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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.

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, Sirot (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 Sirot, 2007). However, as a reasonable explanation, this variability should partly originate in the evolutionary history of the different species or populations (Blumstein, 2006a, b). Sirot (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 Sirot'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 flightness limit the risk of being killed by predators, but increase the amount of energy lost in flights during the season (Sirot, 2007). Thus, basically, Sirot'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 Sirot's (2007) model is also similar to Lytel (2001), but Sirot 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 ψ_a, and, similarly, the number of simple disturbing events is denoted by ψ_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 α is near 0, then the fearful individuals are almost never attacked; conversely, if α is near 1, then the risk is shared more equally by both fearful and bold individuals. The parameter β_f denotes the probability that a fearful individual is captured when selected by the predator, and, similarly, β_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

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

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

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

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

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

respectively, and the total population size is

$$N_t(i+1) = N_t(i) - \beta. \tag{4}$$

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

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

where

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

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

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

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

$$\gamma_f = E - (\psi_a + \psi_d)\varepsilon, \tag{7}$$

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

$$\gamma_b = E - \psi_a\varepsilon. \tag{8}$$