r < 2.38$ , then the fearful population is stable if the population size is small, and the bold population is stable if the population size is large; and (iii) if  $r > 2.38$ , then for both fearful and bold populations, the existence of a periodic or chaotic attractor will be possible.

to see that  $p^*$  can be expressed as

$$p^* = \frac{1}{1-\alpha} \left[ 1 - \frac{1}{N^*} \cdot \frac{\alpha\beta\Phi(\gamma_f)^{1/\psi_a} - \beta\Phi(\gamma_b)^{1/\psi_a}}{\Phi(\gamma_f)^{1/\psi_a} - \Phi(\gamma_b)^{1/\psi_a}} \right], \quad (22)$$

and  $N^*$  is the solution to equation

$$\left( 1 - \frac{\alpha\beta\Phi(\gamma_f)^{1/\psi_a} - \beta\Phi(\gamma_b)^{1/\psi_a}}{\Phi(\gamma_f)^{1/\psi_a} - \Phi(\gamma_b)^{1/\psi_a}} \right)^{\psi_a} \left( 1 - \frac{\psi_a\beta}{N^*} \right) \Phi(\gamma_b)W(N^*) = 1. \quad (23)$$

Clearly,  $(p^*, N^*)$  must be unique if it exists, and  $N^*$  satisfies

$$\frac{\psi_a\beta}{N^*(N^* - \psi_a\beta)} - \frac{r}{K} < 0. \quad (24)$$

It is also easy to see that the interior equilibrium  $(p^*, N^*)$  must be unstable (the proof is given in Appendix A).

From Eq. (22), if the interior equilibrium  $(p^*, N^*)$  exists, i.e.,  $0 < p^* < 1$  and  $N^* > 0$ , then we must have

$$N^* > \frac{\alpha\beta\Phi(\gamma_f)^{1/\psi_a} - \beta\Phi(\gamma_b)^{1/\psi_a}}{\Phi(\gamma_f)^{1/\psi_a} - \Phi(\gamma_b)^{1/\psi_a}}$$

and

$$N^* < \frac{1}{\alpha} \cdot \frac{\alpha\beta\Phi(\gamma_f)^{1/\psi_a} - \beta\Phi(\gamma_b)^{1/\psi_a}}{\Phi(\gamma_f)^{1/\psi_a} - \Phi(\gamma_b)^{1/\psi_a}}.$$

Since  $\partial F_b(p, N)/\partial p < 0$  and  $\partial F_f(p, N)/\partial p < 0$ , i.e.,  $\tilde{N} < N^* < \hat{N}$  if  $p^* \in (0, 1)$  and  $N^* > 0$ , the existence of the interior stable periodic or chaotic attractor is impossible. This shows that if the interior equilibrium  $(p^*, N^*)$  exists, then the two boundary attractors corresponding to boundary equilibria  $(0, \hat{N})$  and  $(1, \tilde{N})$ , respectively, must be stable, where the boundary attractors include the stable fixed points, and periodic and chaotic fluctuations. For the effects of parameter  $r$  on the dynamical behavior of the system, the results of numerical simulation are plotted in Fig. 1.

These results show clearly that the analytic result of Eq. (12) is true.

The stability analysis of Eq. (12) reveals that the phenotypes  $R_f$  and  $R_b$  cannot simply coexist under the natural selection, i.e., if all individuals are pure strategists, then fearful and bold individuals cannot coexist. Biologically, this result can be explained by the ‘dilution effects’ (Hamilton, 1971; Dehn, 1990), i.e., individuals are safer because each individual in a population has a smaller chance of being the one attacked (Dehn, 1990). If most of the individuals in the population are bold, a large population size can reduce the risk of each individual when the population is under predator attacks, i.e., bold individuals have a higher expected fitness than fearful individuals. Conversely, if most of the individuals are fearful, bold individuals will be concentratively attacked when the population is under predator attacks since fearful individuals always leave early. Thus, neither fearfulness, nor boldness is always favored by natural selection.

