

The evolution of crypsis when pigmentation is physiologically costly

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Abstract

The evolution of crypsis when pigmentation is physiologically costly. Predation is one of the main selective forces in nature, frequently selecting for crypsis in prey. Visual crypsis usually implies the deposition of pigments in the integument. However, acquisition, synthesis, mobilisation and maintenance of pigments may be physiologically costly. Here, I develop an optimisation model to analyse how pigmentation costs may affect the evolution of crypsis. The model provides a number of predictions that are easy to test empirically. It predicts that imperfect crypsis should be common in the wild, but in such a way that pigmentation is less than what is required to maximise crypsis. Moreover, optimal crypsis should be closer to “maximal” crypsis as predation risk increases and/or pigmentation costs decrease. The model predicts for intraspecific variation in optimal crypsis, depending on the difference in the predation risk or the costs of pigmentation experienced by different individuals.

Key words: Predation, Pigmentation, Coloration

Resumen

La evolución de la cripsis cuando la pigmentación es fisiológicamente costosa. La depredación es una de las principales fuerzas de selección de la naturaleza y a menudo favorece la cripsis en las presas. Por lo general, la cripsis visual implica el depósito de pigmentos en el tegumento. Sin embargo, adquirir, sintetizar, movilizar y mantener los pigmentos puede ser fisiológicamente costoso. En este estudio he elaborado un modelo de optimización para analizar cómo pueden afectar los costes de la pigmentación a la evolución de la cripsis. El modelo proporciona una serie de predicciones que son fáciles de probar empíricamente. Predice que la cripsis imperfecta debería ser común en la naturaleza, pero de manera que la pigmentación fuera inferior a la necesaria para que la cripsis sea máxima. Además, la cripsis óptima debería estar más cerca de la cripsis “máxima” a medida que aumenta el riesgo de depredación o disminuye el coste de la pigmentación. El modelo también predice la existencia de variación intraespecífica en la cripsis óptima, que depende de la diferencia en el riesgo de depredación o de los costes de la pigmentación que soportan los diferentes individuos.

Palabras clave: Depredación, Pigmentación, Coloración

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Introduction

Predation is one of the main selective forces in nature, so select for potential prey to have a number of adaptations to avoid being devoured (Ruxton et al., 2004; Caro, 2005; Stevens and Merilaita 2011; Cooper and Blumstein, 2015). One of the main means for potential prey to avoid predation is to evade predator detection, frequently by developing cryptic coloration (Endler, 1978; Ruxton et al., 2004; Caro, 2005; Merilaita and Stevens, 2011; Cuthill, 2019). Crypsis by colour matching involves prey presenting coloration similar to the background where they are most often exposed to predator attacks to avoid being detected by visual predators (Endler, 1990; Stevens and Merilaita, 2009; Merilaita et al., 2017). Indeed, experimental studies have shown that less colour difference between the animal and the background, from the predator's perspective (i.e. the greater the degree of visual crypsis), equates to less risk of being depredated (Cooper and Allen, 1994; Bond and Kamil, 2002; Stuart–Fox et al., 2003; Cuthill et al., 2005; Cook et al., 2012; Dimitrova and Merilaita, 2014; Merilaita and Dimitrova, 2014; Troscianko et al., 2016; Michalis et al., 2017; Walton and Stevens, 2018).

Colour is a complex trait that can be defined according to the HSL model, in which *H* is the hue, the 'colour' in common parlance, *S* is the saturation, the purity of the hue, and *L* is lightness, the quantity of light reflected by the surface (Montgomerie, 2006). To attain visual crypsis, animals generally need to deposit pigments in teguments exposed to the visual system of potential predators in order to develop a tegument coloration resembling the background. To this end, animals must acquire or synthesise one or more pigments that provide a hue of coloration similar to the background colour. Once the proper pigment has been produced, its saturation and lightness will provide the correct concealment against the background. For example, given the proper pigment, maximal crypsis may vary according to the degree of saturation, with crypsis declining when saturation deviates from the optimal level (fig. 1). The level of saturation of a colour is typically determined by the concentration of the pigment providing that colour (Ito and Wakamatsu, 2003; McGraw and Gregory, 2004; McGraw and Wakamatsu, 2004; McGraw et al., 2005; Fargallo et al., 2007; McGraw and Toomey, 2010; Roulin et al., 2013).

