Evolutionary Ecology Research, 2011, **13**: 765–778

Evolutionary effects of different dispersal modes on the origin of polymorphic crypsis in predator–prey systems

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ABSTRACT

Scenario: Using adaptive dynamic theory, expose a monomorphic prey population to two habitat types and a visual predator.

Questions: What circumstances can lead to the evolution of polymorphic crypsis? How is the outcome affected by the dispersal pattern of the prey and predator, by the amount of predation, and by the trade-off strength between the habitats?

Mathematical method: I modelled three different dispersal modes: passive dispersal for the prey and a stationary predator; passive dispersal for the prey and habitat choice for the predator; and habitat choice for the prey and no dispersal for the predator.

Conclusions: The different dispersal models produce only minor differences in outcomes. Dispersal rate also seems to have relatively little influence on the evolutionary outcome, with low dispersal rate slightly favouring evolutionary divergence. Other factors (such as the amount of predation and strength of trade-off between the habitats) appear to be more crucial.

Keywords: adaptive dynamics, dispersal, habitat choice, heterogeneous environment, polymorphic crypsis.

INTRODUCTION

Many prey species use camouflage to escape the claws of their predators (Cott, 1940). Crypsis (i.e. background matching) is one of many different camouflage strategies (Stevens and Merilaita, 2009). Some prey have even evolved several morphs that are camouflaged in different environments, including grasshoppers (Dearn, 1990), walking-stick insects (Sandoval, 1994), isopods (Jormalainen *et al.*, 1995; Hargeby *et al.*, 2004), bivalves (Whiteley *et al.*, 1997), land snails (Cook, 1998), crab-spiders (Théry and Casas, 2002), tree frogs (Wente and Phillips, 2003), dragon lizards (Stuart-Fox *et al.*, 2004), and kelp crabs (Hultgren and Stachowicz, 2008). However, how this polymorphism has evolved is in most cases unknown; but, see Bond (2007) for a review of the progress to date.

A number of studies have addressed the maintenance of polymorphic crypsis (Reid, 1987; Sandoval, 1994; Whiteley *et al.*, 1997; Bond and Kamil, 1998, 2002, 2006; Cook, 1998; Merilaita *et al.*, 1999; Théry and Casas, 2002; Wente and Phillips, 2003; Punzalan *et al.*, 2005; Houston *et al.*, 2007; Bolnick and Nosil, 2010). Bond and Kamil

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(2006) performed an experimental study of the evolution of polymorphic crypsis for virtual prey being detected by blue jay predators. Whether the prey became polymorphically cryptic or not depended on the type of background, and whether prey individuals were exposed to one or two backgrounds. In a web-based simulation study, Sherratt *et al.* (2007) let Internet users act as predators trying to detect prey, finding that an initially diverse prey population would easily diverge into two different morphs when presented against different backgrounds. The evolution of polymorphic crypsis was also studied, in a theoretical context, by Nilsson and Ripa (2010), assuming a fixed population density of the predator. Constant abundance for the predator could be a fair assumption, since a generalist predator will feed upon many different types of prey and its abundance will not depend on the availability of only one of them. However, if the predator is a specialist, its density will change with the prey population dynamics. Therefore, incorporating the dynamics of the predator into the modelling can be important. Also, the mode of dispersal between the different habitats for the prey or predator (passive dispersal, habitat choice or isolation) is likely to result in different evolutionary outcomes. The choosing population (the predator or the prey) would most likely not be able to make a perfect choice, which could have an influence on the population dynamics and, as a consequence, evolution.

