

## VISUAL BACKGROUND COMPLEXITY FACILITATES THE EVOLUTION OF CAMOUFLAGE

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**Abstract.**—Cryptic animal coloration or camouflage is an adaptation that decreases the risk of detection. The study of the evolution of camouflage has strongly emphasized the minimization of visual information that predators receive from prey, by means of background matching. However, the evolutionary effects of information processing after its reception have been virtually ignored. I constructed a model that employs an artificial neural network and simulates the evolution of prey coloration in a visually complex and simple habitat. The model suggests: (1) the difficulty of a detection task is related to the visual complexity of the habitat; (2) it is easier to decrease the risk of detection by the means of camouflage in a visually complex habitat; (3) selection on camouflage can exploit limitations in predators information processing; and (4) there are shortcomings in using the degree of background matching as the measure of camouflage.

**Key words.**—Artificial neural network, cognition, cryptic prey coloration, predation, search image.

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Cryptic animal coloration, or camouflage, is a common adaptation that serves to decrease its bearer's risk of detection (Cott 1940; Edmunds 1974). It has been used as a classic example of evolution, but surprisingly little is known about how it actually works. Camouflage has been considered to be tightly related to the resemblance of an animal to its visual background, the better the animal matches its background, the less it is expected to be detected by a predator (Cott 1940; Norris and Lowe 1964; Edmunds 1974; Endler 1978; Edmunds 1990; Endler 1991; Guilford 1992).

Regarding camouflage as synonymous to background matching allows a relatively easy way to estimate camouflage through the measurement of the degree of visual match between the animal and its background (Endler 1978, 1984). This approach appears logical when only the reception of visual information is considered. However, if not only the reception, but also the processing of such information by the predator affects the detection probability, the approach may be biologically unrealistic. The evidence supporting the significance of background matching for camouflage is correlative and some empirical studies show that cryptic animals do not necessarily match their background very closely (Endler 1984; Merilaita 1998). Thus, although background matching certainly is an important determinant of camouflage, other phenomena may be involved as well.

Accordingly, a recent experimental study implies that not only the relationship between colors and patterns of an animal and its background, but also the visual characteristics of the background per se might influence detection (Merilaita et al. 2001). One such property of the background that might influence the probability of detection is the level of its visual complexity. The logic behind this idea is that in a visually complex habitat, there is more visual information to be processed than in a simple habitat, making the detection task more difficult. By constructing a model that uses a genetic algorithm and an artificial neural network to simulate the

evolution of prey coloration and selection caused by predation, respectively, I addressed the hypothesis that requirements for camouflage differ between habitats with high and low visual complexity. More specifically, I studied whether the consequences of an evolutionary constraint on camouflage depend on background complexity.

### MATERIALS AND METHODS

#### *General Procedure*

The present model simulates the evolution of cryptic coloration in a prey, caused by selection from predation. The model consists of three main components: the visual background, the prey, and predation. The predator views its habitat and categorizes the visual samples as prey or background. These samples, and thus also the prey coloration, were described by vectors consisting of eight cells, each cell being occupied by a coloration element. A coloration element can be considered as a color or a figure such as a stripe or a spot.

I used an artificial neural network to simulate predation. Artificial neural networks have been inspired by biological neural systems, and they are used, among other things, for pattern recognition and categorization tasks, as are their biological counterparts (Bishop 1995; Haykin 1999). Artificial neural networks and biological neural systems share the same basic features, such as the network of connections and the parallel processing of information. Therefore, artificial neural networks have become a powerful tool in research that involves cognitive processes. They have also been applied in evolutionary studies on natural and sexual selection imposed by cognition (Enquist and Arak 1993; Johnstone 1994; Enquist and Arak 1998; Phelps and Ryan 1998; Holmgren and Enquist 1999).

The coloration of the prey in the current model has the potential to evolve. The predator's ability to detect the prey imposes a selection pressure on the prey coloration. Thus, predation selects for prey coloration that is difficult for the predator to tell apart from the background. The predator can respond to the prey evolution in a co-adaptive fashion by adjusting its decision criteria for the categorization (i.e. by

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learning). Using this model, I simulated the evolution of cryptic coloration in habitats that differed in their visual complexity. I studied how the effect of an evolutionary constraint on camouflage varied with visual background complexity and compared it with the outcome of unconstrained evolution of coloration.

