Optimization of cryptic coloration in heterogeneous habitats

SAMI MERILAITA*

Department of Animal Ecology, Uppsala University, Norbyvägen 18D, S-752 36 Uppsala, Sweden

JUHA TUOMI

Department of Biology, University of Oulu, FIN-90570 Oulu, Finland

VEIJO JORMALAINEN

Department of Biology, University of Turku, FIN-20014 Turku, Finland

We present a theoretical approach to the optimization of crypsis in heterogeneous habitats. Our model habitat consists of two different microhabitats, and the optimal combination of crypsis in the microhabitats is supposed to maximize the probability of escaping detection by a predator. The probability of escaping detection for a prey is a function of: (i) degree of crypsis, (ii) probability of occurrence in the microhabitats and (iii) probability of encountering a predator in the microhabitats. Because crypsis is background-specific there is a trade-off between crypsis in two visually different microhabitats. Depending on the nature of the trade-off, the optimal coloration is either a compromise between the requirements of the differing microhabitats or entirely adapted to only one of them. An increased risk of predation in one of the microhabitats favours increased crypsis in that microhabitat. Because the trade-off constrains possible optimal solutions, it is not possible to predict the optimal coloration only from factors (i)–(iii). However, habitat choice may fundamentally change the situation. If minimizing predation risk does not incur any costs, the prey should exclusively prefer the microhabitat where it has a lower probability of encountering a predator and better crypsis. The implications of these results for variation in cryptic coloration and polymorphism are discussed.

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ADDITIONAL KEY WORDS:—crypsis – camouflage – microhabitat – habitat choice.

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* Corresponding author. E-mail: sami.merilaita@zoologi.uu.se

INTRODUCTION

Cryptic coloration is an adaptation against visual detection by predators, serving to make a prey animal indistinguishable from its background. Crypsis can be achieved through several mechanisms, such as background matching, disruptive coloration and countershading (Cott, 1940; Edmunds, 1974; Endler, 1978, 1988). Generally, to be cryptic, animal coloration should resemble the visual background (Endler, 1978 and references therein). Consequently, it tends to be background-specific.

Although several studies have attempted to quantify crypsis of animals living in visually varying habitats (Norris & Lowe, 1964; Endler, 1984; Morey, 1990; Harris & Weatherall, 1991; King, 1992, 1993; Kiltie, 1992; Belk & Smith, 1996; Westmoreland & Kiltie, 1996; King & King, 1991), optimization of crypsis in heterogeneous habitats has received surprisingly little theoretical attention. In homogeneous habitats the probability of detection can be decreased simply by increasing the degree of crypsis against that background. In heterogeneous habitats, however, where both the degree of crypsis of a given coloration and the probability of encountering a predator may vary spatially, decreasing the probability of detection by a predator is a more complicated task. In his often-cited paper defining crypsis, Endler (1978) specifically predicted that the optimal coloration should maximize the degree of crypsis in the microhabitat where the prey is most vulnerable to predation. However, one may also imagine situations where the coloration of the prey is an optimal compromise of crypsis in different microhabitats which the prey uses. In such a case, the coloration need not maximize the degree of crypsis in one of the microhabitats but rather provide an optimal crypsis yielding the maximal protection over all of the different microhabitats used. Distinction between these two ways of optimization is important, especially when measurement of crypsis in heterogeneous habitats is considered.

