CONDITIONS FOR THE SPREAD OF CONSPICUOUS WARNING SIGNALS: A NUMERICAL MODEL WITH NOVEL INSIGHTS

MIKAEL PUURTINEN\textsuperscript{1,2} AND VEIJO KAITALA\textsuperscript{1,3}

\textsuperscript{1}Department of Biological and Environmental Science, P.O.B. 35, FIN-40014 University of Jyväskylä, Finland
\textsuperscript{2}E-mail: hemipu@bytl.jyu.fi
\textsuperscript{3}Present address: Department of Biological and Environmental Sciences, P.O.B. 65, FIN-00014 University of Helsinki, Finland

Abstract—The initial evolution of conspicuous warning signals presents an evolutionary problem because selection against rare conspicuous signals is presumed to be strong, and new signals are rare when they first arise. Several possible solutions have been offered to solve this apparent evolutionary paradox, but disagreement persists over the plausibility of some of the proposed mechanisms. In this paper, we construct a deterministic numerical simulation model that allows us to derive the strength of selection on novel warning signals in a wide range of biologically relevant situations. We study the effects of predator psychology (learning, rate of mistaken attacks, and neophobia) on selection. We also study the how prey escape, predation intensity, number of predators, and abundance of different prey types affects selection. The model provides several important results. Selection on novel warning signals is number rather than frequency dependent. In most cases, there exists a threshold number of aposematic individuals below which aposematism is selected against and above which aposematism is selected for. Signal conspicuousness (which increases detection rate) and distinctiveness (which allows predator to distinguish defended from nondefended prey) have opposing effects on evolution of warning signals. A more conspicuous warning signal cannot evolve unless it makes the prey more distinctive from palatable prey, reducing mistaken attacks by predators. A novel warning signal that is learned quickly can spread from lower abundance more easily than a signal that is learned more slowly. However, the relative rate at which the resident signal and the novel signal are learned is irrelevant for the spread of the novel signal. Long-lasting neophobia can facilitate the spread of novel warning signals. Individual selection via the ability of defended prey to escape from predator is not likely to facilitate evolution of conspicuous warning signals if both the resident (cryptic) morph and the novel morph have the same escape probability. Predation intensity (defined as the proportion of palatable prey eaten by the predator) has a strong effect on selection. More intense predation results in strong selection against rare signals, but also strong selective advantage to common signals. The threshold number of aposematic individuals is lower when predation is intense. Thus, the evolution of warning signals may be more likely in environments where predation is intense. The effect of numbers of predators depends on whether predation intensity also changes. When predation intensity is constant, increasing numbers of predators raises the threshold number of aposematic individuals, and thus makes evolution of aposematism more difficult. If predation intensity increases in parallel with number of predators, the threshold number of aposematic individuals does not change much, but selection becomes more intense on both sides of the threshold.

Key words.—Aposematic, conspicuousness, learning, neophobia, predation intensity, recognition errors.

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The initial evolution of warning signals in defended prey (aposematic signals) is considered an evolutionary problem for two reasons. First, if the aposematic morph is more conspicuous than the original (more or less cryptic) morph, it will be detected by predators more often. Second, when the aposematic morph first originates it is likely to be rare. Rarity presents a problem because the per capita mortality during predator education is higher for rare prey types than for abundant prey types (Greenwood et al. 1989; Lindström et al. 2001b). However, if the aposematic morph becomes common, selection may well favor its maintenance and further spread to the population. Because predators are better able to learn, remember, and recognize conspicuous aposematic individuals as unprofitable prey (Gittleman and Harvey 1980; Sillén-Tullberg 1985; Guilford 1986; Roper and Wistow 1986; Roper and Redston 1987; Alatalo and Mappes 1996; Lindström et al. 1999, 2001a), the advantages of enhanced predator avoidance could well compensate for the disadvantage of increased conspicuousness (Endler 1988; Guilford 1990).

Several explanations have been put forward to explain the apparently paradoxical evolution of aposematism. One argument suggests that the assumption of disproportional predation on the rare novel morph is simply wrong (Thomas et al. 2003, 2004; Marples et al. 2005). If predators are reluctant to sample prey items they have not encountered before (neophobia) or if they are very conservative in their choices of food items (dietary conservatism), a novel aposematic prey morph may initially suffer very little predation. However, neophobic aversion is expected to diminish as prey becomes more familiar, and it is not clear whether neophobia can increase the fitness of rare conspicuous prey types in situations where predators and prey interact for extended periods of time (Speed 2001).

