

Animal camouflage: compromise or specialize in a 2 patch-type environment?

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Many animals possess camouflage markings that reduce the risk of detection by visually hunting predators. A key aspect of camouflage involves mimicking the background against which the animal is viewed. However, most animals experience a wide variety of backgrounds and cannot change their external appearance to match each selectively. We investigate whether such animals should adopt camouflage specialized with respect to one background or adopt a compromise between the attributes of multiple backgrounds. We do this using a model consisting of predators that hunt prey in patches of 2 different types, where prey adopt the camouflage that minimizes individual risk of predation. We show that the optimal strategy of the prey is affected by a number of factors, including the relative frequencies of the patch types, the travel time of predators between patches, the mean prey number in each patch type, and the trade-off function between the levels of crypsis in the patch types. We find evidence that both specialist and compromise strategies of prey camouflage are favored under different model parameters, indicating that optimal concealment may not be as straightforward as previously thought. *Key words:* background matching, camouflage, compromise crypsis, optimal foraging, specialization. [*Behav Ecol* 18:769–775 (2007)]

Many animals possess camouflage markings designed to reduce the chance of being detected by visually hunting predators. Most contemporary accounts of camouflage follow Endler's (1978) description of background pattern matching (or crypsis), where optimal concealment is achieved by matching a random sample of the background at the time and location where the risk of predation is greatest. However, it is becoming increasingly apparent that background matching alone may not optimize camouflage and that a range of other strategies (not necessarily mutually exclusive) are important, notably disruptive coloration (Thayer 1909; Cott 1940; Merilaita 1998; Cuthill et al. 2005; Merilaita and Lind 2005; Stevens et al. 2006). Additionally, Thayer (1909) alluded to the possibility that some individuals may be found on a range of backgrounds, or in a range of microhabitats, and so would never be able to match all backgrounds perfectly. In this instance, the optimal strategy may be to possess markings that confer some level of camouflage on all backgrounds, even if this means suboptimal crypsis on any one background. In other words, a generalist rather than a specialist camouflage strategy is optimal. The idea of a "compromise" in camouflage was investigated in a model by Merilaita et al. (1999), with 2 patch types and prey which could either match one background entirely and not the other or be a compromise between the 2 patches. Merilaita et al. (1999) found that prey should adopt a specialist strategy when the risk of predation was unequal between the patches, and when the trade-off in crypsis between the 2 habitats was concave up. However, a compromise strategy was favored when the trade-off was concave down. Support for the efficacy of compromise coloration has also been found by Merilaita et al. (2001) in trials with live birds and artificial prey.

The approach of Merilaita et al. (1999) laid out a clear logic for the conditions under which different camouflage strate-

gies may arise. However, it considered only how the trade-off function between prey camouflage in the 2 patches affected the preys' optimal strategy and assumed predator behavior was fixed. In fact, the predators' behavior (e.g., the time predators spend in the different patches) will also influence (and be influenced by) the optimal strategy. Because predator and prey affect each other's optimal policy, simple intuition cannot guide us to a conclusion. Here, we develop a model consisting of 2 patch types, with predators and prey both optimizing behavior with respect to the other, to investigate the robustness of the conclusions of Merilaita et al. (1999) about how the optimal camouflage strategy changes with conditions.

OPTIMIZING CRYPSIS IN A 2 PATCH ENVIRONMENT

Our model contains prey individuals that are distributed at random, but not necessarily equally, between 2 patch types, 1 and 2. Each patch type contains a Poisson-distributed number of prey with mean number M_i in patches of type i . These prey are hunted by predators that move through the environment seeking to maximize their energetic intake rate (Stephens and Krebs 1986). The phenotype of the prey determines the level of camouflage in each patch type, which is manifested in the capture rate C_i per prey of the predator in patch type i . As such, we define the prey phenotype as that property which affects capture rate by a predator in a habitat. For comparison with a treatment by Merilaita et al. (1999), a low capture rate in a given patch type should be interpreted as the prey having a high level of crypsis on that patch type. We stress that we are not modeling the mechanism by which prey appearance affects conspicuousness to the predator; such a model would have to make specific assumptions about predator perception and cognition (e.g., effects of attention and short-term perceptual filters such as search images).

Because we are not interested in the degenerate case where prey are fully camouflaged on both patch types simultaneously, we specify a trade-off function which links the

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2 capture rates. The capture rate of prey in patch type 2 is related to the capture rate of the prey in patch type 1 by

$$C_2 = 1 - C_1^k, \quad (1)$$

where k is a value which determines the relationship between the capture rates in both patch types (Figure 1). Equation 1 is similar to the trade-off between the degrees of crypsis of prey in 2 microhabitats used by Merilaita et al. (1999), except that here we use a trade-off between capture rates instead of camouflage per se. We note here that in nature there is no reason not to suspect that different, potentially more complex, trade-off functions may also exist, other than the ones that we have presented here. Camouflage is evolutionarily affected by the consequent effects on capture rate (and capture rate obviously affects fitness). A negative relationship is often expected between the capture rates in 2 visually different microhabitats, as it is likely that with greater specialization toward one habitat, an animal's match in other habitats would correspondingly be reduced. That is, as an animal's camouflage markings become a better match toward a given background type, one would expect that camouflage on other backgrounds would be sacrificed, and this would be reflected in the change in capture rates by predators in the different patches. Predators have a specified travel time τ between patches, a proportion p_i of which are of patch type i . Given that prey numbers follow a Poisson distribution, it is optimal to follow a fixed-time rule (i.e., stay in a given patch type for a fixed time, regardless of rewards found [Iwasa et al. 1981; McNamara 1982]). If a predator spends a time T_i in a patch of type i , then its intake rate γ is given by the following equation, where C_i is constrained by Equation 1 (Iwasa et al. 1981):