Nevertheless, the acquisition, synthesis, mobilisation and maintenance of pigmentation may be costly (review in Hill and McGraw, 2006). These costs, though extensively studied in the context of social signals, have received little or no attention in the context of visual crypsis (but see Rodgers et al., 2013). For example, one of the pigments most used in crypsis is melanin (Hubbard et al., 2010; also see Galván et al., 2017), which is also involved in social signals (Jawor and Breitwisch, 2003). Melanin is synthesised from the amino acid tyrosine (with cysteine intervening in the synthesis of pheomelanin) in complex pathways occurring in melanocytes (McGraw, 2006). It is

then stored in organelles called melanosomes and transferred to keratinocytes in the tegument. Melanin-based tegument coloration therefore depends on the concentration of melanin in melanosomes or the concentration of melanosomes in the tegument (Grether et al., 2004). Melanin synthesis may be energetically costly and constrained by a low dietary intake of amino acids (McGraw, 2006). Moreover, the biochemical pathways in which melanin metabolism intervenes and its hormonal regulation may impact on the immune system, oxidative balance, and other physiological processes (Ducrest et al., 2008). But not only pigmented colours may be expensive. For example, white colours, involving unpigmented structural colorations (Prum, 2006), require certain production or maintenance costs (Poston et al., 2005; Moreno–Rueda, 2010; Vágási et al., 2010).

Therefore, maintaining a certain coloration in the integument could prove costly, even in the absence of social selection, and these costs may have an effect on the evolution of crypsis, presumably reducing the optimal level of crypsis. In this paper, I hypothesise that the evolution of crypsis is constrained by the costs of pigmentation. Furthermore, if cryptic pigmentation is costly and these costs differ among individuals, then we can expect intra- and interspecific variation in cryptic coloration. Here, I formally present this hypothesis by examining the evolution of crypsis based on a scenario of costly pigmentation and by developing a simple optimisation model.

The model

Let us consider an animal that, when not preyed upon, reaches its maximal residual fitness, $W = 1$. Its residual fitness would descent to zero if depredated and the probability of being preyed upon is directly related to the probability of being detected by the predator, i.e. the inverse of the animal's degree of crypsis. Assuming that visual crypsis is achieved solely through one pigment, crypsis may be considered a function of the amount of the pigment deposited in the tegument. Therefore, the animal's fitness will be modified by the function $P(x)$, where x is the quantity of pigment deposited and P is the probability of avoiding predator detection through crypsis. Obviously, even with maximal crypsis, there is still a chance of being depredated, but this probability is constant with respect to pigmentation and so it is not considered here. Let us assume that the animal is typically present on only one type of background and has only one type of predator, thus avoiding the heterogeneity due to different backgrounds and predators with different visual systems, which is beyond the scope of this paper.

Hence, a specific amount of pigment provides a maximum degree of crypsis ($x_{crypsis}$). Therefore, when $x = x_{crypsis}$, $P(x_{crypsis}) \sim 1$; that is, the animal has the lowest probability of being preyed upon. However, if $x \neq x_{crypsis}$, $P(x) < 1$, the animal would have a higher probability of being depredated, thereby reducing its fitness. As such, fitness as a consequence of predation is a function of the level of pigment the animal

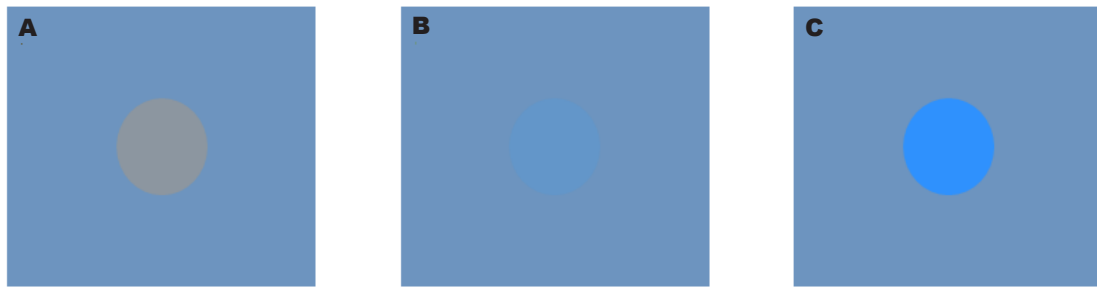


Fig. 1. Example of how the level of saturation may affect visual crypsis. The circle has the same values of hue and lightness as the background ($H = 150$, $L = 150$), but differs in saturation; saturation is 100 for the background and 25 (A), 125 (B) and 250 (C) for the circle. It is evident that the circle is most cryptic in (B), where the overall difference in saturation is the smallest.