Here, I present a system of predator and prey populations living in two visually different habitats, to investigate how different dispersal behaviour of both prey and predator will affect the possibility of polymorphic crypsis through evolutionary branching, and how this relates to changes in dispersal rate, maximal attack rate, strength of trade-off, and predator mortality rate. I use a model similar to that used by Nilsson and Ripa (2010), but with explicit population dynamics for both prey and predator, where evolution towards an optimally cryptic phenotype will decrease predation. I compare three different models of dispersal behaviour, both for the prey and the predator (see Fig. 1). There can be passive dispersal (when a fixed proportion of the population is transferred to the other habitat) or habitat choice (when the predator or the prey can, to some extent, choose which habitat to be in). The first model has one predator and one prey population in each habitat, with the prey populations connected by passive dispersal and the predator populations isolated. In the second model, there is one prey population in each habitat, connected by passive dispersal, and one global predator population with the possibility to redistribute between the two habitats (without cost). The third model has one predator and one prey population in each habitat; the predator populations are isolated and the prey populations are able to affect the propensity for dispersal between the habitats. I find little difference between the three models; the second and third models have slightly smaller parameter areas for branching (for high attack rate in the second model and for high dispersal rate in the third model), and thereby polymorphic crypsis. Generally, I find that polymorphism is likely to evolve for intermediate values of trade-off, predator mortality rate, and maximal attack rate. Dispersal rate seems to have relatively little effect on the evolutionary outcome, although the parameter space for branching is slightly larger for low dispersal rates. Nilsson and Ripa (2010) found a large difference between a type II functional response (when the number of caught prey per predator per time unit increases linearly for low prey abundance, and approaches a maximal value for high prey abundance) and a type III functional response [when the number of caught prey per predator per time unit instead follows a sigmoid curve (Holling, 1959, 1965)], which could be due to the assumption of a fixed predator. Here, in contrast, the result from a type II functional response coincides with the results for the type III functional response in Nilsson and Ripa (2010).

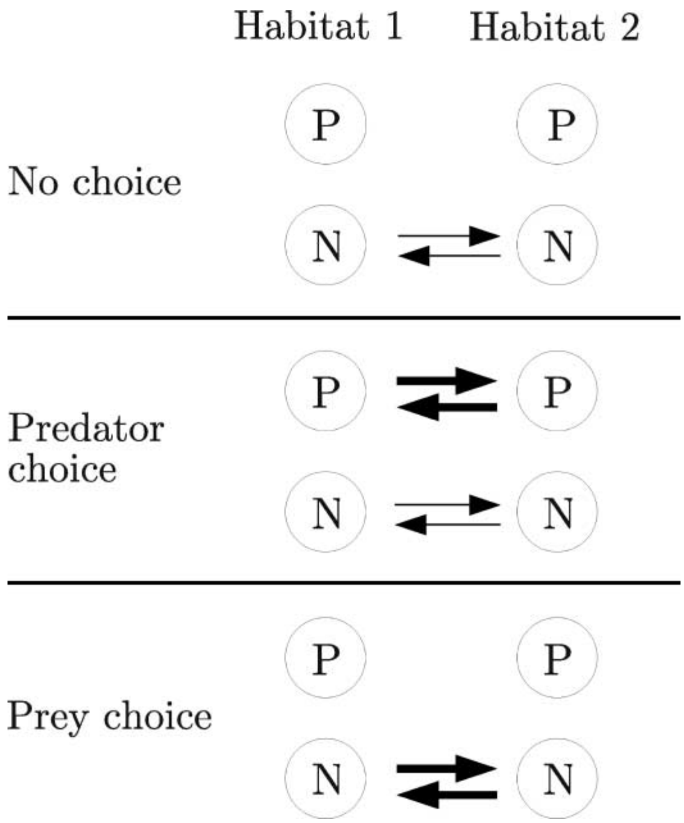

Fig. 1. Schematic representation of the three models. The predator populations are represented by P and the prey populations by N. The arrows show the direction of dispersal between the habitats; thin arrows represent passive dispersal and thick arrows represent habitat choice. If there are no arrows, the populations are isolated.

THE MODELS

I compare three models (‘no choice’, ‘predator choice’, and ‘prey choice’) with different dispersal behaviour of the prey and predator (Fig. 1). All models have a predatory functional response type II. The environment consists of two habitats with visually different backgrounds. Hence, different prey phenotypes will be cryptic in different habitats.

No choice

In this model, there is one prey population and one predator population in each habitat. The prey populations are connected by passive dispersal, and the predator populations are isolated (Fig. 1A). The predators will therefore only feed upon the prey in their respective habitat, and the abundance of a predator population will only depend on the abundance of prey in its own habitat.