$$\gamma = \frac{p_1 M_1 (1 - \exp(-C_1 T_1)) + p_2 M_2 (1 - \exp(-C_2 T_2))}{\tau + p_1 T_1 + p_2 T_2}. \quad (2)$$

For a given value of C_1 (and therefore C_2), we can find the optimal time T_i^* for the predator to spend in a patch of type i . The optimal times maximize γ and hence are given by

$$\frac{\partial \gamma}{\partial T_i} = 0, \quad \text{from which it follows that}$$

$$T_i = \frac{1}{C_i} \ln \left(\frac{C_i M_i}{\gamma} \right) \quad (3) \text{ (cf. Iwasa et al. 1981).}$$

In our model, the optimum strategy for the prey, in terms of the level of compromise between C_1 and C_2 , is that which minimizes the maximum intake rate of the predators (cf. Stewart-Oaten 1982). This strategy may involve specialization toward crypsis in patch type 1 (where C_1 would be small) or patch type 2 (where C_2 would be small) or a compromise strategy where the prey items are optimally camouflaged in neither patch type but have some level of camouflage in both patches. Our model seeks to determine what strategies are favored under varying patch parameters. All results were obtained by writing a custom program in the software MATLAB (The Mathworks Inc., Natick, MA), with each result the product of iteration between Equations 2 and 3 to find the strategy that yields the optimal value of γ for the predator (i.e., the highest value) for a given value of C_1 (and hence C_2). Stability was always reached in less than 20 iterations. This is repeated for a range of C_1 values, and the prey are expected to play the strategy (adopt the value for C_1) for which the iterated value of γ is lowest. It is important to note that we have simplified the problem by assuming that the prey population is monomorphic, so the prey strategy that minimizes the iterative value of γ is also the strategy that minimizes each individual's

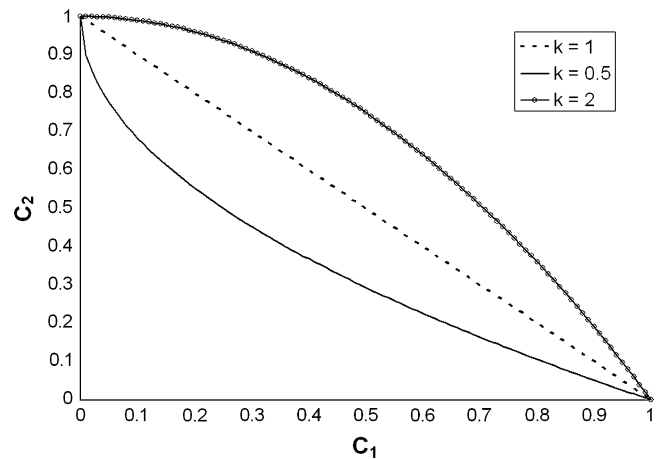


Figure 1
The trade-off function between the capture rate of prey in patch type 1 (C_1) and patch type 2 (C_2). Shown are the trade-off curves for 3 values of k : 0.5, 1.0 and 2.0.

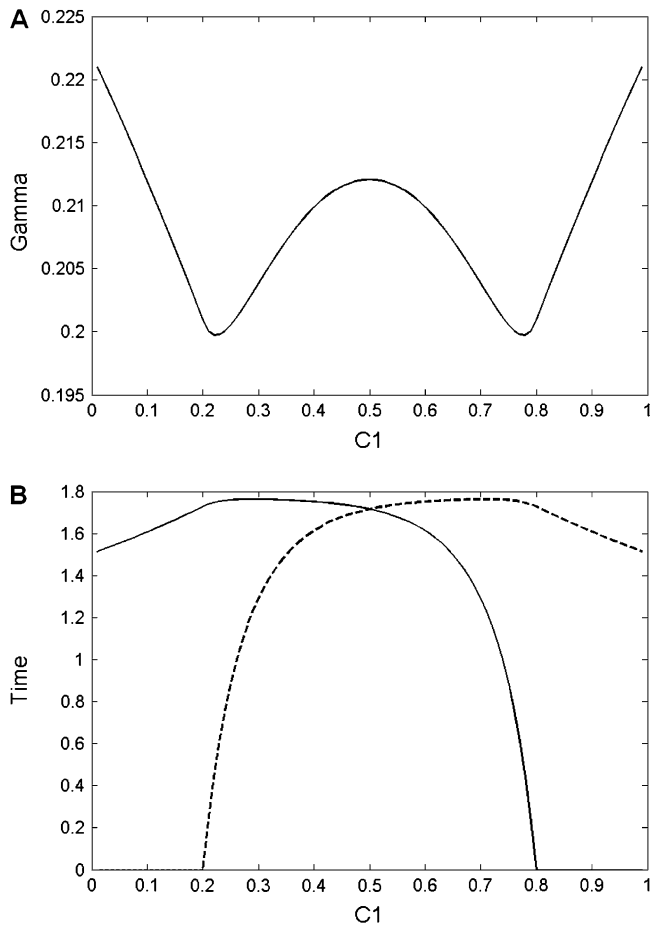
predation risk. Future work needs to consider more complex cases in which more than one form of prey might coexist.