### *The Visual Background*

In the visually complex habitat, the visual background consisted of four different coloration elements (1, 2, 3, and 4), whereas in the simple habitat there were only three elements (1, 2, and 3). In the beginning of each run of the simulation, one of the coloration elements was randomly chosen to be the basal coloration element. Thus, each eight-cell sample of the background in the complex habitat always consisted of two cells of the basal coloration element and two cells of each of the other three elements (e.g., 2,4,3,3,4,1,2,1 or 2,1,1,2,3,4,3,4). In the simple habitat, the samples of the background consisted of two cells of the basal coloration element and three cells of each of the other two elements (e.g., 1,3,3,2,1,2,3,2 or 2,2,2,3,1,3,3,1, in which 1 is the basal element). The order of the cells was not determined, and thus there was a total of 2520 possible different visual samples of the complex habitat and 560 possible different visual samples of the simple habitat. Finally, I ran the simulation in an even more complex habitat to confirm the results. In these additional simulations, the habitat consisted of five elements. Thus, an eight-cell sample of the habitat always consisted of two cells of the basal coloration element, and two, two, one, and one cells occupied by the other four coloration elements (e.g., 5,2,3,2,1,1,4,3 or 3,1,4,1,2,2,3,5 in which 4 and 5 are the elements occupying only one cell each; the number of cells for each element was assigned randomly at the beginning of each run of the simulation). This resulted in 5040 possible different samples of the habitat.

### *The Prey*

The evolution of the prey coloration was simulated with a technique referred to as the genetic algorithm (Sumida et al. 1990; Mitchell 1996). The prey population size was 32 individuals. Each individual had a haploid genome of eight loci. Thus, each locus of the prey genome coded for the coloration element of one cell in the individual's eight-cell body coloration. In the simulations for unconstrained evolution of prey coloration, the prey could produce an allele through mutation corresponding to each background coloration element, i.e. four on the complex background and three on the simple background. In the simulations for constrained evolution, it was possible for the prey to produce a corresponding allele for all except one randomly chosen coloration element of the background. In the beginning of each run of the simulation, all the loci in the prey population had the allele for the basal coloration element. Thus, the coloration element of equally many cells (six) in the initial prey coloration needed to be changed in both the habitats for the prey to perfectly match the background.

The prey generations were nonoverlapping. Camouflage determined prey fitness, but the population size remained constant between generations. During each prey generation,

the prey population was first exposed to predation. In practice, the prey population was presented to the artificial neural network that simulated predation, and the output value was used as a camouflage score for ranking the prey colorations. The least cryptic 25% of the prey population did not survive to reproduction. Each individual belonging to the most cryptic 75% of the population produced one offspring that received a copy of its parent's genotype. In addition, the most cryptic 25% formed four random pairs that produced two offspring each. Each pair of siblings received a recombined copy of their parents' haploid eight-loci chromosomes. The recombination resulted from a single crossing-over at a random point. In addition, each generation was exposed to three point mutations. A mutation changed one allele to another. For each mutation, the locus and the offspring individual were chosen randomly. The recombination and point mutations produced genetic variation necessary for the evolution of prey coloration to take place.

The coloration and genetics of the model are obviously simplifications, but they loosely correspond to species whose colors and patterns are determined by simple genetics. Examples of such species are the isopod *Idotea baltica*, in which the presence of each pattern (a central stripe, two lateral stripes, white spots, and mottled pattern) is determined by separate loci (Tinturier-Hamelin 1963), the Hawaiian happy-face spider *Theridion grallator* whose various patterns are coded by multiple alleles at a single locus (Oxford and Gillespie 1996), and the walking-stick *Timema cristinae* whose color (green, gray, or red) and pattern (striped or unstriped) are controlled by two separate loci (Sandoval 1994).