The dynamics of the prey, N_k, and the predator, P_k, for habitat $k = 1, 2$ are given by

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - \frac{a_1(u) N_1 P_1}{1 + a_1(u) h N_1} - DN_1 + DN_2 \tag{1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - \frac{a_2(u) N_2 P_2}{1 + a_2(u) h N_2} - DN_2 + DN_1 \tag{2}$$

$$\frac{dP_1}{dt} = c\,\frac{a_1(u) N_1 P_1}{1 + a_1(u) h N_1} - m_1 P_1 \tag{3}$$

$$\frac{dP_2}{dt} = c\,\frac{a_2(u) N_2 P_2}{1 + a_2(u) h N_2} - m_2 P_2 \tag{4}$$

where r_k is the intrinsic growth rate in habitat k, K_k is the habitat-specific carrying capacity, D is the symmetric dispersal rate between the habitats, h is the prey handling time, c is a conversion coefficient that describes how efficiently consumed prey are turned into new predators, and m is the mortality rate of the predator. $a_i(u)$ is the attack rate, which depends on the crypticity of the prey:

$$a_k(u) = a_{\max} \mid u - U_k \mid^{x} \tag{5}$$

where $a_{\max}$ is the maximal attack rate, x is the trade-off between the habitats, and u is the value of the evolvable trait that determines how cryptic the prey is against the local background. The habitat-specific optimal trait value is given by U_k(with $U_1 \leq u \leq U_2$ and $0 \leq U_k \leq 1$), and the crypticity of the prey increases when the difference $\mid u - U_k \mid$ decreases. Trade-off is defined as the relative change of adaptation to the two habitats for a small change in trait value (similar to Merilaita *et al.*, 1999 and Sherratt *et al.*, 2007), described here by the function $\mid u - U_k \mid^{x}$. This function is concave for $0 < x < 1$ (strong trade-off), convex for $x > 1$ (weak trade-off) and, when the function is linear (for $x = 1$), trade-off is neutral.

Predator choice

For the 'predator choice' model, the prey has two local populations, N_1 and N_2, connected by passive dispersal, while the predator has only one, global, population, P (Fig. 1B). The predator has some knowledge about the abundance of prey and their crypticity in both habitats and can (without any cost) travel between the habitats. The population dynamics are described by

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - \frac{\beta_1 a_1(u) N_1 P}{1 + \beta_1 a_1(u) h N_1 + \beta_2 a_2(u) h N_2} - DN_1 + DN_2 \tag{6}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - \frac{\beta_2 a_2(u) N_2 P}{1 + \beta_1 a_1(u) h N_1 + \beta_2 a_2(u) h N_2} - DN_2 + DN_1 \tag{7}$$

$$\frac{dP}{dt} = cP\,\frac{\beta_1 a_1(u) N_1 + \beta_2 a_2(u) N_2}{1 + \beta_1 a_1(u) h N_1 + \beta_2 a_2(u) h N_2} - mP \tag{8}$$

Depending on the availability of prey (i.e. the size of the prey population, N_k, as well as the prey's visibility, $a_k(u)$), a predator can choose between the two habitats with the choice function β (Fryxell and Lundberg, 1997), with β_k being the probability for a predator to be in habitat k:

$$\beta_1 = \begin{cases} \dfrac{1}{1 + e^{-z_\beta\left(\frac{N_1 a_1}{N_2 a_2} - 1\right)}}, & N_1 a_1 \geq N_2 a_2 \\ 1 - \dfrac{1}{1 + e^{-z_\beta\left(\frac{N_2 a_2}{N_1 a_1} - 1\right)}}, & N_1 a_1 < N_2 a_2 \end{cases} \tag{9}$$

$$\beta_2 = \begin{cases} 1 - \dfrac{1}{1 + e^{-z_\beta\left(\frac{N_1 a_1}{N_2 a_2} - 1\right)}}, & N_1 a_1 \geq N_2 a_2 \\ \dfrac{1}{1 + e^{-z_\beta\left(\frac{N_2 a_2}{N_1 a_1} - 1\right)}}, & N_1 a_1 < N_2 a_2 \end{cases} \tag{10}$$

β_k is a sigmoid function, where β_1 is maximized when $N_1 a_1 \gg N_2 a_2$, and β_2 is maximized when $N_2 a_2 \gg N_1 a_1$. The parameter z_β determines how well the predator is able to make a correct decision. When z_β is very large, the function is close to a step function and the predator always chooses the best habitat. For smaller z_β, the predator is more prone to make mistakes when choosing a habitat. Note that $\beta_1 + \beta_2 = 1$, as the predator must decide to be in one of the habitats. When $N_1 a_1 = N_2 a_2$, the habitats are equally good, and the predator population will be equally distributed between the habitats with $\beta_1 = \beta_2 = 0.5$.