THE EFFECT OF PATCH PROPORTIONS

For all the following examples, $M_1 = 1.0$, $M_2 = 1.0$, $\tau = 1.0$ and $k = 1.0$. By varying the relative patch proportions and running the model for a range of values of C_1 (from 0.01 to 0.99 in steps of 0.01), we can determine the optimal strategy of the prey and the time predators spend in both patch types. When the proportions of the 2 patch types are equal ($P_i = 0.5$), we find that the optimum strategy of the prey is largely specialization toward camouflage in either patch type, although with some level of compromise (Figure 2A), showing that there can be more than one local minimum. We inevitably end up with a symmetrical figure featuring 2 equal minima because of the inherent symmetry of the situation brought on by the assumptions that $M_1 = M_2$, $P_1 = P_2$ and $k = 1$; any deviation away from these assumptions would destroy the perfect symmetry of this figure. In this situation, predators do not always forage in both patches; for instance, predators do not forage in patch type 1 (i.e., $T_1 = 0$) when prey are captured at a low rate in this patch type (i.e., prey are well camouflaged) (Figure 2B). If the patch proportions are altered so that patch type 1 is now the dominant patch type in the environment (e.g., $P_1 = 0.8$, $P_2 = 0.2$), the optimal strategy for the prey becomes specialization toward being cryptic in patch type 1 (though still with a small level of camouflage toward patch type 2) (Figure 3A). Therefore, the greater the proportion of a given patch type in the habitat, the greater the level of crypsis toward that particular patch type prey should adopt.

THE EFFECT OF TRAVEL TIME BETWEEN PATCHES

The most significant and potentially intriguing results found from the model are those when the travel time of the predators between patches is altered. For example, if the travel time between patches is increased from 1.0 (as above with all patch parameters equal; Figure 2A) to a value of 20.0, the optimal strategy of the prey to minimize the predators' intake rate becomes a strong specialization toward being cryptic in either patch type 1 or patch type 2 (Figure 4A); any level of compromise is strongly disfavored. In contrast, markedly decrease the travel time between patches (to 0.2) and the optimal strategy is now a compromise between being cryptic in the 2 patch

**Figure 2**

(A) The intake rate of the predators (gamma) as a function of C_1 , where $k = 1.0$, $P_1 = 0.5$, $P_2 = 0.5$, $M_1 = 1.0$, $M_2 = 1.0$, and $\tau = 1.0$. The graph shows a symmetrical relationship where the optimal strategy of the prey (which minimizes gamma) is largely specialization toward either patch type but with some compromise toward the opposing patch type. (B) The time that the predators spend in patch type 1 (dashed line) and patch type 2 (solid line) as a function of C_1 . This shows that predators do not always forage in both patch types in an effort to maximize their intake rate.

types (Figure 4B). Therefore, the travel time between patches has a strong influence on the optimal prey strategy and can lead to either specialization or compromise in the model.

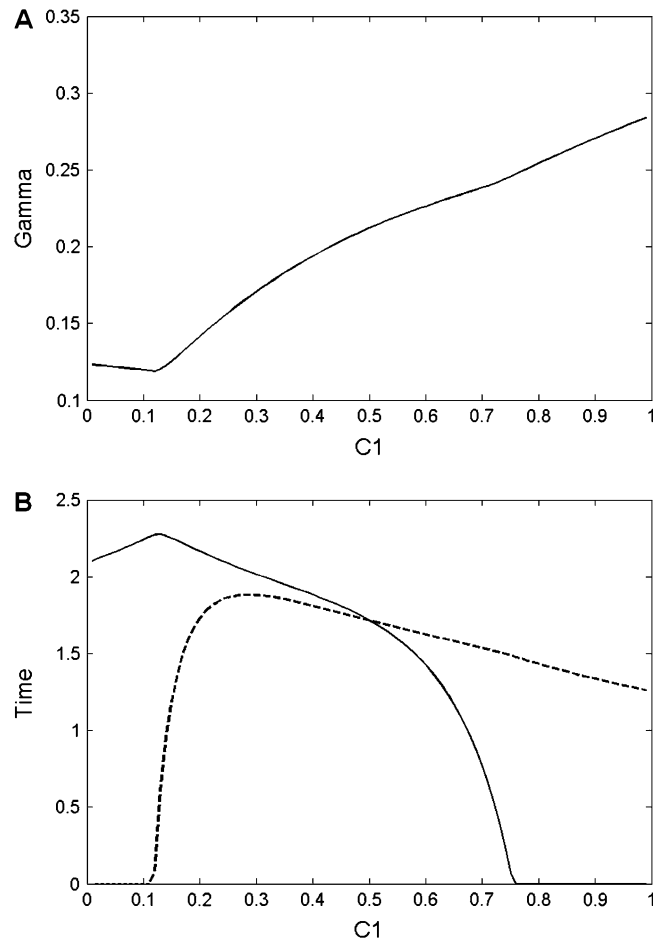
THE EFFECT OF THE NUMBER OF PREY ITEMS IN A PATCH