We formalized the basic ideas of optimization of crypsis in a heterogeneous habitat. When selection acts on the protective coloration of the prey, the optimal combination of microhabitat-specific crypsis should give the best chance of escaping detection over the entire array of microhabitats. Below, we first derive the probability that the prey will escape detection by predators. Second, we study optimal combinations of microhabitat-specific crypsis that maximize the overall probability of escaping detection in spatially heterogeneous environments. The environmental heterogeneity corresponds to Levins' (1968) fine-grained environment in the sense that the prey experiences all the microhabitats within its habitat. Our formalization is based on static optimization procedures (e.g. Levins, 1968; Chiang, 1984) and shares the general assumptions of optimization models in evolutionary ecology (Stearns, 1976; Parker & Maynard Smith, 1990).
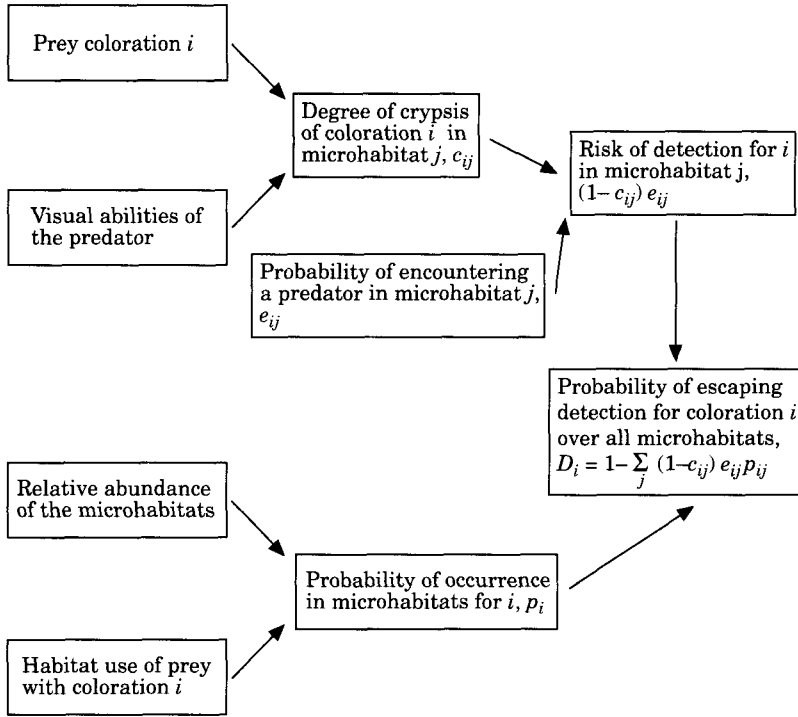
Figure 1.Components of the probability of escaping detection by a predator for a prey with coloration i in a heterogeneous habitat as defined in Eq. (1).

CRYPSIS AND THE PROBABILITY OF ESCAPING DETECTION

Let c_{ij} denote the degree of crypsis of coloration i in microhabitat j $(0 \le c_{ij} \le 1)$ (Fig. 1). Degree of crypsis achieves the minimum value of zero when each prey individual of phenotype i that encounters a predator in microhabitat j will be detected by the predator. The maximum value $c_{ij} = 1$ indicates that no prey individual encountering a predator will be detected. We assume that the prey cannot respond to a change of microhabitat with an immediate adjustment of coloration.

Moreover, let e_{ij} be the probability that an individual of phenotype i encounters a predator in microhabitat j $(0 \le e_{ij} \le 1)$. Then the expression $(1 - c_{ij})e_{ij}$ will correspond to the probability that an individual of phenotype i will be detected by a predator in microhabitat j. If we now assume that the probability of an individual of phenotype i to occur in microhabitat j is p_{ij} $(0 \le p_{ij} \le 1; \sum_j p_{ij} = 1)$, the probability for an individual of type i to be detected by a predator will be $\sum_j (1 - c_{ij})e_{ij}p_{ij}$, and the probability of escaping detection for phenotype i will thus be

$$D_i = 1 - \sum_j (1 - c_{ij})e_{ij}p_{ij}. \tag{1}$$

The probability of occurrence in a certain microhabitat (p_{ij}) is determined by both the relative proportions of the microhabitats and the microhabitat preferences of the phenotype (Fig. 1). Let us denote the proportion of microhabitat j by h_j. If

habitat choice is random, then p_{ij} simply corresponds to h_j. Taking into account microhabitat preferences, we further assume in Eq. (1) that $p_{ij} = h_j + \delta_{ij}$, where δ_{ij} is the deviation from $p_{ij} = h_j$ due to non-random microhabitat choice $(\sum_j \delta_{ij} = 0)$.