Fig. 1. Ejemplo de cómo el grado de saturación puede afectar a la cripsis visual. El círculo tiene los mismos valores de matiz y luminosidad que el fondo ($H = 150$, $L = 150$), pero difiere en saturación; la saturación es 100 para el fondo y 25 (A), 125 (B) y 250 (C) para el círculo. Es evidente que el círculo más críptico es el (B), donde se produce la menor diferencia general en la saturación.

uses for crypsis. At the same time, if the acquisition, synthesis, deposition or maintenance of the pigment imposes a physiological cost on the animal in other fitness parameters (energy, immunity, oxidative balance, etc.), then fitness would also be reduced according to a function that depend directly on the quantity of pigment used for crypsis: $C(x)$. Therefore, the fitness of an animal adopting a strategy of visual crypsis (everything being equal) may be defined by the equation:

$$W = [1 - C(x)] \cdot P(x) \quad [1]$$

In this equation fitness ranges from 0 to 1, it is reduced by the function $C(x)$ whose values lies between 0 and 1 and modified by a probability function of escaping predator detection, $P(x)$. Note that this includes the extreme possibilities in which the physiological costs are so high that the animal dies, when $C(x) = 1$, or when there is no cost for the case of $C(x) = 0$.

The effect of quantity of pigment deposited on the probability of being depredated can be considered a quadratic function such that:

$$P(x) = 1 - b(x_{cryspsis} - x)^2,$$

where b is a parameter related to the strength of the selective pressure from predators; that is, b indicates how much fitness decreases as a consequence of increased predation risk as the degree of crypsis deviates from maximal crypsis ($x_{cryspsis}$) (fig. 2). Higher values of b indicate a steeper decrease in fitness as the level of crypsis declines (fig. 2). Meanwhile, C can be approached as a linear function such as $C(x) = cx$, where c is the degree to which fitness is affected by the quantity of pigment (x) deposited in the tegument (fig. 2). Given these equations, fitness can be expressed as:

$$W = [1 - cx] \cdot [1 - b(x_{cryspsis} - x)^2] \quad [2]$$

Results

To examine how the optimal pigmentation values (x^*) vary depending on the three parameters defined in the model (c , b and $x_{cryspsis}$), I ran computer simulations where the values of a specific parameter were allowed to vary along a continuum (0 to 1) while the other two parameters remained fixed, and the value of x^* (which maximises fitness) was estimated. The results show that higher values of both b and $x_{cryspsis}$ increase the optimal value of x . On the other hand, the optimal value of x decreases monotonically with an increase in the costs c of depositing pigment in the tegument (fig. 3). In other words, the optimal pigmentation level increases when greater pigmentation is necessary for maximal crypsis and also when fitness decreases steeply if crypsis diminishes; however, the optimal pigmentation level decreases when the cost of pigmentation increases.

The model also shows that x^* is typically smaller than $x_{cryspsis}$ except when $c = 0$. That is, the costs associated with pigmentation mean that optimal pigmentation is below the level that produces maximum visual crypsis. Moreover, the function of x^* according to b depended on the costs; the function was smoother for low values of c , while x^* was relatively higher for low values of b (fig. 4).

Discussion

The model indicates that when greater quantities of pigment are needed for maximal crypsis ($x_{cryspsis}$), the optimal quantity of pigment (x^*) the animal should deposit in its tegument is also higher. This finding implies that in the case of crypsis resulting from eumelanin, for example, darker substrates require the incorporation of more eumelanin in the teguments.