Symmetrical patch parameters

Increasing the number of prey items in a patch has an effect on the model results that are readily understood intuitively. For larger values of M , when M is increased by the same amount in both patch types, the intake rate of the predators increases. Changes to the number of prey items in a patch in this way do not affect the shape of the gamma (γ) curve (Figure 2A) and so have no influence on the optimal strategy of the prey.

Asymmetrical patch parameters

Increasing the number of prey items contained in one patch type, relative to the number of prey items in the other patch type, affects the optimal strategy of the prey in minimizing the

**Figure 3**

(A) The intake rate of the predators (gamma) as a function of C_1 . The graph shows an asymmetrical relationship when the patch proportions are not equal ($P_1 = 0.8$, $P_2 = 0.2$). The optimal strategy of the prey (which minimizes gamma) is specialization toward patch type 1 and with only a small level of compromise toward patch type 2. (B) The time that the predators spend in patch type 1 (dashed line) and patch type 2 (solid line) as a function of C_1 . Predators now spend time foraging over a greater range of values of C_1 than when the patch proportions are equal.

predators' intake rate. For example, when M_1 is increased from 1.0 to 10.0 but M_2 remains unchanged, the optimal strategy of the prey is now one of specialization toward avoiding capture in patch type 1 (Figure 5A). As can be seen from Figure 5B, predators forage almost exclusively in patch type 1 for values of C_1 down to about 0.02, despite both patch types occurring in equal proportions. This occurs because each prey individual is more likely at any given time to be on a type 1 patch than a type 2 patch, and so type 1 patches are more profitable to predators. However, as Figure 5A shows, prey should adopt a strategy of pure specialization $C_1 \approx 0.0$, and at this point, predators stop foraging in patch type 1 and forage exclusively in patch type 2. Therefore, our model makes the initially counterintuitive prediction that, in some circumstances, prey should optimize concealment in a habitat where predators rarely, or even never, occur; this is effectively the opposite of what would be expected based on Endler's (1978) definition of crypsis. This also raises the question of how much specialization is possible; for example, whether it is biologically realistic for a prey animal to perfectly match one background (i.e., whether C_1 would be expected to be constrained to values above zero).

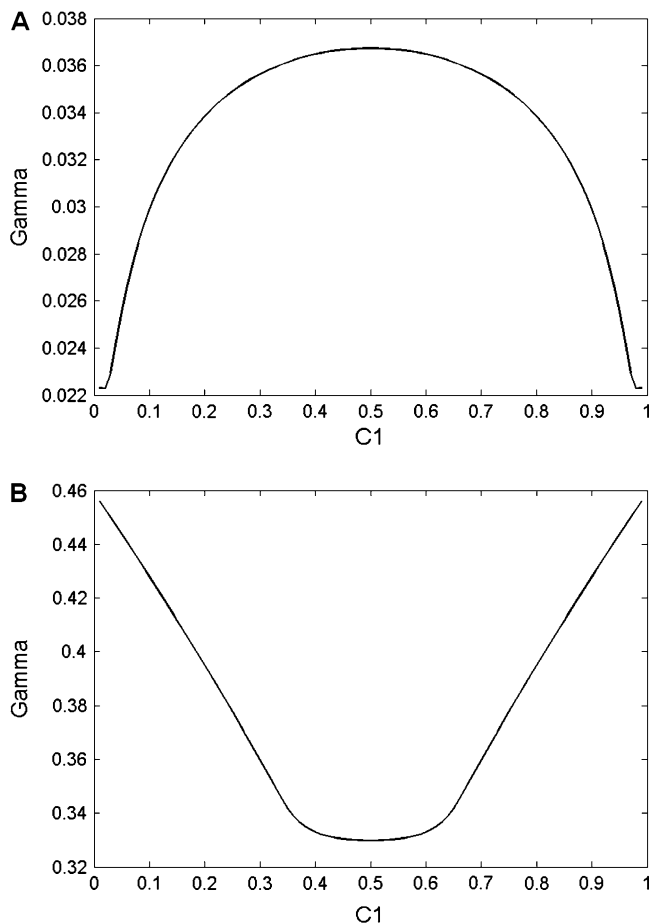


Figure 4
 (A) The intake rate of the predators (gamma) as a function of C_1 when $\tau = 20$. The optimal strategy of the prey to minimize the predators' intake rate is specialization toward either patch type but with no compromise in between. (B) The intake rate of the predators (gamma) as a function of C_1 , when $\tau = 0.2$. The optimal strategy of the prey is now to be a compromise in crypsis between the 2 patch types. Specialized camouflage strategies are strongly disfavored.