OPTIMIZING CRYPSIS IN HETEROGENEOUS HABITATS

Random habitat choice

Let us assume a habitat consisting of two visually different microhabitats, 1 and 2. If habitat choice is random, the probability that phenotype i escapes detection will be

$$D_i = 1 - (1 - c_{i1})e_1h_1 - (1 - c_{i2})e_2h_2. \tag{2}$$

For given relative proportions of microhabitat 1 and 2 the probability of escaping detection remains constant over the whole habitat when the total differential is zero, or

$$dD_i = \frac{\partial D_i}{\partial c_{i1}}dc_{i1} + \frac{\partial D_i}{\partial c_{i2}}dc_{i2} = 0 \tag{3}$$

giving

$$\frac{dc_{i2}}{dc_{i1}} = -\frac{\partial D_i/\partial c_{i1}}{\partial D_i/\partial c_{i2}}. \tag{4}$$

Since $\dfrac{\partial D_i}{\partial c_{i1}} = e_{i1}h_1$ and $\dfrac{\partial D_i}{\partial c_{i2}} = e_{i2}h_2$ we obtain the condition

$$\frac{dc_{i2}}{dc_{i1}} = -\frac{e_{i1}h_1}{e_{i2}h_2} \tag{5}$$

which defines for given values of e_{ij} and h_j $(j = 1,2)$ the combinations of c_{i1} and c_{i2} giving the same probability of escaping detection. Graphically, these combinations can be presented as straight lines with a constant D_i and the slope given by Eq. (5).

The more complete the visual resemblance between the animal coloration and one of the microhabitats becomes, the less the coloration can resemble the other microhabitat (Edmunds, 1974; Endler, 1978; Sandoval, 1994a). In other words, there should be a trade-off between c_{i1} and c_{i2}. We assume a general trade-off function

$$c_{i2} = f_i(c_{i1}) \tag{6}$$

between the degree of crypsis in the two microhabitats, giving the highest possible c_{i2} the prey can produce for each value of c_{i1}. The highest probability of escaping
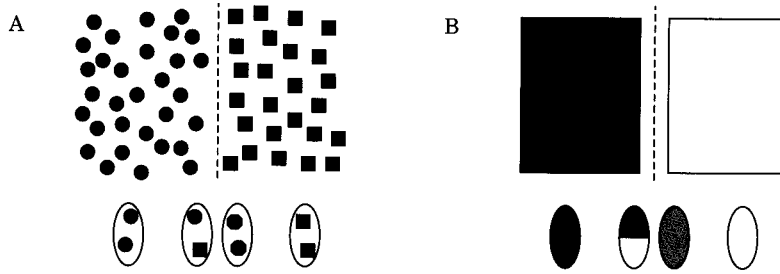
Figure 2. Two hypothetical examples of heterogeneous habitats and animals relying on crypsis through background matching. In (A) the habitat consists of two different microhabitats, one with circular and the other with square-formed elements. The two outermost of the four animals have adapted to the microhabitats with respective patterns only. The two animals in the middle, one with a circle and a square to the left and one with two octagons to the right, represent compromised adaptations for crypsis in both microhabitats. Successfully compromised colorations give the trade-off between crypsis in these microhabitats a convex form. In (B) one microhabitat is black and the other is white. Again, the outermost animals represent adaptations to one microhabitat only. However, this time the compromised colorations in the middle are apparently very poor, making the trade-off between crypsis in the two microhabitats concave.

detection by a predator $D_i(max)$ for the given prey coloration and relative proportions of microhabitats is found among the points in the trade-off curve where the slope dc_{i2}/dc_{i1} is equal to $-e_{i1}h_1/e_{i2}h_2$. We denote the microhabitat-specific crypsis which corresponds to $D_i(max)$ by c^*_{i1} and c^*_{i2} for the two microhabitats. Notice that if the habitat consists of more than two microhabitats, the number of c_{ij} axes as well as the dimensions of the trade-off function and the function describing $D_i(max)$ as combinations of c_{ij} increase to equal the number of different microhabitats (cf. Levins, 1968). Note also that we describe trade-off functions as concave and convex following Levins (1968) and other ecological literature, not as they are defined in mathematical literature (e.g. Chiang, 1984).