#### 4. Evolutionarily stable strategy

In the above section, we consider only the dynamical properties of the pure strategy model, i.e., all individuals are pure strategists. In this section, ESS for the trade-off between survival and reproduction is considered.

Suppose that an individual uses a mixed strategy, denoted by  $\mathbf{u} = (u, 1 - u)$ , i.e., when the population is disturbed, this individual exhibits phenotype  $R_f$  with probability  $u$ , and phenotype  $R_b$  with complementary probability  $1 - u$ . According to this definition, phenotypes  $R_f$  and  $R_b$  can be also denoted by  $(1, 0)$  and  $(0, 1)$ , respectively. In a population with fearfulness level  $p$  (i.e., the frequency of phenotype  $R_f$  in the population is  $p$ ), the fitness of an individual with phenotype  $\mathbf{u}$ , denoted by  $F_{\mathbf{u}}(p, N)$ , is given by

$$F_{\mathbf{u}}(p, N) = H_{\mathbf{u}}\Phi(\gamma_{\mathbf{u}})W(N), \quad (25)$$

where

$$H_{\mathbf{u}} = \left(1 - \frac{(u\alpha + (1-u))\beta}{(\alpha p + (1-p)N)}\right)^{\psi_a} \left(1 - \frac{\psi_a\beta}{N}\right) \quad (26)$$

with that  $V_{\mathbf{u}} = H_{\mathbf{u}}U(p)$  is the expected survival probability of individuals with phenotype  $\mathbf{u}$  (see the definitions and assumptions in Section 2), and

$$\gamma_{\mathbf{u}} = E - (\psi_a + u\psi_d)\varepsilon \quad (27)$$

the level of energy reserves. Notice that fitness exhibits the constant term  $(1 - \psi_a\beta/N)W(N)$ . Thus, in order to define an ESS, we can use the function

$$G_{\mathbf{u}}(p, N) = \left(1 - \frac{(u\alpha + (1-u))\beta}{(\alpha p + (1-p)N)}\right)^{\psi_a} \Phi(\gamma_{\mathbf{u}}) \quad (28)$$

to represent fitness.

It is easy to show that equation  $\partial G_{\mathbf{u}}(p, N)/\partial u = 0$  must have a unique solution, denoted by  $u_{\max}(p, N)$ , that corresponds to the maximum of  $G_{\mathbf{u}}(p, N)$  (see Appendix A). From this property, we can define that for given  $(p, N)$ ,  $u_{\text{opt}}(p, N)$  corresponds to an optimal strategy, denoted by  $\mathbf{u}_{\text{opt}}(p, N) = (u_{\text{opt}}, 1 - u_{\text{opt}})$ , where  $u_{\text{opt}} = 1$  if  $u_{\max} \geq 1$ ,  $u_{\text{opt}} = u_{\max}$  if  $u_{\max} \in (0, 1)$ , and  $u_{\text{opt}} = 0$  if  $u_{\max} < 0$  (see also Sirot, 2007).

Let  $\mathbf{u}^* = (u^*, 1 - u^*)$  be an ESS, i.e., if all individuals adopt strategy  $\mathbf{u}^*$ , then no mutant strategy could invade the population under the influence of natural selection (Maynard Smith, 1982). Then, we have

$$G_{\mathbf{u}^*}(u^*, N) > G_{\mathbf{u}}(u^*, N) \quad (29)$$

for all possible  $\mathbf{u} \neq \mathbf{u}^*$ . This is a strict Nash equilibrium (Maynard Smith, 1982; Cressman, 1992; Hofbauer and Sigmund, 1998). Obviously, the pure strategy  $R_f$  is an ESS if

$$N < \frac{(1-\alpha)\beta\psi_a}{\alpha} \left[ \frac{a\psi_d\varepsilon}{\Phi(\gamma_f)} (1 - \Phi(\gamma_f)) \right]^{-1} + \beta \quad (30)$$