### *Predation*

The artificial neural network that I used to simulate selection on prey coloration caused by predation, consisted of eight input cells, a layer of five neurons referred as the hidden layer, and one neuron on the output layer. The neural network was saturated so that each neuron on the hidden layer was connected to every input cell and to the neuron on the output layer, with a total of 45 connections. The neural network was a feed-forward network and thus the signals from the input cells traversed only to one direction through the hidden layer to the output layer (for a schematic figure of a feed-forward network see e.g., Enquist and Arak 1993, 1998). Each neuron consisted of specific weights for every incoming connection, a bias, and a transfer function. The weight value is comparable with the strength of a synaptic connection, and it can be negative or positive to describe inhibitory or excitatory synapses of different strengths. The bias adjusts the input in relation to the transfer function, and it can be considered a weighted connection with a constant input of 1. Thus, when the neural network received an input, all input cells forwarded the received signals simultaneously through the connections to the hidden layer. The neurons on the hidden layer operated in parallel. All the signals coming into a neuron were first multiplied with the connection-specific weights. The sum of these weighted signals and the bias formed the input to the log-sigmoid transfer function. Then, each neuron forwarded the output of its transfer function to the output neuron. There,

the incoming signals were processed in the same way to produce the output of the network.

The response of an artificial neural network to a given input depends on its weight and bias values. When a neural network is trained, these values are adjusted such that for a given input, a desired output is received. Training also affects the neural networks generalization ability, that is the ability to correctly categorize data that it has not encountered previously (Bishop 1995; Haykin 1999). Such ability to make correct decisions in new situations also characterizes adaptive animal behavior. In this model, the target outputs were 0 for background and 1 for prey. The input data (i.e., the visual sample vectors) were scaled to range from  $-1$  to  $1$ .

The starting point for the simulation was the presumption that the predator was able to tell apart the background from a coloration consisting only of the basal coloration elements, the coloration of the prey in the beginning. Therefore, in the beginning of each run of the simulation, the neural network was first trained for this. The training data set consisted of a total of 100 eight-cell vectors of which 50 were randomly chosen different samples of the background and the other 50 were copies of the vector consisting only of the basal coloration element. Equal number of prey and background samples in the training data set ensured that both pattern categories had an equal impact on the performance measures of the network during the training. The training was done with batch training, the weights and biases of the neural network were adjusted after the whole training data set and the corresponding target outputs had been presented to the neural network, and these presentations of the training data set were repeated until the performance goal was met. The performance was measured as mean square error of the output. The performance goal was  $2 \times 10^{-6}$  (this was the smallest value that was reached in all the simulations) and it took about 300 training rounds to reach it. The neural network was trained with a gradient descent back-propagation algorithm with an adaptive learning rate and momentum (Bishop 1995; Haykin 1999; Demuth and Beale 2000). This algorithm updated the weight and bias values to the direction of the steepest gradient of the performance function. The adaptive-learning rate increases the learning rate (i.e. change in weight values) when it does not increase the error, and the momentum allows the algorithm to ignore local changes in the performance function.

After the initial training, the neural network was trained with incremental training during each prey generation as a co-adaptive response to prey evolution. In incremental training, the weights and biases are updated each time a training vector and the corresponding correct output is presented to the neural network. This simulated predator learning from interaction with prey and background. First, the prey individuals were presented to the neural network, and the output was used as a measure of camouflage that also determined prey fitness (see above). The output ranged from zero to one. The closer it was to one, the poorer the camouflage it indicated, whereas the output of zero indicated that the neural network incorrectly categorized a prey as a part of the background. The training set was formed from a subset of the current prey population and randomly chosen samples of the background. For this purpose, the prey were ranked according

to their camouflage. The four highest ranked individuals were excluded from the training set because a highly cryptic coloration has to be common before a predator effectively learns it. Then, any repetitions among the remaining individuals were excluded so that only one copy of each phenotype was included in the training set. Also, because the predator was assumed not to be able to tell apart a prey exactly matching a sample of the background from a sample of the background, any prey individual with coloration that equaled any of the possible background samples was excluded from the training set. Finally, randomly chosen samples of the background were added to the training set until it contained equally many prey and background samples. The vectors of the current training set were then presented to the neural network once and in a random order.