At least two scenarios can be envisaged, depending on the form of the trade-off curve. First, we may assume that the microhabitats are sufficiently similar to enable a coloration to be cryptic in both microhabitats, degree of crypsis in one being thus a convex function of degree of crypsis in the other (Figs 2A, 3A). In this case, the prey obtains the highest probability of escaping detection by compromising the requirements of the two microhabitats, so that the improvement of the coloration is more directed by the microhabitat where the prey has a higher probability of spending time, and of encountering a predator. The higher the degree of crypsis that can be acquired in one of the microhabitats, the better the coloration should be adapted to it (Fig. 3B).

Second, the visual properties of the microhabitats may be so different that no coloration can provide a high degree of crypsis in both microhabitats (Fig. 2B). Now, degree of crypsis in one microhabitat is a concave function of degree of crypsis in the other. In this case the probability of escaping detection is maximized by maximizing the degree of crypsis in the microhabitat where the product of the probability of occurring and the probability of encountering a predator is higher (Fig. 3C). With a certain slope, say $-e_{i1}h_1/e_{i2}h_2=k$, we could expect two different phenotypes specialized to be cryptic in different microhabitats to coexist (Fig. 3D). However, even the slightest deviation from k would lead to one of the two phenotypes being superior in the given habitat structure.
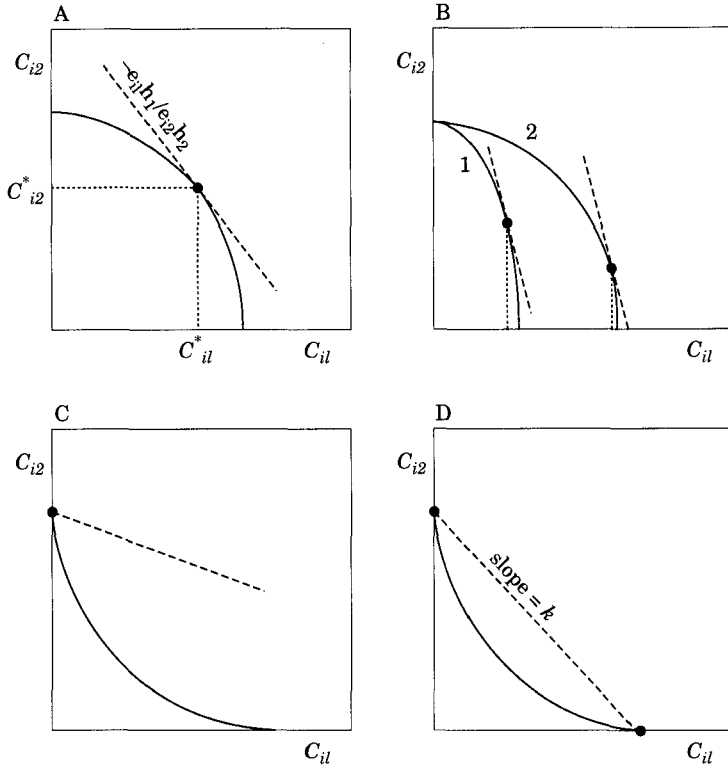
Figure 3. (A) When the slope of the trade-off curve between the degree of crypsis in microhabitats 1 and 2 is convex the local maximum of the probability of escaping predation giving the optimal degree of crypsis in the microhabitats is a compromise between the requirements of the two microhabitats. It is found where the slope equals $-e_{i1}h_1/e_{i2}h_2$. (B) The higher the degree of crypsis the animal can achieve in one of the microhabitats the more the optimal coloration will be affected by the requirements of this microhabitat. Accordingly, trade-off curve 2 yields a higher degree of crypsis in microhabitat 1 than curve 1 does. (C) If the slope of the trade-off is concave the point where its slope equals $-e_{i1}h_1/e_{i2}h_2$ gives a local minimum, and the best solution is, instead, to maximize the degree of crypsis purely in one of the microhabitats. (D) For trade-offs which are partly or wholly concave there exists a special case $-e_{i1}h_1/e_{i2}h_2 = k$ in which there are two distinct optima. A slight change in $-e_{i1}h_1/e_{i2}h_2$ when it's close to k can dramatically switch the optimal coloration from one optimum to the other.