since  $G_f(1, N) > G_{\mathbf{u}}(1, N)$  with  $u < 1$  is equivalent to  $u_{\text{opt}}(1, N) \geq 1$ , i.e.,

$$\left. \frac{dG_{\mathbf{u}}(1, N)}{du} \right|_{u=1} \geq 0.$$

Similarly, the pure strategy  $R_b$  is an ESS if

$$N > \frac{(1-\alpha)\beta\psi_a}{\alpha} \left[ \frac{a\psi_d\varepsilon}{\Phi(\gamma_b)} (1 - \Phi(\gamma_b)) \right]^{-1} + \frac{\beta}{\alpha}. \quad (31)$$

Finally, a mixed strategy  $\mathbf{u}^* = (u^*, 1 - u^*)$  is an ESS if and only if the optimal strategy  $\mathbf{u}_{\text{opt}}(u^*, N)$  corresponding to  $G_{\mathbf{u}}(u^*, N)$  satisfies: (i)  $u_{\text{opt}}(u^*, N)$  is in the interval  $0 < u_{\text{opt}}(u^*, N) < 1$ , which holds if and only if

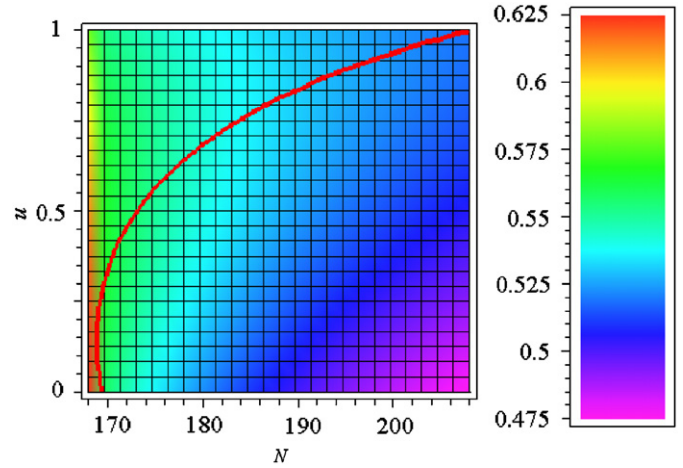
$$\frac{(1-\alpha)\beta\psi_a}{(\alpha u^* + (1-u^*))N - \beta} > \frac{a\psi_d\varepsilon}{\Phi(\gamma_b)} (1 - \Phi(\gamma_b)),$$

$$\frac{(1-\alpha)\beta\psi_a}{(\alpha u^* + (1-u^*))N - \alpha\beta} < \frac{a\psi_d\varepsilon}{\Phi(\gamma_f)} (1 - \Phi(\gamma_f)) \quad (32)$$

and (ii)  $u^*$  is the solution to the equation  $u_{\text{opt}}(u^*, N) = u^*$ .

Eqs. (30)–(32) show that the ESS conditions depend strongly on the population size. The ESS conditions for the pure strategies fearfulness and boldness imply that a small population size is favorable to the phenotype  $R_f$ , but a large population size is favorable to the phenotype  $R_b$ , i.e., the fearfulness is an ESS if the population size is less than the threshold

$$((1-\alpha)\beta\psi_a/\alpha)[a\psi_d\varepsilon(1-\Phi(\gamma_f))/\Phi(\gamma_f)]^{-1} + \beta,$$