A second class of arguments envisions chance or genetic factors that could raise the frequency of the aposematic morph over the threshold where learned predator avoidance selects for aposematism. Mallet and Singer (1987) suggested that the aposematic morph could increase in frequency in small local populations by genetic drift and then spread through the population because of its higher overall fitness. A model by Harvey et al. (1982) suggested that aposematism could evolve in a species that lives in gregarious family groups, provided that predators are better able to learn to avoid groups of aposematic siblings than groups of cryptic individuals (see Alatalo and Mappes 1996; Riipi et al. 2001). Brodie and Agrawal (2001) suggested that such groups of aposematic...
siblings could easily arise if the aposematic phenotype was expressed by the offspring of the individual carrying the gene (a maternal effect gene) rather than by the individual itself. However, all these models make rather unspecified assumptions about the strength of selection on the aposematic morph, making it difficult to apply the models to different systems.

A third class of arguments suggests that conspicuous warning signals could evolve by individual selection. There are two different mechanisms by which individual selection could work. One is the idea of peak-shift, where aversion of predators is strongest against more conspicuous prey than the prey that predators have actually learned to avoid. The disadvantage of increased conspicuousness could then be counterbalanced by predators being less likely to attack new, more conspicuous prey types (Leimar et al. 1986; Mallet and Singer 1987; Yachi and Higashi 1998; Mallet and Joron 1999). Empirical studies have provided some support for this hypothesis, but more studies are needed to evaluate the general importance of peak-shift phenomenon in the context of warning-signal evolution (Gamberale and Tullberg 1996; Lindström et al. 1999). Individual selection might allow aposematism to evolve also if defended prey are able to survive predator attacks. Predators could then learn to avoid aposematic individuals (including the one attacked) in future encounters (Sillén-Tullberg and Bryant 1983; Engen et al. 1986). However, this idea of individual selection by prey escape has not been examined in the context of selection against rare morphs, and the theoretical plausibility of the argument thus remains unclear (Mallet and Singer 1987; Mallet and Joron 1999; Ruxton et al. 2004, p. 110).

Yet another class of explanations was proposed by Merilaita and Kaitala (2002), who argued that the evolution of aposematism can be approached by looking at the ecology of aposematism. In some cases, switching to a new host plant may enable the initial evolution of aposematism (Harvey and Paxton 1981; Guilford 1988; Endler 1991; Merilaita and Kaitala 2002). In particular, the herbivorous prey may gain from the new host plant compounds useful for defense against predation. However, the prey may be conspicuous on the new host plant, which may initiate evolution of aposematism (Gittleman and Harvey 1980; Guilford 1990).

The role of predation intensity in determining the strength and shape of selection on warning signals has received relatively little attention from researchers. In this paper, predation intensity is explicitly defined as the proportion of palatable prey individuals that succumb to predation during the season. As we describe below in the model section, predation intensity on palatable prey has a direct relationship with intensity of predation on defended prey species, making it a very useful concept for studying evolution of warning coloration. It is conceivable that predation intensity varies among different environments. For example, predation on insects is probably more intense in tropical rainforests than in highly seasonal habitats like arctic tundra. Predation intensity is important for evolution of warning signals because predation, by definition, is the selective force responsible for warning signal evolution (Guilford 1988). Predation intensity is thus intimately linked to intensity of selection on warning signals. However, the effect of predation intensity on evolution of warning signals is not easy to predict without a formal mathematical model. Intensive predation can make it very difficult for a rare aposematic morph to spread to a population, whereas aposematic signaling has no selective benefit in the absence of predation.

Many different hypotheses have been proposed to explain the evolution of conspicuous warning signals under the rare conspicuous mutant scenario (for a review see Ruxton et al. 2004). However, the exact properties of frequency-dependent selection under the rare conspicuous mutant scenario are poorly understood. Servedio (2000) built an analytical model for the effects of predator learning, forgetting, and recognition errors on the evolution of warning coloration. Her model analytically showed that predation results in frequency-dependent selection and that predator cognitive abilities determine the position of the frequency threshold above which aposematism is favored. However, the shape and strength of selection is not easily derived from her analytical model. Here, we develop an extended numerical simulation model based on Servedio’s (2000) original approach that allows us to derive the strength of selection on aposematic phenotypes for many different situations. With our model, we study the effects of predator learning, predator recognition errors, predator neophobia, prey escape probability, predation intensity, number of predators, and numbers of different prey types on the evolution of conspicuous warning signals.