Linear and partially concave trade-off functions represent specific modifications of Figure 3C and D. First, if the trade-off curve were linear with a slope differing from k, the probability of escaping detection is maximized by maximizing the degree of crypsis in the microhabitat where the product of the probability of occurring and the probability of encountering a predator is higher (cf. Fig. 3C). However, in case of multiple equilibria (the slope of the linear trade-off $= k$), instead of only two points, all the points along the trade-off curve are optimal (cf. Fig. 3D). Second, we can also imagine cases in which the shape of the trade-off curve is partially convex and partially concave. Although, generally speaking, the optimization is now specific for each shape of trade-off, the array of optimal colorations is discontinuous for partially concave trade-offs and may lead to coexistence of phenotypes which do not necessarily maximize crypsis (c_{i1} or c_{i2}) in any of the microhabitats as in Figure 3D, but each of

them puts a proportionally greater weight for crypsis in one of the available microhabitats.

Non-random habitat choice

Let us again assume two microhabitats, 1 and 2. However, now the habitat choice of the prey deviates from random. Since we have defined $\Sigma h_j = 1$ and $\Sigma \delta_{ij} = 0$, we can substitute for $h_2 = 1 - h_1$ and $\delta_{i2} = -\delta_{i1}$ in Eq. (1). The probability of escaping detection will now be

$$D_i = 1 - [(1 - c_{i1})e_{i1} - (1 - c_{i2})e_{i2}](h_1 + \delta_{i1}) - (1 - c_{i2})e_{i2} \tag{7}$$

where δ_{i1} can vary between $-h_1$ (all individuals choose microhabitat 2) and h_2 (all individuals choose microhabitat 1). When $\delta_{i1} = 0$, Eq. (7) reduces to the earlier case of random habitat choice (Eq. 2).

In Eq. (7) D_i is a linear function of δ_{i1}. Therefore, we have two possibilities for optimal habitat choice: all individuals should choose either microhabitat 1 ($\partial D_i / \partial \delta_{i1} > 0$) or microhabitat 2 ($\partial D_i / \partial \delta_{i1} < 0$). Differentiating D_i in Eq. (7) in relation to δ_{i1} and keeping the other parameters constant, we can solve the condition for the former possibility

$$(1 - c_{i2})e_{i2} > (1 - c_{i1})e_{i1}. \tag{8}$$

In other words, when the prey has a free choice between the microhabitats, it should prefer microhabitat 1 when the probability of becoming detected by a predator is lower in microhabitat 1 than in microhabitat 2. When the opposite is true, the prey should prefer microhabitat 2. These situations correspond with the optima $\delta_{i1} = h_2$ and $\delta_{i1} = -h_1$ respectively.

When taking the total differential of D_i in relation to unit changes in c_{i1} and c_{i2}, we arrive at the condition

$$\frac{dc_{i2}}{dc_{i1}} = -\frac{e_{i1}(h_1 + \delta_{i1})}{e_{i2}(h_2 - \delta_{i1})} \tag{9}$$

which defines the slope of the trade-off curve for the combination of c_{i1} and c_{i2} giving the maximal probability of escaping detection by predators and the optimal crypsis for the given habitat composition and habitat use pattern. It is now evident that non-random habitat choice can change the slope fundamentally. When $\delta_{i1} = h_2$, the tangent will be parallel with the vertical axis and the optimal crypsis is achieved by maximizing crypsis in microhabitat 1. When $\delta_{i1} = -h_1$, the slope will be zero and the tangent will be parallel with the horizontal axis and the optimal crypsis is achieved by maximizing crypsis in microhabitat 2. The microhabitat choice may be affected also by other factors in addition to predation risk, such as the distribution of resources. In this case the coloration is optimized the same way as when the microhabitat choice is random, except that the deviation from random microhabitat choice is taken into account.