**Fig. 2.** A mixed strategy  $\mathbf{u}^* = (u^*, 1 - u^*)$  is an ESS if and only if (i)  $u_{\text{opt}}(u^*, N)$  is in the interval  $0 < u_{\text{opt}}(u^*, N) < 1$  and (ii)  $u^*$  is the solution to the equation  $u_{\text{opt}}(u^*, N) = u^*$  (see the text). Here, as an example, the parameters are taken as  $\alpha = 0.4$ ,  $\beta = 0.8$ ,  $\psi_a = 50$ ,  $\psi_d = 50$ ,  $a = 0.1$ ,  $E = 20$ , and  $\varepsilon = 0.1$ . The red curve represents the function  $u^*(N)$  (i.e., the solution to equation  $u_{\text{opt}}(u^*, N) = u^*$ ), which corresponds to a mixed ESS strategy. A mixed ESS depends strongly on the population size, and for the existence of a mixed ESS, the population size must be in the interval  $167 < N < 208$ . For convenience, in this figure, the fitness of individual with phenotype  $\mathbf{u} = (u, 1 - u)$  is represented by the color (where the fitness value is denoted by the color bar). It is easy to see that for a given population size  $N$  in the interval  $167 < N < 208$ , the fitness of a  $\mathbf{u}^*$ -strategist must be bigger than the fitness of a  $\mathbf{u}$ -strategist for all possible  $u \neq u^*$ .

and boldness is an ESS if the population size is larger than the threshold

$$((1-\alpha)\beta\psi_a/\alpha)[a\psi_d\varepsilon(1-\Phi(\gamma_b))/\Phi(\gamma_b)]^{-1} + \beta/\alpha.$$

Theoretically, a mixed ESS strategy seems to be possible in our simple model, and it may represent a reasonable trade-off between survival and reproduction at individual level, but we have to notice also that the conditions of a mixed ESS strategy are very rigorous, i.e., if a mixed strategy  $\mathbf{u}^*$  is an ESS, then it must be the solution to the equation  $u_{\text{opt}}(u^*, N) = u^*$ , i.e.,  $u^*$  should be in general a function of population size  $N$ , where  $N$  is in a given interval that is determined by Eq. (32) (see Fig. 2). Thus, if we assume that only two pure strategies (fearfulness and boldness) are possible, then we may have no any prior reasons, or evidences, to believe that a mixed ESS strategy can be maintained in a real biological system.

## 5. Summary

In this paper, the evolutionary dynamics of fearfulness and boldness and evolutionarily stable strategy (ESS) for the trade-off between survival and reproduction are investigated using a simple two-phenotype model. The basic framework of the model is mainly from Sirot (2007). In this paper we focus our attention on the relationship between the dynamical properties of the system and evolutionary stability of behavior traits compared to Sirot's (2007) results. For the dynamical stability of the pure strategy model, our results show that the simple coexistence of two pure strategies, fearfulness and boldness, is impossible, i.e., if all individuals are pure-strategists, then fearful and bold individuals cannot coexist. This means that no any interior stable attractor can exist, and the system state will be eventually attracted by the boundary attractors. Biologically, this result implies that neither fearfulness nor boldness is always favored by natural selection. For the evolutionary stability of behavior traits, we show that the ESS conditions depend strongly on the population size. The ESS conditions for the pure strategies imply

that a small population size is favorable to fearfulness, but a large population size is favorable to boldness. On the other hand, the existence of a mixed ESS strategy is possible in our simple model, and it may represent a trade-off between survival and reproduction with evolutionary advantages, but its conditions are very rigorous. Thus, it remains difficult to explain whether a mixed ESS strategy can occur in a real biological system. Finally, we show that the dynamics of population density is crucial for a proper understanding of the strategy dynamics, and the main difference between our results and Sirots (2007) is that Sirots considered only the situation with fixed population size but we show clearly the relationship between the evolutionary stability of fearfulness (boldness) and population size.

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**Appendix A**

**A.1. Derivation of Eq. (5)**

Notice that at the end of generation  $t$  the expected numbers of fearful and bold individuals are

$$n_t(\psi_a) = n_t \prod_{i=0}^{\psi_a-1} (1 - q_t(i)),$$

$$m_t(\psi_a) = m_t \prod_{i=0}^{\psi_a-1} (1 - s_t(i)), \tag{33}$$

respectively. Notice also that

$$\frac{n_t(\psi_a)}{m_t(\psi_a)} \approx \frac{n_t}{m_t} \left( \frac{1 - q_t(0)}{1 - s_t(0)} \right)^{\psi_a}$$