THE EFFECT OF K

The parameter k in the model affects the shape of the trade-off function between the capture rate of the prey items in patch type 1 and patch type 2, given by Equation 1 (Figure 1). By altering k , and therefore the relationship between C_1 and C_2 , we can determine the effect this has on the optimal strategy of the prey. So far, our model has used a value of $k = 1.0$ and so has provided a linear and symmetrical relationship between C_1 and C_2 (Figure 2A): any reduction in capture rate (increased crypsis) that a compromise form experiences in patch type 1 is offset by an equal and opposite increase in type 2. Increasing the value of k to 2.0 creates a concave-down trade-off function that is also asymmetric (the changes in C_1 and C_2 near $C_1 = 1$ are not the same as the changes near $C_2 = 1$). It is also important to note that because we model trade-offs in terms of capture rates, not crypsis, our concave-down trade-off for capture rates is the equivalent of concave-up function of Merilaita et al. (1999) for crypsis and vice versa. When $k = 2.0$, a situation is encountered similar to when $k = 1.0$, except that, because of the asymmetry in the trade-off, while there are 2 good compromise strategies for the prey to adopt, one strategy is better than the other (Figure 6A). The relationship between gamma and C_1 is still broadly that the prey should

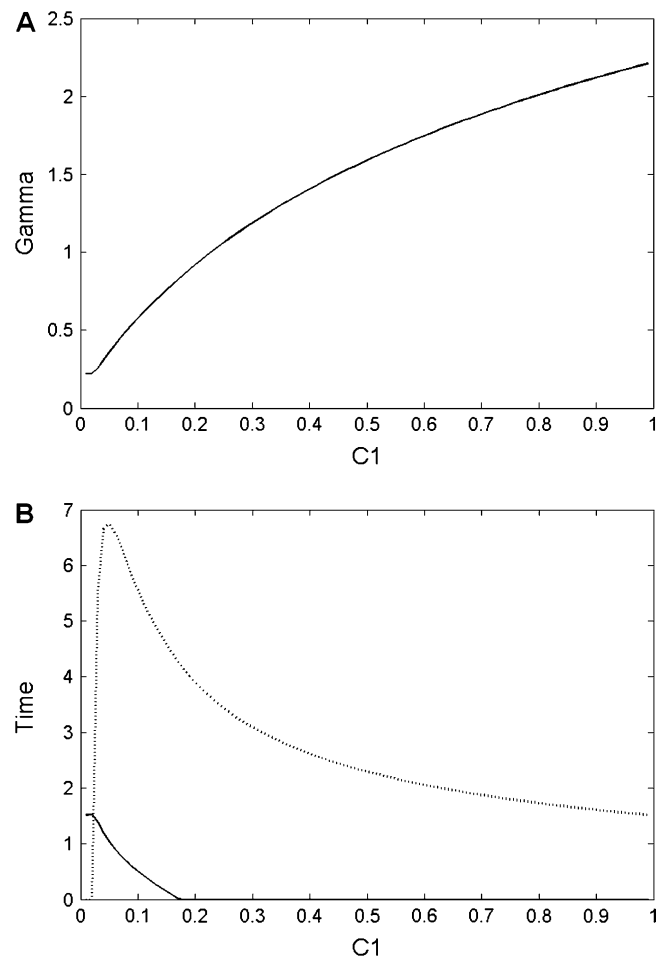


Figure 5
 (A) The intake rate of the predators (gamma) as a function of C_1 , when $M_1 = 10$ and $M_2 = 1.0$. The optimal strategy of the prey (which minimizes gamma) when patch type one contains 10 times as many prey items per patch is specialization toward patch type 1. (B) The time that the predators spend in patch type 1 (dashed line) and patch type 2 (solid line) as a function of C_1 . When patch type 1 contains 10 times as many prey items per patch compared with patch type 2, the predators forage almost exclusively in patch type 1.

largely specialize toward being cryptic in either patch type but with some compromise. However, the optimal strategy, which minimizes gamma, is toward being well camouflaged in patch type 2 with relatively little compromise ($C_1 = 0.9$ approximately). The other locally good solution which prey can adopt involves closely matching patch type 1 ($C_1 = 0.2$ approximately), but this requires a greater level of compromise and also produces a larger predator intake rate. These results therefore indicate that the shape of the trade-off function can create situations with more than one favorable strategy (local optimum), but with one global optimal solution. Creating an asymmetrical, concave-down trade-off function also creates an optimal strategy where C_1 equals approximately 0.9; this is a greater degree of specialization than when the trade-off is linear and symmetrical ($k = 1.0$), although still not a strategy of pure specialization.

Decreasing the value of k in the model to 0.5 (concave-up trade-off) shifts the optimal strategy toward being cryptic in patch type 1, but again with a level of compromise (Figure 6B). Here, compromise strategies in general do quite well, and strong specialization is not favored, particularly with respect to patch type 2.