DISCUSSION

In summary, according to our model the optimal coloration in a heterogeneous habitat is achieved either by compromising the degree of crypsis between the microhabitats, or by improving the degree of crypsis in one of the microhabitats at the expense of the other. The form of the trade-off function describing how improved crypsis in one microhabitat impairs crypsis in the other plays a central role in the optimization. When the trade-off between the degree of crypsis in the two micro-habitats is convex, the coloration should evolve to a compromise between the visual elements of the microhabitats. The optimal coloration is achieved by weighting it with the relative probability of occurrence in the microhabitats and encountering a predator there. If the trade-off is concave or linear, the coloration should evolve towards the highest possible degree of crypsis in the microhabitat where the probability of occurrence and encountering a predator is the highest. These pre-dictions hold also when the habitat choice deviates from random. Preference for one of the microhabitats strengthens the selection for crypsis there. On the other hand, if a prey with a certain coloration has a free choice between microhabitats, and only predation risk is considered, then it should stay only in the microhabitat where it has the lowest probability of encountering and being detected by a predator. Habitat choice based purely on maximization of crypsis can, however, be expected to be costly in terms of decreased quantity or quality of resources accessible for the animal. Therefore, we expect that microhabitat choice is affected jointly by resource distribution and predation risk which together determine selection for crypsis and the evolution of coloration.

Our finding that the optimal coloration can, theoretically, sometimes be a compromise between the requirements of the two microhabitats contradicts the idea that the optimal coloration should always be the one which maximizes crypsis in that microhabitat where the prey is most vulnerable to predation (Endler, 1978). In fact, Endler's (1978) proposal can be considered as a specific outcome of a more general theory of optimization of crypsis. We therefore suggest that when quantitative measures of crypsis are made, it is important that the microhabitat proportions and the patterns of habitat use of the animals are known, because some cryptic colorations may have evolved to combine the requirements of the different microhabitats used.

The shape of the trade-off curve is affected by physical and biological constraints in the production of a cryptic coloration, and the visual abilities of the predator. First, the visual difference between the microhabitats sets the physical constraint limiting the simultaneous resemblance of the two backgrounds, and thus determines the best theoretical compromise of background elements (patterns and colours) in the microhabitats for each habitat composition. Similarity in the appearance of the microhabitats makes the trade-off curve more convex and a combination of their requirements more beneficial. Conversely, differences in the visual elements between the two microhabitats make the trade-off curve more concave and the optimal solution approaches maximal degree of crypsis in one of the microhabitats. If we imagine for example a chess board-coloured habitat with purely white and black microhabitats, it is obvious that a good compromise giving a relatively high degree of crypsis in both white and black microhabitats is impossible (Fig. 2B). Also, different mechanisms of achieving crypsis are likely to differ in their background specificity with less background-specific mechanisms producing better compromises. For example, crypsis achieved by disruptive coloration can be less background-specific and

therefore a better option for a compromising coloration than crypsis achieved by background matching (Merilaita, 1998).

Second, although a certain compromise between the visual elements of the two backgrounds would be physically possible, it may be biologically constrained due to lack of genetic variation (Belk & Smith, 1996), high costs of producing such a coloration, or opposing selection for thermal capacity (Gibson & Falls, 1988) or opposing sexual selection (Endler, 1978). Some traits of the coloration may for example vary discontinuously due to simple Mendelian genetics or have a threshold of expression (Roff, 1996), and consequently the trade-off curve can be discontinuous or at least partly have a concave shape.

Third, the visual abilities of the predator affect the form of the trade-off curve. High visual acuity increases the probability of its detecting any deviations from a complete visual resemblance of a microhabitat, and therefore decreases the crypsis of any compromise. On the other hand, if the predator can sense only a narrow spectrum of wavelengths or is unable to distinguish between some wavelengths (cf. colour blindness), the prey can more easily achieve crypsis and successfully use compromises. In other words, a poor visual acuity of the predator can make the shape of the trade-off curve more convex.