Our model clarifies the role of predator learning and neophobia in warning signal evolution and emphasizes the importance of distinguishing signal conspicuousness from signal distinctiveness. The model also sheds light on the issue of whether prey escape combined with predator learning can facilitate evolution of warning signals by individual selection. Perhaps the most interesting results of the model are that selection on aposematic morph is number rather than frequency dependent and that predation intensity and predator numbers can have a strong effect on warning signal evolution.

The Model

We model the changes in numbers of different prey types over one generation of the prey’s life cycle (a season). The model is fully deterministic. We assume that in the beginning of the season the predator(s) are naive with respect to all prey types. The prey community consists of one defended prey species with two morphs, aposematic (bright) and cryptic (dull). In addition to the defended species, there is a palatable species (or a group of palatable species) upon which the predator relies as food. For simplicity, we assume that the palatable species and the dull morph of the defended species are equally conspicuous.

During the season, predator(s) make attacks on prey until a predetermined fraction of the palatable prey population has been consumed by predator(s). We call the proportion of palatable prey eaten during the season predation intensity; the larger the proportion of palatable prey eaten, the higher the predation intensity. It is worth noting that the total number of attacks on all prey types over the whole season is not fixed, but depends on the numbers of different prey types in the beginning of the season (and on predator learning capabilities). The main advantage of using predation intensity to define season length is that, with constant predation in-
tensity, selection on the defended species is independent of the number of individuals in the palatable species. This is because fixed predation intensity on palatable prey results in the same number of attacks on the defended prey, irrespective of the number of palatable prey in the beginning of the season (assuming the numbers of aposematic and dull defended prey in the beginning of the season are the same). For example, when palatable individuals are rare, the predator will make many attacks on defended prey before it succeeds to find and predate the palatable prey. However, if palatable individuals are very numerous, the predator will make a very large total number of attacks during the season. The fraction of these numerous attacks directed toward defended prey amounts to exactly the same number of attacks as when the palatable prey are rare, because the season length adjusts to precisely compensate for the variation in palatable prey numbers. Thus, assuming fixed predation intensity and same numbers of the defended prey types, the abundance of palatable prey does not affect selection on the aposematic morph.

Fitness of the aposematic morph is calculated as the relative per capita survival of the bright morph in relation to the survival of the dull morph

\[ W = \frac{N_B(\text{end})/N_B(1)}{N_D(\text{end})/N_D(1)}, \]

where \( N_B(1) \) and \( N_B(\text{end}) \) denote numbers of bright (aposematic) individuals of the defended species in the beginning and in the end of the season, and \( N_D(1) \) and \( N_D(\text{end}) \) are the corresponding numbers of dull (cryptic) individuals of the defended species.

If \( W > 1 \), the aposematic form increases in frequency relative to the cryptic morph and can invade the population. If \( W < 1 \), the aposematic morph decreases in relative frequency during the course of the season. Assuming that each prey generation faces a naive population of predators, the aposematic morph will not be able to invade unless \( W > 1 \).

We model the season of predation as consisting of discrete time steps. During each time step, the predator makes one attack on a prey individual. To calculate the change in prey numbers from time step \( t \) to time step \( t + 1 \), we first calculate the proportion of individuals belonging to the defended species \( (x) \) at time \( t \):

\[ x(t) = \frac{N_B(t) + N_B(t)}{N_p(t) + N_D(t) + N_B(t)}, \]

where \( N_p \) denotes the number of individuals in the palatable species. Next, we calculate the proportion of aposematic individuals in the defended species:

\[ b(t) = \frac{N_B(t)}{N_B(t) + N_D(t) + N_B(t)}. \]

The relative probabilities with which the different prey types are detected by the predator at time \( t \) are:

\[ P_B(t) = cx(t)b(t)[cx(t)b(t) - x(t)b(t) + 1], \]

and

\[ P_D(t) = x(t)[1 - b(t)][cx(t)b(t) - x(t)b(t) + 1], \]

where \( c \) is the relative conspicuousness of the aposematic morph \( (c > 1) \).

Next we define the probabilities that each prey type is attacked if detected. The probability that a palatable species is attacked when detected is always one \( (g_B = 1) \). The probabilities that defended prey types will be attacked when detected at time step \( t \) are given by:

\[ g_B(t) = [1 - v_B(t)m_B][1 - n(t)] \quad \text{and} \quad \quad \quad \quad \quad \quad \quad \text{(5a)} \]

\[ g_D(t) = 1 - v_D(t)m_D, \quad \text{(5b)} \]

where \( v_B \) and \( v_D \) are learned aversions toward bright and dull defended prey, respectively, \( n \) is the probability that the predator will not attack the bright prey due to neophobic aversion, and \( m \) is the probability that the predator correctly identifies the defended prey if learning has taken place (signal distinctiveness). We assume that aposematic prey are more easily distinguished from palatable prey than the dull prey, and thus the probability of correct identification is higher for aposematic than dull prey \( (m_B > m_D) \).