The presentation of the visual samples to the neural network corresponds to a predator that scans its environment and directs its attention to "interesting" patches (e.g., patches that resemble prey in size or shape). Because the visual elements may represent figures as well as colors, this means that the input signals have already gone through the early levels of processing (i.e. the edges and simple shapes have been detected). Thus, the visual information coming in to the neural network simulates signals that have reached the restricted "window of attention" rather than simulating all the signals reaching the retina. There are several reasons to include only the focal patch in a visual sample (i.e. the window of attention) and use stored information in the categorization, instead of also including a part of the surrounding background. First, difference between the focal patch and the adjacent patch is not a reliable cue in prey searching because divergence between adjacent patches of background is common in heterogeneous habitats. Second, attending one target at a time is consistent with how recognition of complex patterns is performed (e.g., Desimone and Duncan 1995). Third, from a methodological point of view, including cells of the adjacent background surrounding the potential prey patch in the visual samples would not contribute any useful information for the neural network in the categorization because they would not correlate with the correct output. Instead, the weights of the neurons that receive signals from these surrounding cells would fluctuate wildly during the training, and consequently those cells would be a source of noise.

### *Simulation*

I wrote the simulation model program, using the software Matlab (version 6.1) and its Neural Network Toolbox (version 4.0) (The MathWorks, Inc., Natick, MA). Each simulation was run until the prey susceptibility to predation had decreased below a threshold value—when the mean output of the neural network for the most cryptic 25% of the prey population was below 0.001. The benefits of this measure are, when compared to a measure based on the mean of the whole population, that it responds more rapidly to a new cryptic coloration that is spreading, and that it is insensitive to the inferior colorations possibly produced each generation by the mutations and recombination. If the threshold was not reached in 200 generations, the simulation run was interrupted. From each simulation run, I recorded the number of

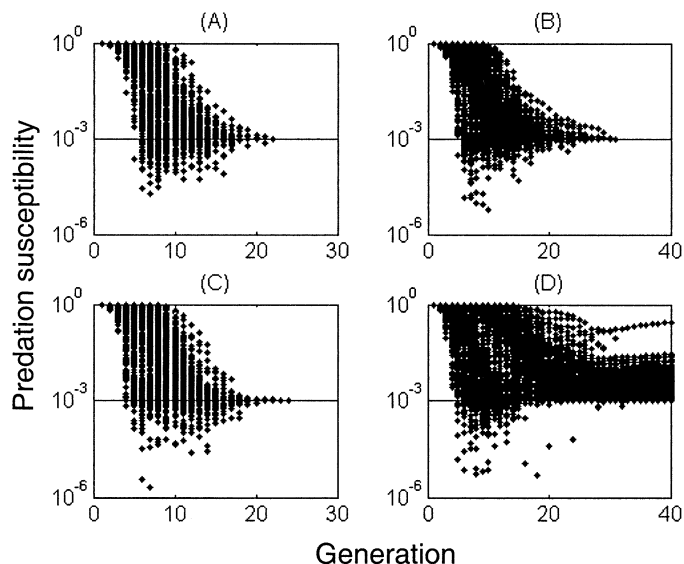


FIG. 1. The predation susceptibility of the prey per generation, measured as the mean output of the neural network for the most cryptic 25% of the prey population; (A) unconstrained evolution in the complex habitat; (B) constrained evolution in the complex habitat; (C) unconstrained evolution in the simple habitat; and (D) constrained evolution in the simple habitat. A simulation run ( $N = 500$  in each category) was stopped when the predation susceptibility threshold value of  $10^3$  was reached. In (D) 34% runs of the simulation did not reach the threshold value in 200 generations. One dot may represent multiple points.

prey generations it took to reach the predation susceptibility threshold. In the end of a simulation run, I also recorded the most cryptic prey coloration (i.e. the coloration that was least likely to be detected by the neural network). As a measure of background matching, I calculated the shortest Euclidian distance between the most cryptic prey coloration of each generation and any habitat sample.

## RESULTS

The prey susceptibility to predation generally decreased between generations, indicating that evolution of cryptic prey coloration took place (Fig. 1). Also, the background matching of prey was improved from the initial values (Fig. 2). Thus, the shortest Euclidian distance between the best prey coloration and any member of the background sample set decreased  $56.6 \pm 0.52\%$  (mean  $\pm$  SE) in the complex habitat without the evolutionary constraint,  $50.1 \pm 0.54\%$  in the complex habitat with the evolutionary constraint,  $51.8 \pm 0.88\%$  in the simple habitat without the evolutionary constraint, and  $37.8 \pm 0.68\%$  in the simple habitat with the evolutionary constraint; Fig. 3).