Prey choice

In the 'prey choice' model, the predator has two local, isolated, populations, while the prey can affect the amount of dispersal between the habitats, as the prey has some knowledge about the amount of competition and predation in both habitats (Fig. 1C). Based upon this, the probability of a prey being dispersed will increase or decrease. Hence, dispersal is no longer passive and not necessarily symmetric. The dynamics of this model are

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - \frac{a_1(u) N_1 P_1}{1 + a_1(u) h N_1} - \mu_1 D N_1 + \mu_2 D N_2 \tag{11}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - \frac{a_2(u) N_2 P_2}{1 + a_2(u) h N_2} - \mu_2 D N_2 + \mu_1 D N_1 \tag{12}$$

$$\frac{dP_1}{dt} = c \frac{a_1(u) N_1 P_1}{1 + a_1(u) h N_1} - m_1 P_1 \tag{13}$$

$$\frac{dP_2}{dt} = c \frac{a_2(u) N_2 P_2}{1 + a_2(u) h N_2} - m_2 P_2 \tag{14}$$

The prey can choose to increase or decrease the amount of dispersal between the habitats with the prey choice function μ. $\mu_1 D$ thus describes the dispersal from habitat 1 to habitat 2, and $\mu_2 D$ describes dispersal from habitat 2 to habitat 1. The dispersal coefficients μ_k are calculated according to

$$\mu_1 = \frac{2}{1 + e^{-z_\mu\left(\frac{\gamma_1}{\gamma_2} - 1\right)}} \tag{15}$$

$$\mu_2 = \frac{2}{1 + e^{-z_\mu\left(\frac{\gamma_2}{\gamma_1} - 1\right)}} \tag{16}$$

where

$$\gamma_k = \frac{N_k}{K_k} + \frac{a_k P_k}{1 + a_k h N_k} \tag{17}$$

z_μ is a measure of how accurately the prey makes a decision, similar to z_β for the β function, with a high value of z_μ for a prey that always makes the right decision, and a low value of z_μ for a prey that makes mistakes. The prey in habitat k is trying to avoid local competition (N_k / K_k) and predation $\left(\frac{a_k P_k}{1 + a_k h N_k}\right)$, which is described by the γ_k function.

If $\gamma_1 \gg \gamma_2$, it is beneficial for the prey to increase dispersal from habitat 1 (i.e. a large value of μ_1) but remain in habitat 2 (small value of μ_2), whereas if $\gamma_1 \ll \gamma_2$, the direction of dispersal would preferably be from habitat 2 to habitat 1. The maximal value of μ_k is 2, and the minimal value is 0, which means that the dispersal rate can vary between 0 and $2D$. When the two habitats are equally good, i.e. for $\mu_1 = \mu_2 = 1$, this will give the same model as when there is no preference (the 'no choice' model, equations 1–4), with the symmetric dispersal rate D.

Evolution

New trait values are introduced into the system by mutants from the resident population. A mutant population is assumed to be of negligible size initially, and will thus not experience competition from its own population, only from the resident. Also, the functional response of the predator will be determined by the majority of the prey (i.e. the resident population). Thus the amount of competition, as well as the shape of the functional response, will be determined by the resident population. The resident population is assumed to reach equilibrium, N_k^*, between invasion events.

The prey dynamics of an invading prey mutant, N', with trait value u' invading the resident population with trait value u can be generalized to

$$\frac{dN'_1}{dt} = w_{I,1}(u', u)N'_1 - \mu_1 D N'_1 + \mu_2 D N'_2 \tag{18}$$

$$\frac{dN'_2}{dt} = w_{I,2}(u', u)N'_2 - \mu_2 D N'_2 + \mu_1 D N'_1 \tag{19}$$

where I denotes the model (1 for the 'no choice' model, 2 for the 'predator choice' model, and 3 for the 'prey choice' model), with $\mu_1 = \mu_2 = 1$ for model 1 and 2. The respective