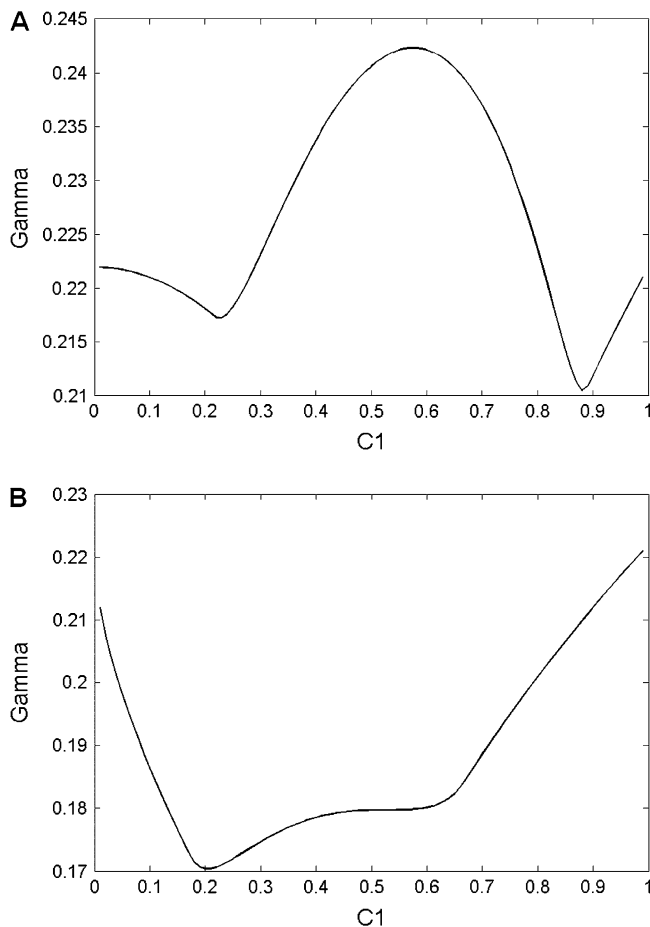


Figure 6
 (A) The intake rate of the predators (gamma) as a function of C_1 where $k = 2.0$. The graph shows an asymmetrical relationship where specialization toward either patch type is favored, but the optimal strategy is to be specialized toward patch type 2. (B) The intake rate of the predators (gamma) as a function of C_1 where $k = 0.5$. The graph shows an asymmetrical relationship where compromise prey morphs are largely favored, but the optimal strategy contains some specialization toward patch type 1.

DISCUSSION

In recent years, the view that optimal camouflage will be achieved by an animal matching a random sample of the background environment has been challenged (Merilaita 1998; Merilaita et al. 1999; Cuthill et al. 2005; Merilaita and Lind 2005). In particular, a model set out by Merilaita et al. (1999) has indicated that there may be situations where animals should bear some markings from a range of different backgrounds in a heterogeneous environment, instead of optimizing camouflage with respect to a single background type. In this article, we have also set out a model examining the optimal strategy for camouflaged prey in a 2 patch type environment. Like Merilaita et al. (1999), we considered the effect of the trade-off function between camouflage (in our model this function is between prey capture rates, which increase as camouflage decreases) in the different patch types and its effect on the optimal strategy of the prey. However, we also allowed predator behavior to change (optimally) in response to the prey, as a function of the travel time of predators between patches, the number of prey items in a patch, and the proportion of the 2 patch types in the habitat. Our model has indicated different situations where compromise camouflage

or specialization may be favored. Indeed, there is evidence in natural systems for both specialization toward specific backgrounds (Sandoval 1994; Wente and Phillips 2003) and of compromise coloration in conspicuous signals (Macedonia et al. 2003).

In our model, the proportion of the 2 patch types affects the optimal camouflage strategy of the prey. Even with a linear trade-off between crypsis in the 2 habitats, with equal patch proportions, specialization toward either patch type is generally favored, although with some compromise toward the opposing patch type. As expected, if the proportion of one patch type is increased, prey should increase their level of specialization toward this patch type, although this change is not directly proportional to the change in patch proportions. In this situation, prey are more likely to be found in one patch type and therefore will gain more from being camouflaged toward this microhabitat. Cooper and Allen (1994) found that in experiments with wild birds and artificial prey, prey suffered a higher risk of predation on backgrounds when they matched backgrounds that were rarer.

One of the strongest effects of the model is that of changing the travel time of the predators between the different patches. A short travel time between patches results in a compromise camouflage strategy being strongly favored, and a relatively large travel time between patches results in a strategy of specialization toward either patch type. This implies that different strategies may be favored in a habitat depending on how clumped the different patches are. In a habitat, where patches are separated from the other patch types by a relatively large distance, specialization toward either patch type may be favored. Essentially, one can think of this effect in terms of how predator foraging is affected by the relative travel times. If the travel time between patches is low, then the relative investment by predators in reaching a patch is small, and as such, there is little cost to the predator in leaving an unprofitable patch. This allows predators to specialize on one patch type alone because they can simply leave any unattractive patch that they encounter. Here, specialization is not favored by the prey toward one patch type because predators would respond by foraging largely on the other patch type. Conversely, when the travel time between patches is long, predators are relatively more constrained to a patch because they have invested more in reaching it. As such, predators are unlikely to abandon a patch immediately and so predators are unable to concentrate their foraging on one patch type so strongly. Given that predators will therefore spend time foraging in both patch types, in this instance, the prey benefit by optimizing concealment in a given patch type. The elegant experiments by Bond and Kamil (2006) on optimal camouflage against coarse- or fine-grained heterogeneous backgrounds would seem relevant here, but there are important differences that make direct comparison with our model difficult. Their experiments involved blue jays (*Cyanocitta cristata*) foraging for artificial prey on computer screens where the prey patterns were allowed to evolve by a genetic algorithm, subject to selection imposed by predation. On the coarse-grained background, a dimorphism of 2 different specialist morphs evolved to match the different patch types, whereas on a fine-grained background generalist morphs evolved (Bond and Kamil 2006). However, this is a situation where all patches are similar, albeit heterogeneous, whereas we and Merilaita et al. (1999) consider spatially separated patches (background types) that predators can recognize and choose between. A full account of crypsis will require both levels of analysis.