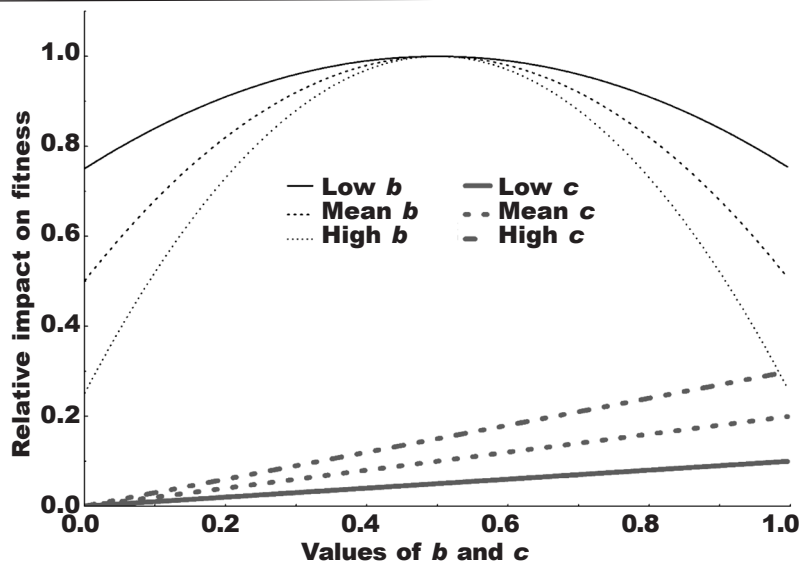


Fig. 2. Fitness associated with different values of b and c according to the level of pigmentation (x). The data consider a maximal crypsis at a pigmentation level of 0.5 ($x_{\text{crypsis}} = 0.5$). The higher the risk of predation when non-cryptic (b), the steeper the function of fitness related to pigmentation. The higher the cost of pigmentation, the greater the fitness lost.

Fig. 2. Eficacia biológica asociada a diferentes valores de b y c según el grado de pigmentación (x). Los datos apuntan que la cripsis es máxima cuando el grado de pigmentación es de 0,5 ($x_{\text{cripsis}} = 0,5$). Cuanto mayor es el riesgo de depredación en ausencia de cripsis (b), más pronunciada es la función de la eficacia biológica relacionada con la pigmentación. Cuanto mayor sea el coste de la pigmentación, mayor será la pérdida de eficacia biológica.

On the other hand, the optimal quantity of eumelanin would be lower for light substrates. Thus, one prediction from the model is a match between the background colour and the quantity of pigment used for crypsis, which is supported by a number of studies that have reported a relationship between substrate hue and animal coloration (Nachman et al., 2003; Laurent et al., 2016).

However, the model also predicts that x^* will generally be smaller than x_{crypsis} , so crypsis is not usually maximal. Typically, imperfect crypsis has been attributed to background heterogeneity (Hughes et al., 2019), gene flow (Rosenblum, 2006), constrictions for crypsis (Cutchill, 2019), or a conflict with other selective pressures on coloration such as sexual selection (Martin and Badyaev, 1996). As such, the present model suggests that imperfect crypsis may be widespread in the wild. According to the model, maximal crypsis is only reached when the cost of pigmentation is null, so $x^* = x_{\text{crypsis}}$. Pigmentation costs could be zero if animals compensate for it, such as in the case of an excess of amino-acids required in pigment synthesis. Nevertheless, for very high predation-risk values (b) and/or reduced pigmentation costs (c), the optimal level of pigmentation may be very close to the level needed for maximal crypsis. Mathematically, if $b \gg c$, then $x^* \sim x_{\text{crypsis}}$. Notice that

the model not only predicts imperfect crypsis, but also that animals will deposit less pigment than the amount required to maximise crypsis. This means that animals should have less saturated coloration than necessary for maximal crypsis rather than an excess of pigment. As far as I am aware, this prediction from the model has not been studied empirically.

Parameter b is an indicator of how the risk of being depredated varies as crypsis deviates from maximum, i.e. the crypsis-dependent risk of predation. The higher the b , the quicker fitness is lost because the tegument coloration differs from the background (fig. 2). The model predicts higher values of x^* for a greater crypsis-dependent risk of predation. Endler (1978) stated that if selection by predation is weak, crypsis may not be very accurate. My model conceptualises why the level of crypsis depends on the risk of predation, the key factor being the cost associated with pigmentation. Although b is determined by the predator's perception, if pigmentation costs were null, crypsis would be maximal even for a very low predation risk. In other words, in the long evolutionary run, and with no other selective pressures intervening, a weak predation risk would only allow reduced visual crypsis if pigmentation were costly. However, if the risk is very high, the optimal level of pigmentation will approach that of maximal crypsis even for high pigmentation costs (fig. 4).