$w_{I,k}(u', u)$ (which give the per capita growth rate of an invader in habitat k using model I, without dispersal) for the different models are

$$w_{1,k}(u', u) = r_k\left(1 - \frac{N_k^*}{K_k}\right) - \frac{a_k(u')P_k}{1 + a_k(u)hN_k^*} \tag{20}$$

$$w_{2,k}(u', u) = r_k\left(1 - \frac{N_k^*}{K_k}\right) - \frac{\beta_k a_k(u')P}{1 + \beta_k a_k(u)hN_k^* + \beta_j a_j(u)hN_j^*} \tag{21}$$

$$w_{3,k}(u', u) = r_k\left(1 - \frac{N_k^*}{K_k}\right) - \frac{a_k(u')P_k}{1 + a_k(u)hN_k^*} \tag{22}$$

A matrix M can be derived from the linear equations (18, 19):

$$M = \begin{bmatrix} w_{I,1}(u') - \mu_1 D & \mu_2 D \\ \mu_1 D & w_{I,2}(u') - \mu_2 D \end{bmatrix} \tag{23}$$

The fitness of an invading mutant is acquired by calculating the dominant eigenvalue of M (Holt and Gaines, 1992; Meszéna *et al.*, 1997; Kawecki and Holt, 2002).

Following the framework of adaptive dynamics (e.g. Geritz *et al.*, 1998), an invasion fitness landscape can be generated by calculating the fitness for all possible invaders (with a trait value $U_1 \leq u' \leq U_2$) trying to invade a resident population with trait value u. Due to frequency dependence, the invasion fitness landscape will change for different values of u. This makes evolution towards a fitness minimum possible, and by that branching.

I only consider mutants as invaders (the system is closed to invaders from elsewhere) and mutations are assumed to be small. Consequently, evolution will be gradual. The direction of evolution will therefore be decided by the slope of the invasion fitness landscape at u, the trait value of the resident population (Iwasa *et al.*, 1991). A singular point is found when the slope of the invasion fitness landscape is 0 at u (Geritz *et al.*, 1998).

RESULTS

I chose to vary the following parameters: maximal attack rate ($a_{\max}$), dispersal rate (D), trade-off (x), and the mortality rate for the predator (m), as well as compare the three models ('no choice', 'predator choice', and 'prey choice'). These parameters were chosen to represent changes in prey (D and x), predator (m) or both ($a_{\max}$).

Pairwise invasibility plots [PIPs (see Geritz *et al.*, 1998)] for different evolutionary outcomes are shown in Fig. 2. The evolutionary properties of the system for varied parameters, as well as the differences between the models, are shown in Fig. 3.

Singular points

There are four different evolutionary outcomes here, with one or three singular points in the system. When there is only one singular point, the intermediate trait value can be a convergent-stable evolutionarily stable strategy (ESS; Fig. 2A and black areas in Fig. 3) or a branching point (Fig. 2B and dark grey areas in Fig. 3). When the resident population is at the ESS singular point, evolution will stop.

When there are three singular points, the intermediate trait value will be a repeller with two singular points symmetrically situated on both sides of it. These specialist singular

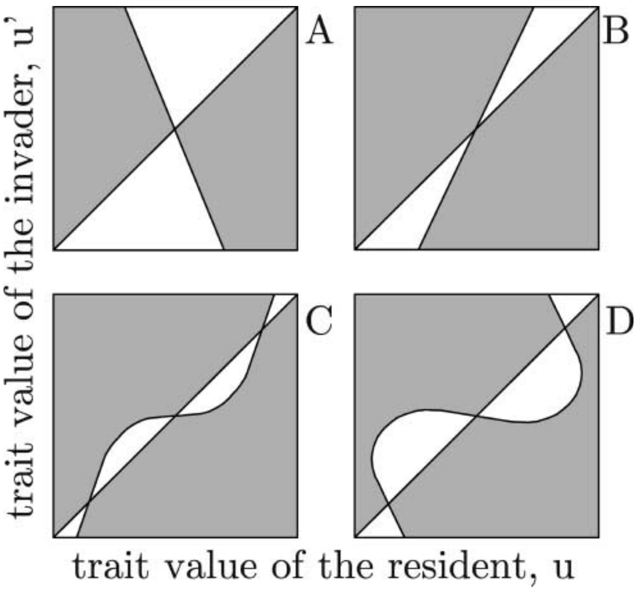

Fig. 2. Pairwise invasibility plots. For the dark areas the invader has higher fitness than the resident, and will be able to invade and replace the resident. In the white areas the resident has higher fitness than the invader, and there will be no successful invasion. (A) Intermediate ESS, (B) intermediate branching point, (C) intermediate repeller and specialist branching points, and (D) intermediate repeller and specialist ESSs.

points can be located anywhere from close to the intermediate trait value to the extreme trait values (U_1 and U_2). The specialist trait values can be either branching points (Fig. 2C and light grey areas in Fig. 3) or ESSs (Fig. 2D and white areas in Fig. 3). When the population is at a specialist ESS, the system could possibly be invaded from elsewhere by a morph specialized on the other habitat (however, this possibility is not considered here).