As expected, when the number of prey items in a patch is increased in the model, this increases the intake rate of the predators because there is more available food. When this intake occurs symmetrically across patch types, this has no

effect on the optimal camouflage strategy of the prey. However, when the number of prey items is increased in one patch type relative to the other, this causes an increase in the level of specialization by the prey toward that patch type. This strategy of specialization is linked closely to the result that the predators almost exclusively forage in the patch type with a greater number of prey items, and so it is more important for prey to be camouflaged with respect to this background type.

The effect of changing the trade-off function between the capture rates of the prey items in the 2 patch types is perhaps the most complicated aspect of the model. Merilaita et al. (1999) found that when trade-off is convex between the levels of camouflage in the 2 patch types, then prey should adopt a compromise strategy. However, when trade-off is concave, then prey should specialize. Our trade-off function is not between the degree of crypsis of the prey in the 2 patch types per se but instead is between the capture rates of the prey in the 2 patch types, which is negatively related to the degree of crypsis. A potential advantage of our formulation is that measuring capture rates empirically in real systems may be easier than directly assessing the degree of crypsis. When there is a concave-up relationship between C_1 and C_2 ($k < 1$), compromise strategies do well and the different patch types may be similar enough to enable this compromise in crypsis. In contrast, when the trade-off between C_1 and C_2 is concave down ($k > 1$), specialization is more strongly favored, specifically toward one of the patch types. However, unlike in the model of Merilaita et al., when the trade-off function is concave down (concave-up in model of Merilaita et al.), pure specialization is not favored, and some level of compromise is. This indicates that small levels of compromise in camouflage may be favored, even when asymmetrical trade-offs exist in nature. Merilaita et al. (1999) argue that concave-down situations may be encountered when both patch types are so dissimilar that successful compromise forms are hard to evolve. The concavity of the trade-off function creates 2 "good" solutions for the prey to adopt (specialization points close to either patch type), although not pure specialization as in the results of Merilaita et al. (1999) (because in our model, predator optimal behavior is also included). The asymmetry in the trade-off function also leads to one strategy being marginally better than the other. This has interesting implications in that prey species may be unable to evolve between "adaptive peaks," due to disadvantageous phenotypes in between the 2 strategies. Species may be phenotypically constrained to a successful, but not optimal, level of camouflage. Therefore, different types of prey, with only slightly different ecologies, could have entirely different phenotypes because they lie on either side of the divide or have evolved from different directions (Van Tienderen 1991; Merilaita et al. 1999; Ruxton et al. 2004). Furthermore, if the environment in which a species is found changes, so that previously well-camouflaged animals no longer have an optimal phenotype, it may be difficult for the species' phenotype to evolve toward the new optimum as small changes in phenotype are worse than the current situation; only a macromutation may be beneficial (Ruxton et al. 2004). To some extent, the potential problems associated with living in a heterogeneous environment may be overcome if an animal can select a specific background type to rest on, for which there is some evidence (Sargent 1966, 1968; Kettlewell and Conn 1977). This may allow for high levels of specialization toward one background type. However, effective background selection may not circumvent the need for compromise markings when the environmental conditions fluctuate unpredictably or frequently. For example, Sasaki and De Jong (1999) found that when there is unpredictable habitat change between the development of, and natural selection on, an individual, an evolutionarily stable compromise situa-

tion can be established between the phenotypic optima in the different patch types. Conversely, in unpredictable environments, there may be selection for animals to actively search for the appropriate background because the information stored in the genotype is no longer a reliable cue to the current conditions. Therefore, while spatial variation is likely to have a large influence on an optimal strategy, temporal change and environmental predictability must also be considered.

Our model of camouflage has indicated the contrasting situations where different strategies of camouflage may be favored. It is becoming increasingly clear that there may be no simple rule dictating how optimal camouflage should be achieved and, instead, that camouflage is a flexible and potentially variable strategy that may be influenced by many factors in a habitat. The existence of "imperfect camouflage," just as with what appears to be imperfect mimicry (Cuthill and Bennett 1993; Ditttrich et al. 1993; Howse and Allen 1994; Edmunds 2000; Sherratt 2002), may be at least partly explained by the benefits of a compromise strategy against multiple backgrounds. In addition to compromise camouflage (Merilaita et al. 1999, 2001) and disruptive coloration (Cuthill et al. 2005; Merilaita and Lind 2005), a range of other factors are also likely to be important in successful concealment, such as the relative proportion and distribution of patches in a habitat and the behavior of those predators searching for their prey. Different predators' behavior or ecology for instance can affect their success rate at finding prey (Kothbauer-Hellmann and Winkler 1997). Furthermore, compromises in concealing patterns may also occur between the visual systems of different predators (Endler 1978; Ruxton et al. 2004) and the ability of predators to process visual information while searching for prey (Dukas and Ellner 1993). Animal markings are the result of many interacting factors in an environment; future research should aim to determine the relative importance of such factors, both in real and artificial systems.