The form of the trade-off curve can be studied by measuring the crypsis of an animal coloration in the two different microhabitats it is using. A relatively high degree of crypsis in both microhabitats would suggest a compromising coloration with convex trade-off. A large difference in the degree of crypsis between the two microhabitats would suggest that the coloration is adapted primarily to one of the microhabitats having a concave trade-off. Obviously, the trade-off can be solved for those parts only for which there exist adapted colorations. Therefore, animals with variable colour phenotypes and animals which can adjust their coloration according to their background can be expected to provide most information about the nature of the trade-offs. Also, animals in which the relative proportions of microhabitats vary among populations can be useful in studies about the trade-offs.

Several examples for the outcomes from our model can be found in nature. A cichlid fish, *Telmatochromis temporalis*, provides an example of a coloration corresponding to the concave trade-off with no compromises. The individuals of this species acquire either a pale or dark coloration depending on the proportions of well-illuminated and shaded areas in their territories (Mboko & Kohda, 1995). Similarly, in the pattern dimorphic walking-stick, *Timema cristinae*, either morph is strongly associated with such patches in which the shrub, on which the morph has higher crypsis, is more abundant (Sandoval, 1994b). There are also several examples of animals living in visually heterogeneous habitats with a coloration adapted primarily to one of the microhabitats, which increase their crypsis by choosing microhabitats on the basis of their visual characters (Broadman *et al.*, 1974; Gillis, 1982; Steen *et al.*, 1992), or by regulating their coloration according to their background (Jormalainen & Tuomi, 1989; Marshall & Messenger, 1996; Ramachandran *et al.*, 1996).

Also, examples of species corresponding to the convex trade-offs with compromised colorations between the microhabitats can be found in nature. The desert spiny lizard, *Sceloporus magister*, living on a substratum of variable colour, has a coloration compromising the reflectance spectrum of its background colours (Norris & Lowe, 1964). Several background generalist and semi-generalist moths had their highest degree of crypsis in combined backgrounds rather than on specific backgrounds (Endler, 1984).

Some implications for colour polymorphism can also be found from our model. First, it is possible that more than one coloration yields the same optimal solution because their degrees of crypsis are equal, which could enhance the probability of coexistence of these morphs (cf. Endler, 1978, 1988). Second, when the trade-off is concave, there exists a special case with two alternative colorations with different degrees of crypsis in the two microhabitats having equal probability of escaping detection (Fig. 3D: $-e_{i1}h_1/e_{i2}h_2 = k$). It is, however, improbable that this kind of labile equilibrium could result in stable colour polymorphism without any further assumptions. The third and the most interesting prediction from this model, when colour polymorphism is considered, is that when $-e_{i1}h_1/e_{i2}h_2$ is close to k, even a slight change in the slope can shift it over k and switch the optimal coloration to a completely different one. Thus, when two populations of a prey species are considered, we suggest that in some cases a minute difference in microhabitat proportions or microhabitat-specific predation risks may lead in selection favouring very different colorations in the two populations. Consequently, a slight or gradual variation between populations in habitat composition can result in discrete variation in optimal animal colorations, which together with gene flow between the populations could maintain polymorphism (Felsenstein, 1976).

There can also be selection for different colorations within populations if the microhabitat choice differs between individuals. Such differences in coloration correlated with habitat use are common between different states of life cycle but can also be found between sexes (Stepien, 1987; Calver & Bradley, 1991; Forsman & Shine, 1995; Merilaita & Jormalainen, 1997).

To conclude, the optimal cryptic coloration can either be a compromise between the two microhabitats or shaped entirely by the requirements of only one of them. The trade-off between crypsis in the two microhabitats plays an important role. In some cases a slight change in proportion or probability of encountering a predator can switch the optimal coloration to a very different one. When studying crypsis in heterogeneous habitats it is important to know the microhabitat proportions, the habitat use pattern of an animal, its degree of crypsis and risk of encountering a predator in all the microhabitats it uses.

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