$$= \frac{p_t}{1 - p_t} \left( \frac{1 - q_t(0)}{1 - s_t(0)} \right)^{\psi_a} \tag{34}$$

since

$$\frac{1 - q_t(i)}{1 - s_t(i)} = \frac{1 - q_t(i+1)}{1 - s_t(i+1)} + O(1/N_t^2) \tag{35}$$

for all  $i = 1, 2, \dots, \psi_a - 1$ . Thus, Eq. (35) can be rewritten as

$$n_t(\psi_a) = (N_t - \psi_a \beta) \frac{p_t(1 - q_t(0))^{\psi_a}}{p_t(1 - q_t(0))^{\psi_a} + (1 - p_t)(1 - s_t(0))^{\psi_a}}$$

$$= n_t(1 - q_t(0))^{\psi_a} \left( 1 - \frac{\psi_a \beta}{N_t} \right) U(p_t),$$

$$m_t(\psi_a) = (N_t - \psi_a \beta) \frac{(1 - p_t)(1 - s_t(0))^{\psi_a}}{p_t(1 - q_t(0))^{\psi_a} + (1 - p_t)(1 - s_t(0))^{\psi_a}}$$

$$= m_t(1 - s_t(0))^{\psi_a} \left( 1 - \frac{\psi_a \beta}{N_t} \right) U(p_t), \tag{36}$$

where  $U(p_t)$  is given in Eq. (6). So, Eq. (5) can be obtained.

**A.2. Stability analysis of interior equilibrium  $(p^*, N^*)$**

The Jacobian matrix of Eq. (12) about the interior equilibrium  $(p^*, N^*)$  is

$$\mathbf{J}_{(p^*, N^*)} = \begin{pmatrix} 1 + p(1 - p) \left( \frac{\partial F_f}{\partial p} - \frac{\partial F_b}{\partial p} \right) & p(1 - p) \left( \frac{\partial F_f}{\partial N} - \frac{\partial F_b}{\partial N} \right) \\ N \left( p \frac{\partial F_f}{\partial p} + (1 - p) \frac{\partial F_b}{\partial p} \right) & 1 + N \left( p \frac{\partial F_f}{\partial N} + (1 - p) \frac{\partial F_b}{\partial N} \right) \end{pmatrix} \bigg|_{(p^*, N^*)} \tag{37}$$

where

$$\frac{\partial F_f(p, N)}{\partial p} \bigg|_{(p^*, N^*)} = - \frac{\alpha(1 - \alpha)\beta\psi_a}{(\alpha p^* + (1 - p^*))H_f},$$

$$\frac{\partial F_b(p, N)}{\partial p} \bigg|_{(p^*, N^*)} = - \frac{(1 - \alpha)\beta\psi_a}{(\alpha p^* + (1 - p^*))H_b},$$

$$\frac{\partial F_f(p, N)}{\partial N} \bigg|_{(p^*, N^*)} = \frac{\alpha\beta\psi_a}{N^*H_f} + \frac{\psi_a\beta}{N^*(N^* - \psi_a\beta)} - \frac{r}{K},$$

$$\frac{\partial F_b(p, N)}{\partial N} \bigg|_{(p^*, N^*)} = \frac{\beta\psi_a}{N^*H_b} + \frac{\psi_a\beta}{N^*(N^* - \psi_a\beta)} - \frac{r}{K}, \tag{38}$$

where

$$H_f = (\alpha p^* + (1 - p^*))N^* - \alpha\beta,$$

$$H_b = (\alpha p^* + (1 - p^*))N^* - \beta. \tag{39}$$

The characteristic equation of the matrix  $\mathbf{J}_{(p^*, N^*)}$  is given by

$$U(\lambda) = \lambda^2 - \lambda(2 + A) + (1 + A) + B = 0, \tag{40}$$

where

$$A = p^*(1 - p^*) \left( \frac{\partial F_f}{\partial p} - \frac{\partial F_b}{\partial p} \right) + N^* \left( p^* \frac{\partial F_f}{\partial N} + (1 - p^*) \frac{\partial F_b}{\partial N} \right),$$