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REFERENCES

- Bond AB, Kamil AC. 2006. Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *Proc Natl Acad Sci USA*. 103:3214–3219.
- Cooper JM, Allen JA. 1994. Selection by wild birds on artificial dimorphic prey on varied backgrounds. *Biol J Linn Soc*. 51:433–446.
- Cott HB. 1940. *Adaptive coloration in animals*. London: Methuen & Co. Ltd.
- Cuthill IC, Bennett ATD. 1993. Mimicry and the eye of the beholder. *Proc R Soc Lond B Biol Sci*. 253:203–204.
- Cuthill IC, Stevens M, Sheppard J, Maddocks T, Párraga CA, Troscianko TS. 2005. Disruptive coloration and background pattern matching. *Nature*. 434:72–74.
- Ditttrich W, Gilbert F, Green P, McGregor P, Grewcock D. 1993. Imperfect mimicry: a pigeon's perspective. *Proc R Soc Lond B Biol Sci*. 251:195.
- Dukas R, Ellner S. 1993. Information processing and prey detection. *Ecology*. 74:1337–1346.
- Edmunds M. 2000. Why are there good and poor mimics? *Biol J Linn Soc*. 70:459–466.
- Endler JA. 1978. A predator's view of animal color patterns. *Evol Biol*. 11:319–364.
- Howse PE, Allen JA. 1994. Satyric mimicry: evolution of apparent imperfection. *Proc R Soc Lond B Biol Sci*. 275:111–114.

- Iwasa Y, Higashi M, Yamamura N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *Am Nat.* 117:710–723.
- Kettlewell HBD, Conn DLT. 1977. Further background-choice experiments on cryptic Lepidoptera. *J Zool.* 181:371–376.
- Kothbauer-Hellmann R, Winkler H. 1997. Prey detection in two tit species, *Parus ater* and *P. cristatus*. *Ethology.* 103:339–349.
- Macedonia JM, Echternacht AC, Walguarnery JW. 2003. Color variation, habitat light, and background contrast in *Anolis carolinensis* along a geographical transect in Florida. *J Herpetol.* 37:467–478.
- McNamara JM. 1982. Optimal patch use in a stochastic environment. *Theor Popul Biol.* 21:269–288.
- Merilaita S. 1998. Crypsis through disruptive coloration in an isopod. *Proc R Soc Lond B Biol Sci.* 265:1059–1064.
- Merilaita S, Lind J. 2005. Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proc R Soc Lond B Biol Sci.* 272:665–670.
- Merilaita S, Lytinen A, Mappes J. 2001. Selection for cryptic coloration in a visually heterogeneous environment. *Proc R Soc Lond B Biol Sci.* 268:1925–1929.
- Merilaita S, Toumi J, Jormalainen V. 1999. Optimization of cryptic coloration in heterogeneous habitats. *Biol J Linn Soc.* 67:151–161.
- Ruxton GD, Sherratt TN, Speed MP. 2004. *Avoiding attack.* Oxford: Oxford University Press.
- Sandoval CP. 1994. Differential visual predation on morphs of *Timema cristinae* (Phasmatoidea: Timemidae) and its consequences for host range. *Biol J Linn Soc.* 52:341–356.
- Sargent TD. 1966. Background selections of geometrid and noctuid moths. *Science.* 154:1674–1675.
- Sargent TD. 1968. Cryptic moths: effects on background selections of painting the circumocular scales. *Science.* 159:100–101.
- Sasaki A, De Jong G. 1999. Density dependence and unpredictable selection in a heterogeneous environment: compromise and polymorphism in the ESS reaction norm. *Evolution.* 53:1329–1342.
- Sherratt TN. 2002. The evolution of imperfect mimicry. *Behav Ecol.* 13:821–826.
- Stephens DW, Krebs JR. 1986. *Foraging theory.* Princeton (NJ): Princeton University Press.
- Stevens M, Cuthill IC, Párraga CA, Troscianko T. 2006. The effectiveness of disruptive coloration as a concealment strategy. In: Alonso J-M, Macknik S, Martinez L, Tse P, Martinez-Conde S, editors. *Progress in brain research.* Vol. 155. Amsterdam (The Netherlands): Elsevier. p. 49–65.
- Stewart-Oaten A. 1982. Minimax strategies for a predator-prey game. *Theor Popul Biol.* 22:410–424.
- Thayer GH. 1909. *Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries.* New York: Macmillan.
- Van Tienderen PH. 1991. Evolution of generalists and specialist in spatially heterogeneous environments. *Evolution.* 45:1317–1331.
- Wente WH, Phillips JB. 2003. Fixed green and brown color morphs and a novel color-changing morph of the pacific tree frog *Hyla regilla*. *Am Nat.* 162:461–473.