For polymorphism to arise, the prey population must evolve to a branching point (grey areas in Fig. 3). Here, the population will experience disruptive selection, and the initially monomorphic population can diverge into two co-existing morphs.

Effects of predation

The amount of predation depends on how abundant the predator is, which is here determined by the predator mortality rate, m (Fig. 3A–I), and how efficient the predator is, i.e. the maximal attack rate, $a_{\max}$ (Fig. 3A–C, J–O). Branching, and thereby polymorphism, is likely to occur at intermediate amounts of predation (intermediate predator mortality rate, m, and intermediate maximal attack rate, $a_{\max}$). For too little predation (i.e. for high predator mortality rate, large m, or low maximal attack rate, small $a_{\max}$), the intermediate trait value will be an ESS, and polymorphism will not evolve. When predation is low, the prey populations in both habitats will be large and of approximately the same size. Hence, adaptation for the prey to both habitats is equally important, and the intermediate trait value will be optimal (unless the trade-off is too strong).

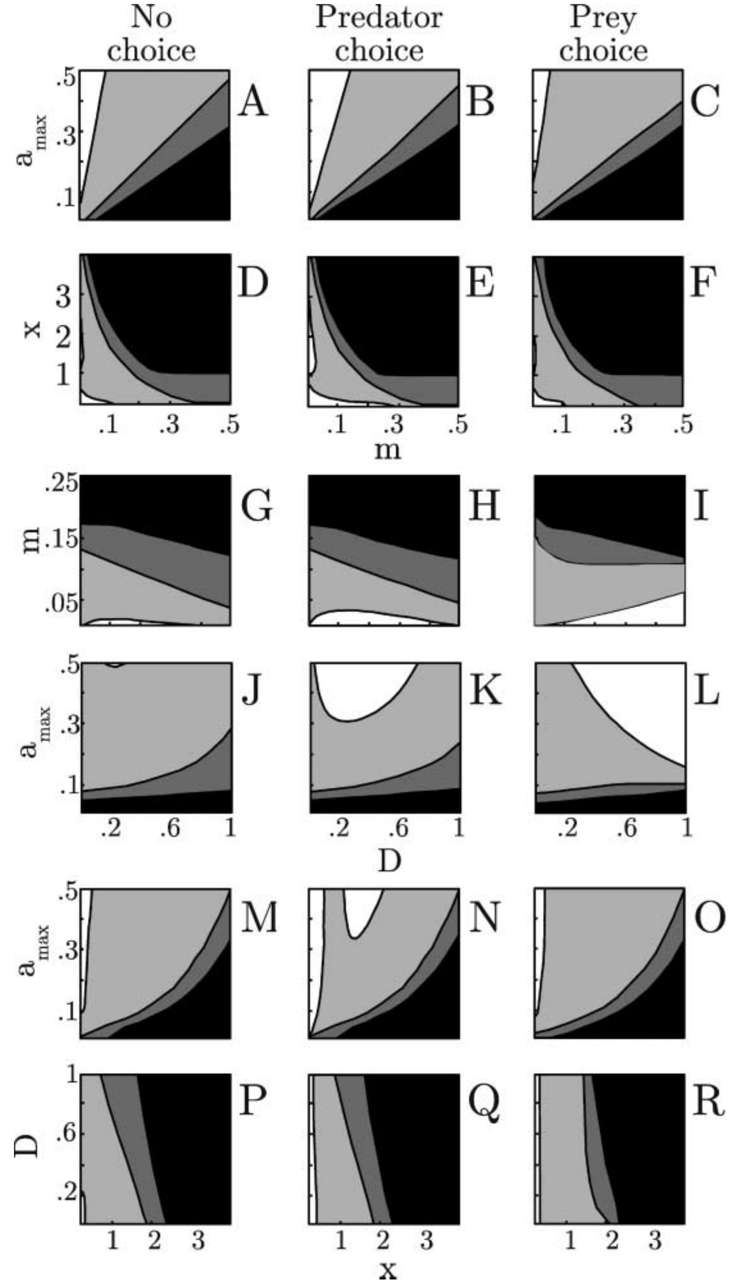

Fig. 3. Singular points for various values of the parameters x, D, a_{max}, and m for the three models ('no choice', 'predator choice', and 'prey choice'). Black areas are intermediate ESSs, dark grey areas are intermediate branching points, light grey areas are specialist branching points, and white areas are specialist ESSs. Parameter values for (A–C): $x = 1.5$, $D = 0.1$; (D–F): $a_{max} = 0.1$, $D = 0.1$; (G–I): $a_{max} = 0.1$, $x = 1.5$; (J–L): $x = 1.5$, $m = 0.1$; (M–O): $D = 0.1$, $m = 0.1$; (P–R): $a_{max} = 0.1$, $m = 0.1$. Other parameter values are $U_1 = 0$, $U_2 = 1$, $K = 100$, $c = 0.05$, $r = 1$, $h = 0.01$ and, for the choice models, $z_\beta = z_\mu = 4$.

When predation is too high (for low predator mortality rate, m, or high maximal attack rate, $a_{\max}$), there will instead be a specialist ESS, which also prevents evolution of polymorphism. Higher predation will increase the difference in abundance of prey between the two populations, and the less cryptic population will be much smaller. The probability for any individual to be in the more cryptic population is therefore greater, and increased crypticity for this population is favoured.

Effects of trade-off strength

The trade-off between the habitats, x (Fig. 3D–F, M–R), is considered strong when $0 < x < 1$, and weak when $x > 1$. At $x = 1$, the trade-off is linear and considered neutral. Divergence through evolutionary branching will typically occur for intermediate trade-off, close to neutral (x close to 1).