$$B = p^*(1 - p^*)N^* \left( \frac{\partial F_f}{\partial p} \cdot \frac{\partial F_b}{\partial N} - \frac{\partial F_b}{\partial p} \cdot \frac{\partial F_f}{\partial N} \right), \tag{41}$$

where

$$\frac{\partial F_f}{\partial p} - \frac{\partial F_b}{\partial p} = \frac{(1 - \alpha)^2 \beta \psi_a N^*}{H_f H_b},$$

$$p^* \frac{\partial F_f}{\partial N} + (1 - p^*) \frac{\partial F_b}{\partial N} = \frac{\beta \psi_a}{H_f H_b N^*} [(\alpha p^* + (1 - p^*)) \times (p^* \alpha + (1 - p^*))N^* - \alpha \beta]$$

$$+ \frac{\psi_a \beta}{N^*(N^* - \psi_a \beta)} - \frac{r}{K},$$

$$\frac{\partial F_f}{\partial p} \cdot \frac{\partial F_b}{\partial N} - \frac{\partial F_b}{\partial p} \cdot \frac{\partial F_f}{\partial N} = \frac{(1 - \alpha)^2 \beta \psi_a N^*}{H_f H_b} \left( \frac{\psi_a \beta}{N^*(N^* - \psi_a \beta)} - \frac{r}{K} \right). \tag{42}$$

Notice that the eigenvalues of the matrix  $\mathbf{J}_{(p^*, N^*)}$ , i.e., the solution to equation  $U(\lambda) = 0$ , are given by

$$\lambda_{1,2} = 1 + \frac{A \pm \sqrt{A^2 - 4B}}{2}. \tag{43}$$

Thus, the interior equilibrium  $(p^*, N^*)$  must be unstable since  $B < 0$ .

**A.3. Existence and uniqueness of the solution to equation  $\partial G_{\mathbf{u}}(p, N) = 0$**

From Eq. (28), notice that

$$\frac{\partial \ln G_{\mathbf{u}}(p, N)}{\partial u} = \frac{(1 - \alpha)\beta\psi_a}{(\alpha p + (1 - p))N - u\alpha\beta - (1 - u)\beta}$$

$$- \frac{a\psi_d \varepsilon}{\Phi(\gamma_{\mathbf{u}})} (1 - \Phi(\gamma_{\mathbf{u}})),$$

$$\frac{\partial^2 \ln G_{\mathbf{u}}(p, N)}{\partial u^2} = - \frac{(-\alpha)^2 \beta^2 \psi_a}{[(\alpha p + (1 - p))N - u\alpha\beta - (1 - u)\beta]^2}$$

$$- \frac{(a\psi_d \varepsilon)^2}{\Phi(\gamma_{\mathbf{u}})} (1 - \Phi(\gamma_{\mathbf{u}})) < 0, \tag{44}$$

and that

$$\begin{aligned} \frac{\partial}{\partial u} \left[ \frac{(1-\alpha)\beta\psi_a}{(\alpha p + (1-p))N - u\alpha\beta - (1-u)\beta} \right] \\ = - \frac{(1-\alpha)^2\beta^2\psi_a}{[(\alpha p + (1-p))N - u\alpha\beta - (1-u)\beta]^2} \\ < 0, \\ \frac{\partial}{\partial u} \left[ \frac{a\psi_d\varepsilon}{\Phi(\gamma_u)} (1 - \Phi(\gamma_u)) \right] = \frac{(a\psi_d\varepsilon)^2}{\Phi(\gamma_u)^2} (1 - \Phi(\gamma_u)) > 0, \end{aligned} \quad (45)$$

for given  $(p, N)$ . Thus, equation  $\partial G_u(p, N)/\partial u = 0$  must have a unique solution, denoted by  $u_{\max}(p, N)$ , that corresponds to the maximum of  $G_u(p, N)$ .

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