In the simulations with unconstrained evolution, the prey successfully evolved coloration reaching the predation susceptibility threshold during every run of the model. In the complex four-element habitat, it took normally (median (min.–max.)) 10 (5–22) prey generations and in the simpler three-elements habitat, 12 (5–31) prey generations (Fig. 1A–B). Also, the constrained evolution in the complex habitat always resulted in prey coloration reaching the predation susceptibility threshold (Fig. 1C). It took normally 12 (4–24)

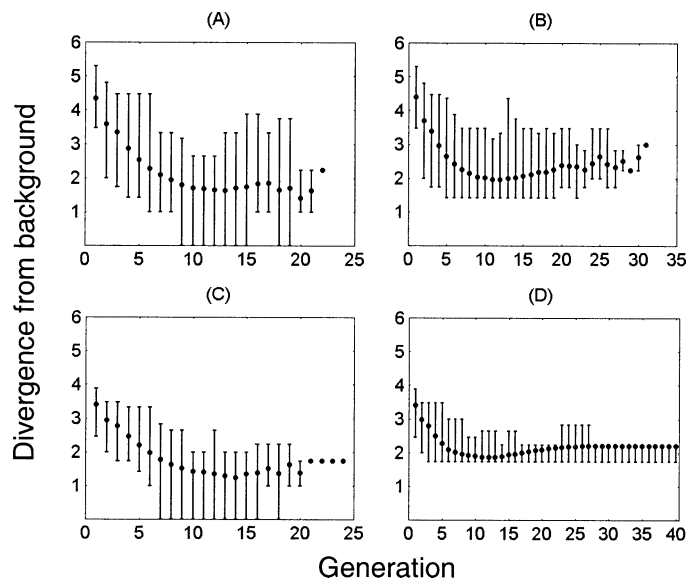


FIG. 2. Background matching, that is, visual divergence from the background, measured as the shortest Euclidian distance between the most cryptic prey of a generation and a habitat sample (mean and range); (A) unconstrained evolution in the complex habitat; (B) constrained evolution in the complex habitat; (C) unconstrained evolution in the simple habitat; and (D) constrained evolution in the simple habitat.

prey generations. In the simple habitat when the evolution of coloration was constrained, however, the outcome was dramatically different from the other simulations (Fig. 1D). In 34.0% of the simulation runs (170 of 500), the prey could not produce coloration reaching the predation susceptibility threshold within 200 generations. The median number of generations needed to produce a coloration that reached the threshold was 13 (min. = 5). This result shows that it was more demanding to evolve a cryptic coloration yielding a given level of protection in the visually simple habitat than in the complex one.

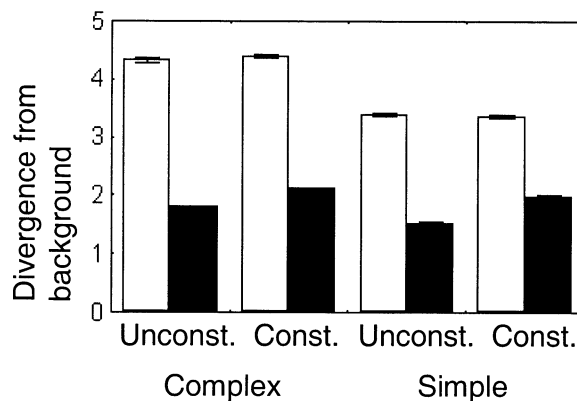


FIG. 3. The improvement of prey background matching during the simulations. Visual divergence from the background was measured as the shortest Euclidian distance between the most cryptic prey of a generation and a habitat sample (mean and SE) for unconstrained and constrained evolution of prey coloration in the complex and simple habitat. White bars represent the background matching at the beginning and black bars at the end of the simulation runs.

The additional simulations in the even more complex five-element habitat confirm the result that visual background complexity facilitates the evolution of camouflage. Both the evolutionary unconstrained prey and the constrained prey evolved coloration reaching the predation susceptibility threshold in every run of the simulation. For the unconstrained prey, the median time was 10 (4–27) generation and for the constrained prey it was 11 (4–36) generations.