If the trade-off is too weak (large x), there will be an intermediate ESS, since evolution towards the intermediate trait value will increase crypticity in the less cryptic habitat relatively more than it will decrease in the more cryptic habitat, making it beneficial for the prey to evolve towards the intermediate trait value.

Too strong a trade-off (small x) will produce a specialist ESS. When the trade-off is strong, evolution from the intermediate trait value towards a specialist will increase crypticity for the more cryptic population relatively more than it will decrease for the less cryptic population. Since the more cryptic population is also the more abundant one, adaptation to this habitat will be favoured.

Effects of dispersal

Dispersal varies in two ways in this study: the rate of dispersal between the habitats and different dispersal models, both for prey and predator.

Regardless of whether dispersal is passive or if the prey can choose habitat, the dispersal parameter, D (Fig. 3G–L, P–R), determines the amount (or maximal amount, $2D$, in the 'prey choice' model) of movement between the habitats. The effect of varied dispersal rate is not very pronounced, but there are some general trends.

For low dispersal (small D), an individual is likely to stay in the same habitat. Hence, it is beneficial to be locally adapted, and the parameter space for a branching point is slightly larger. When the dispersal rate is too high (large D), it is probable that an individual will experience both habitats, which will favour an intermediate trait, equally cryptic in both habitats.

The three different dispersal models give very similar results (left-hand column for the 'no choice' model in Fig. 3, middle column for the 'predator choice' model, and right-hand column for the 'prey choice' model). The 'predator choice' and the 'prey choice' models have slightly larger areas for a specialist ESS, resulting in a somewhat smaller parameter range for branching. For the 'predator choice' model, this occurs at a high maximal attack rate (large $a_{\max}$, Fig. 3K, N). At this specialist singular point, there will be more predators in the habitat with the more cryptic population for the 'predator choice' model compared with the other two models, since some predators will make the wrong decision. Hence, a small shift towards the intermediate trait value will be very unfavourable for the more cryptic population.

In the ‘prey choice’ model, there will be specialist ESSs at high dispersal rate (large D) in combination with a high maximal attack rate (large a_{max}, Fig. 3L) or low mortality rate for the predator (small m, Fig. 3I). High dispersal in combination with high predation will increase the differences between the habitats. This will in turn cause a more asymmetric dispersal, with a net flow of dispersers into the habitat where the prey is more cryptic, favouring adaptation to this habitat.