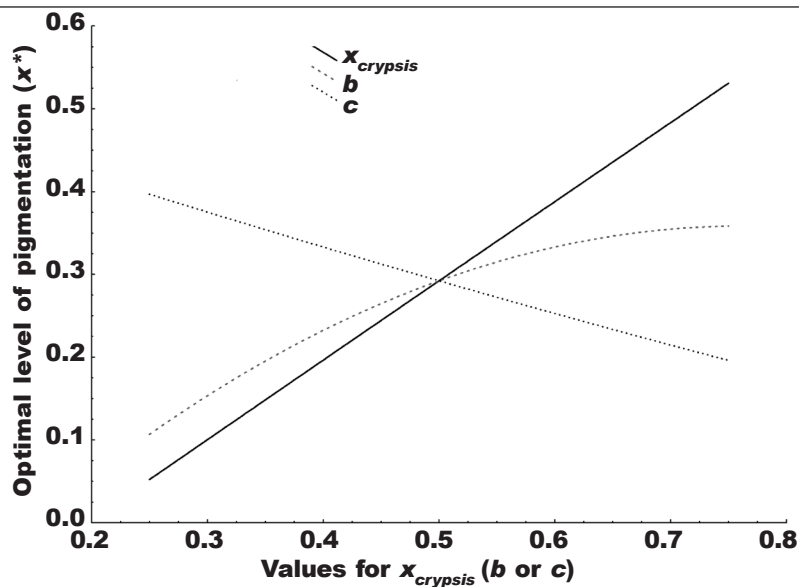


Fig. 3. Optimal level of pigmentation (x^*) as a function of pigmentation level that maximises crypsis (x_{crypsis}), predation risk when non-cryptic (b) and costs associated with pigmentation (c).

Fig. 3. Grado óptimo de pigmentación (x^*) en función del grado de pigmentación en el que la cripsis es máxima (x_{crypsis}), el riesgo de depredación en ausencia de cripsis (b) y los costes asociados a la pigmentación (c).

The costs of pigmentation, on the other hand, affect the way in which x^* varies with predation risk, with lower values and steeper functions as the costs become higher (fig. 4). The model therefore predicts that crypsis should be higher as predation risk increases; this conjecture is supported by some studies (e.g. Endler, 1980). Nevertheless, the model also stresses that, at the intraspecific level, individuals with a higher predation risk (e.g. those with a lower capacity for escape) are expected to be more cryptic (provided all else is equal, i.e. no other antipredator strategies are involved).

As expected, the optimal level of pigmentation, which maximises fitness, should decline as the cost of pigmentation increases. As explained earlier, acquisition, mobilisation, synthesis and maintenance of pigmentation may be costly, at least under certain circumstances. An important implication of the model is that if pigmentation costs vary between individuals, then the optimal level of crypsis should also vary between individuals. To the best of my knowledge, the literature is bereft of any studies on this aspect. So the model predicts that, all else being equal, individuals for whom pigmentation is more costly should be less cryptic than those with less costly pigmentation. For example, given that grooming is very costly in terms of time and energy (Walther and Clayton, 2005), unwell individuals might reduce time spent grooming (Yorinks and Atkinson, 2000) and hence plumage coloration fades (Zampiga et al., 2004). These less cryptic individuals may therefore favour alternative

antipredator strategies, such as aposematism (Merilaita and Tullberg, 2005), or their lower crypsis (and hence higher mortality prospects) may affect their life history, for example, favouring fast life styles (Roff, 2002). What is more, costs might not be limited to pigmentation but also affect pigmentation patterning, which is very important for camouflage (Merilaita and Lind, 2005). In conclusion, if pigmentation for crypsis is costly, it involves several ecological and evolutionary implications that require further investigation.