In the simple three-element habitat the evolutionary constraint of the prey missing the allele for one of the visual elements resulted in a minimum deviation of three cells between any eight-cell habitat sample and the prey, whereas in the complex four-element habitat the minimum deviation was only two cells. One could argue that this difference might account for the lower likelihood of constrained evolution producing successful camouflage in the simple habitat. However, a modification of the simulation so that the constraint caused a minimum deviation of three cells also in the complex habitat (the habitat samples consisted of two cells of the constrained visual element, and one, two, and three cells of the remaining three elements, respectively) did not significantly change the number of generations needed to reach the predation susceptibility threshold value (Mann-Whitney *U*-test:  $N_1 = N_2 = 500$ ,  $Z = 0.70$ ,  $P = 0.48$ ).

A comparison of the best final colorations (i.e. the best coloration of the last generation of a simulation run) within and between the constrained evolution simulations sheds more light on the effect of the evolutionary constraint. In the simple habitat simulation with the evolutionary constraint, the best final colorations matched the background significantly better in the runs that reached the predation susceptibility threshold value within 200 generations than in those that did not reach it (Mann-Whitney *U*-test:  $N_1 = 330$ ,  $N_2 = 170$ ,  $Z = -15.49$ ,  $P < 0.001$ ). However, the best final colorations in the complex habitat simulation with constrained evolution matched the background significantly worse than the best final colorations in the simple habitat simulation with constrained evolution (Mann-Whitney *U*-test:  $N_1 = N_2 = 500$ ,  $Z = 4.95$ ,  $P < 0.001$ ; Fig. 3). Even in those runs of the simulation of constrained evolution in the simple habitat, which did not reach the predation susceptibility threshold in 200 generations, the best final coloration matched the background better in 22.0% and equally well in 71.4% of the runs than in the simulation of constrained evolution in the complex habitat. These results demonstrate that the degree of background matching alone did not account for the difficulty of the constrained evolution to reach the predation susceptibility threshold value in the simple habitat.

Background matching did not continuously increase between generations, but after an initial increase in background matching, decrease of the prey susceptibility was frequently achieved also by a decrease in the background matching (Fig. 2). For instance, when the push of the last generation below the predation susceptibility threshold value involved a change in the level of the background matching of the best coloration in the population, this change was a decrease in the matching in 46.3%–75.4% of the cases in the four simulations.

#### DISCUSSION

The present model resulted in evolution of cryptic prey coloration, as was shown by the decrease of predation sus-

ceptibility of the prey. The model, however, suggests that it is easier to decrease the risk of detection to a given level by the means of cryptic coloration in a visually complex habitat than in a simple habitat because in the simple habitat the evolutionary constraint had a much more severe impact on predation susceptibility. This result has wide importance, as it appears that the evolution of camouflage is susceptible to several kinds of constraints (Merilaita et al. 1999). To begin with, the production of some coloration elements that could be used to achieve camouflage may be constrained. Further, in heterogeneous habitats, camouflage may be constrained by conflicting requirements among different parts of the habitat (Merilaita et al. 1999). Camouflage may also be constrained by other functions of coloration, such as signalling or thermoregulation (Endler 1978).

The difficulties of the prey in the simple habitat reaching the predation susceptibility threshold with constrained coloration were not caused by an inferior background matching, but by a higher probability of detection of a constrained coloration in the simple habitat than in the complex habitat. This first suggests that not only is the probability of detection determined by the resemblance between animal coloration and background, but the degree of camouflage of an animal coloration also depends on the visual complexity of the background. To put it more generally, it proposes that the difficulty of a detection task is related to the complexity of the background. The result also suggests, that in addition to relying on background matching, camouflage can exploit predators' information processing or, rather, shortcomings in the information processing (cf. Dukas 1998). This idea is supported by a previous predation experiment in which the risk of detection did not vary simply in accordance with background matching of the prey (Merilaita et al. 2001).