DISCUSSION

The rate of dispersal has previously been shown to be important for the evolutionary outcome in a heterogeneous environment. Less dispersal between different habitats is known to increase the possibility for local adaptations (Räsänen and Hendry, 2008). Nosil (2009) confirmed that local camouflage is more likely when the migration rate between different habitats is low. Also, in an experimental study with blue jays searching for virtual moths in different habitats, Bond and Kamil (2006) found that the evolution of polymorphic crypsis occurred when the moths were exposed to the same background (remaining in the same habitat), but not when the background varied (dispersal between the habitats). In the present study, I found that a change in dispersal rate from low to high could change the branching point from being at the intermediate trait value to being at a more specialized trait value, and increased dispersal can even change a branching point into an intermediate ESS. However, other parameters seem to be more important, i.e. trade-off between the habitats, mortality rate of the predator, and maximal attack rate. Bond and Kamil (2006) also compared different kinds of backgrounds, which could be comparable to the trade-off in this study (with little difference between the habitats corresponding to a weak trade-off and a large difference between the habitats equivalent to a strong trade-off). Bond and Kamil found that polymorphism only evolved for the backgrounds that differed the most (i.e. for strong trade-off). This coincides with the findings of this study, as the trade-off should not be too weak, lest an intermediate ESS will evolve. However, if the trade-off is too strong, a specialist ESS would be the evolutionary outcome, also preventing branching. In a web-based simulation study, Sherratt *et al.* (2007) found the trade-off to be either strong or close to neutral, resulting in polymorphic crypsis with specialist morphs, but no intermediate (‘jack-of-all-trades’) generalists. This is in line with the present study, in that it is clear that an intermediate generalist only evolves for a weak trade-off, while neutral and strong trade-offs will result in an intermediate branching point, specialist branching points or specialist ESSs. That Sherratt *et al.* (2007) did not obtain a specialist ESS is probably due to the fact that they started with a broad spectrum of different morphs, and therefore the prey did not have to evolve to a branching point to become polymorphic. As I have only considered evolution for one homogeneous population, the event of a specialist ESS being invaded by another specialist morph is a possibility (cf. Nilsson and Ripa, 2010), but this is outside the scope of this study. After polymorphism has evolved, prey individuals tend to stay in the habitat where they are cryptic (Endler, 1978; Gillis, 1982). This will reinforce the isolation between habitats and may be a step towards speciation.

I found that polymorphic crypsis can arise through evolutionary branching for intermediate trade-off strength and predation (determined by the maximal attack rate and predator mortality), but dispersal seems to have a relatively minor effect (although low dispersal rate will make the parameter space for branching slightly larger). These results are very similar to the results for the type III functional response in Nilsson and Ripa (2010).

Nilsson and Ripa used a model similar to the 'no choice' model, but with constant predator abundance. Hence, predation was added as an extra mortality rate for the prey. Presumably, when explicit predator dynamics is used, low prey abundance will decrease the predator populations enough to reduce predation and give the same result as a type III functional response with constant predator density.

I have compared three different models of dispersal in a predator–prey system, with passive dispersal or habitat choice, to identify key processes in the evolution of polymorphism. Different dispersal models might be expected to give different evolutionary outcomes, since the behaviour of both prey and predator differ substantially between the models. However, I found little difference between the evolutionary outcomes for all models, as only in detail did the models show disparate results (instead of branching at a specialist trait value, there will be an evolutionarily stable specialist at a high maximal attack rate for the 'predator choice' model, and at a high dispersal rate in combination with high maximal attack rate or low predator mortality rate for the 'prey choice' model). Hence, even though the prey and the predator were able (to some extent) to choose habitat, but were unable to make a perfect decision, the evolutionary outcome of the models still gave similar results. Instead, other factors (such as strength of trade-off and amount of predation) seem to be more important. Here, only predation by detection is driving the evolution of prey polymorphism. Apostatic selection, when the predator chooses common over rare prey (e.g. if the predator uses a search image when hunting for prey), has been suggested to facilitate polymorphism (Allen, 1988). Franks and Oxford (2011) found apostatic selection to be neither required nor sufficient for polymorphic crypsis to evolve, but that it is indeed facilitated by dietary wariness of the predator. Features like these should be accounted for to increase the realism of the model and thus identify the key factors of evolution of polymorphic crypsis.

ACKNOWLEDGEMENTS

I would like to thank Jörgen Ripa and Jacob Johansson for valuable comments and discussions. This study was supported financially by the Swedish Research Council.

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