This model, however, is a first approach and has a number of limitations. Firstly, it assumes that only one pigment is involved in tegument coloration. This situation is probably very rare in nature, where coloration typically results in a mix of pigments and structural traits (Grether et al., 2004). Moreover, changes in tegument coloration can be achieved not only by varying the concentration of a pigment, but also by changing the pigment (e.g. replacing eumelanin with pheomelanin) or by pigment abrasion (Negro et al., 2019). In such cases, if each pigment is associated with a different cost, increasing crypsis could result in a lower physiological cost than remaining less cryptic (Grether et al., 2004). Furthermore, camouflage frequently results from a pattern of several colours providing disruptive crypsis (Cuthill et al., 2005), a complication that is not captured by the model. The model only considers what happens when the prey moves across one type of substrate and has one type of predator. Heterogeneity regarding the microhabitats the prey uses is known to constrain

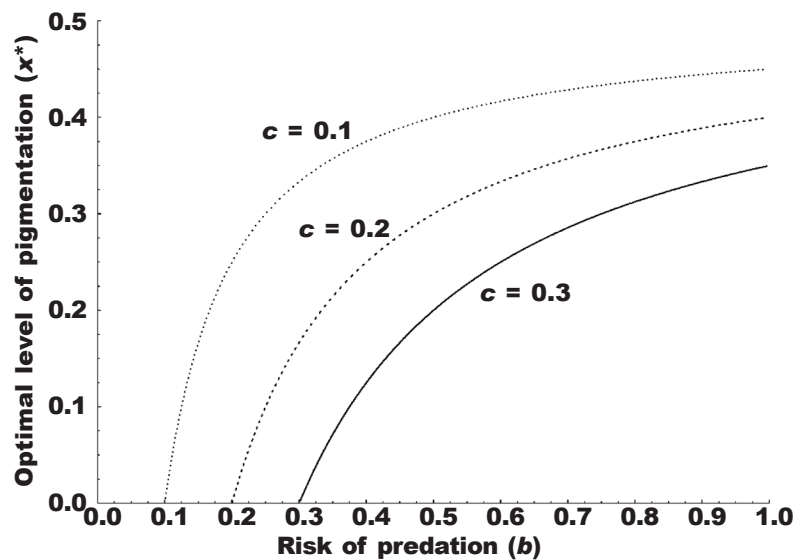


Fig. 4. Optimal level of pigmentation (x^*) for maximal crypsis at a pigmentation level of 0.5 ($x_{\text{crypsis}} = 0.5$), as a function of the predation risk when non-cryptic (b) for different pigmentation costs (c). The optimal level of pigmentation increases monotonically with the risk of predation, approaching an asymptote at $x_{\text{crypsis}} = 0.5$. The higher the pigmentation cost, the lower the optimal pigmentation for a given risk predation and the asymptote is reached more slowly.

Fig. 4. Grado óptimo de pigmentación (x^*) para una cripsis máxima a un grado de pigmentación de 0,5 ($x_{\text{crypsis}} = 0,5$), en función del riesgo de depredación (b), para diferentes costes de pigmentación (c). El grado óptimo de pigmentación aumenta con el riesgo de depredación y se acerca a una asíntota en $x_{\text{crypsis}} = 0,5$. Cuanto mayor es el coste de pigmentación, menor es la pigmentación óptima para una depredación de riesgo dada y más lentamente se alcanza la asíntota.

the evolution of crypsis (Hughes et al., 2019). Prey found living in several habitats are predicted to evolve a compromise coloration or customise their crypsis for a specific microhabitat, usually the most frequent or that in which they are at most risk (Merilaita et al., 1999; Houston et al., 2007; Nilsson and Ripa, 2010). Incorporating pigmentation costs in these models might modify their predictions as prey could specialise their crypsis for microhabitats where it is less costly. Regarding the effect of multiple predators, theory predicts the evolution of monomorphic prey (cryptic against the most danger predator) or a polymorphism (Endler, 1988). The consideration of pigmentation costs would probably affect these predictions, favouring the less expensive crypsis under certain circumstances. The movement of prey may also affect the effectiveness of crypsis (Hall et al., 2013). Future extensions of this model should explore all these limitations.

In conclusion, this model suggests that crypsis evolution may be strongly affected by pigmentation costs. The model presented here provides a number of new predictions that are simple to test empirically: (1) imperfect crypsis should be common in the wild; (2) the level of pigmentation should typically be lower (not higher) than the level of maximum crypsis; (3) crypsis should be closer to maximum when risk of

predation is higher; (4) crypsis should be closer to maximum when the cost of pigmentation is lower; and (5) crypsis should present intraspecific variation: individuals that are generally more exposed to predators and those for which pigments are less costly should show more cryptic coloration.

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