An explanation for this result is that the categorization task can be expected to be more demanding in the complex habitat in which the number of possible different visual samples,  $4^8$ , is ten-fold more than the  $3^8$  of the simple habitat. Also, the ability of a neural network to generalize (i.e. correctly categorize data that it has not encountered during training), which is traded off against the accuracy of the categorization of previously encountered data, is decreased by the complexity of the categorization task (Haykin 1999). Another important point contributing the result is limitations in a predator's ability to process visual information (e.g., Dukas 1998). The trade-off that natural predators experience between search rate and prey detection probability demonstrates such limitation in information processing capacity (Gendron and Staddon 1983; Gendron 1986). Thus, predator's need to meet its minimum capture rate constrains the time that it can use to search a given area, constraining also thoroughness of the search and the detection probability. Correspondingly, in the current model the predator's detection ability was limited, which was indicated in that the unconstrained prey only seldom evolved a coloration that perfectly matched the background. The consequence of such limitation for a natural predator as well as for the artificial neural network is that instead of being able to use every aspect of the patterns, it is restricted to only use some aspects of them in the pattern recognition, resulting in decreased accuracy of detection. To conclude, the increase in the amount of visual information

with increasing visual complexity, combined with limitations in predator's information processing, results in requirements for camouflage being more stringent in complex than simple habitats.

For the validity of any evolutionary conclusions based on the present model, it is important that the essential aspects of the behavior of the artificial neural network are consistent with the behavior of biological neural systems. Experimental studies confirm this. Accordingly, experiments on humans show that the difficulty of a visual detection task increases with increasing complexity of background patterns and colors (Gordon 1968; Farmer and Taylor 1980).

The model has several important implications for the study of the evolution of camouflage. First, the model predicts that in the evolution of cryptic coloration, the requirement of background matching is less stringent in a visually complex habitat than in a simple habitat and therefore the appearance of the optimal coloration is more loosely determined in a complex habitat. Consequently, it may be easier to decrease the risk of detection to a given level by the means of cryptic coloration in a visually complex habitat. Further, it has previously been suggested that a visually complex background may facilitate color polymorphism because in such habitats there should be several ways to resemble the background (Endler 1978). However, the current model suggests that in complex habitats the conditions for polymorphism may be even less stringent than that because less exact background matching is required in such habitats.

Second, by suggesting that visual background complexity and predators' information processing affect the risk of detection, this study questions the use of background matching as the measure of camouflage, especially between different habitats or within a habitat when it is not visually uniform and simple. This conclusion is of paramount importance because the protection from cryptic coloration has not before been considered to be related to the visual characteristics of the background, but rather a given degree of background matching has been assumed to yield equal camouflage on any background (Endler 1978, 1984).

Third, biases and constraints in predators' information processing, such as the less stringent requirement of background matching in visually complex habitats, may allow a more effective use of other means to improve camouflage. First, it has been suggested that camouflage can be improved by disruptive coloration, a coloration that conceals prey characters such as body shape or shape of specific parts of the body used by predators in detection and identification of prey (Cott 1940). Maximization of such effect is not always in accordance with maximization of background matching of the geometry and colors of the coloration (Merilaita 1998). Second, in visually heterogeneous habitats the optimal coloration is sometimes coloration that is a compromise between the requirements of several microhabitats instead of matching any one microhabitat (Norris and Lowe 1964; Shreeve 1990; Merilaita et al. 1999, 2001). Such compromise is more likely to be favored if the requirement for background matching is not stringent (Merilaita et al. 1999).

Although the evolution of prey coloration generally improved background matching in the model, the improvement was not continual, but instead the degree of background

matching fluctuated. This observation corresponds well to the idea of predators' limited and shifting attention, which has been suggested to account for the so-called "search image" (Dawkins 1971; Pietrewich and Kamil 1979; Dukas and Kamil 2001). Thus, instead of using all the visual information available, the predator's attention is limited to some characteristics sufficient for conducting the detection task. Consequently, the prey's co-adaptive response is not necessarily to increase its background matching, but to make impossible a detection based on that aspect of the coloration, in which the predator has focused its attention. This, in turn, should cause the predator to shift its attention to another aspect of the coloration.

To summarize, the current model predicts that the evolution of camouflage is less demanding in visually complex habitats because a lower degree of background matching is required there than in simple habitats. The model also suggests that protection from camouflage depends on the visual characteristics of the habitat and, therefore, the degree of background matching is not a reliable measure of camouflage when measurements from visually different backgrounds are compared.

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