In the simulations we usually assume that there is no neophobia \( (n = 0) \), unless specifically stated. In simulations with neophobia, predators have neophobic aversion only toward aposematic prey. Neophobia is modeled as an initial aversion toward aposematic prey \( (n[1] = 1) \), but this aversion diminishes by factor \( e \) each time an aposematic individual is sighted. Neophobic aversion toward aposematic prey at time \( t \) is:

\[ n(t) = n(t - 1) - P_B(t - 1)e n(t - 1). \]

In the beginning of the season predators are naive, and there is no learned aversion toward either bright or dull defended prey \( (v_B[1] = 0 \text{ and } v_D[1] = 0) \). The learned aversion at time step \( t \) toward aposematic \( (v_B) \) and dull \( (v_D) \) prey are given by:

\[ v_B(t) = v_B(t - 1) + A_B(t - 1)k_B[1 - v_B(t - 1)] \quad \text{and} \quad \quad \quad \quad \quad \quad \quad \text{(7a)} \]

\[ v_D(t) = v_D(t - 1) + A_D(t - 1)k_D[1 - v_D(t - 1)], \quad \text{(7b)} \]

where \( k \) is a factor related to speed of learning the association of prey appearance and prey defenses \( (k_B \approx k_D) \) and \( A(t - 1) \) is the probability of an attack on this prey type at the previous time step. We thus assume that learning the association between prey appearance and prey defenses happens only when the prey is attacked. Further, we assume that predators do not forget this association during the season, which is a reasonable assumption for many vertebrate predators (e.g., Langham 2004).

Now we can calculate the probabilities of predator attack for each prey type during time step \( t \) as:

\[ A_B(t) = P_B(t)g_B(t)[P_B(t)g_B(t) + P_D(t)g_D(t) + P_P(t)], \]

\[ A_D(t) = P_D(t)g_D(t)[P_B(t)g_B(t) + P_D(t)g_D(t) + P_P(t)], \]

and

\[ A_P(t) = P_P(t)[P_B(t)g_B(t) + P_D(t)g_D(t) + P_P(t)], \]

and the probability for each prey type to die during time step \( t \) is calculated as

\[ D_B(t) = (1 - s)A_B(t)p, \]

\[ D_D(t) = (1 - s)A_D(t)p, \]

and

\[ D_P(t) = A_P(t)p. \]

where \( p \) is the number of predators foraging in the area, and \( s \) is the probability that a defended prey will escape unharmed from the predator if attacked.

Finally, the numbers of different prey types at time step \( t + 1 \) are:

\[
N_B(t + 1) = N_B(t) - D_B(t), \quad (10a)
\]

\[
N_D(t + 1) = N_D(t) - D_D(t), \quad \text{and} \quad (10b)
\]

\[
N_p(t + 1) = N_p(t) - D_p(t). \quad (10c)
\]

The season is over (simulation is ended) when

\[
1 - \frac{N_p(t)}{N_p(1)} \geq \text{predation intensity}. \quad (11)
\]

An external test of the model’s ability to mimic true predator behavior is provided by the study of Lindström et al. (2001b). In their study, great tits were allowed to prey on artificial prey in a novel-world experiment. The birds were offered conspicuous unpalatable prey items among palatable cryptic prey items at three different frequencies (4%, 12%, and 32%). The total number of prey items was 200 in each treatment, and the birds were allowed to eat 50 prey items on two consecutive days. On both days the experiment was started with 200 prey items with treatment-specific frequency of aposematic prey items. If we set the conspicuousness of the bright prey to six times that of palatable prey (\( c = 6 \)), a value estimated by Lindström et al. (2001a), and the numbers of the two prey types as in the experiment (4%: \( N_B = 8, N_p = 192 \); 8%: \( N_B = 16, N_p = 184 \); 32%: \( N_B = 64, N_p = 136 \)), and further choose the values of memorability and learning coefficient to maximize the fit of the model to the experimental results (\( m_B = 1, k_B = 0.25 \)), we obtain results nearly identical to the experimental ones (cf. Figs. 1A and 1B). The model can thus reproduce patterns of true predator learning quite accurately, which gives confidence to the simulation results.

**RESULTS**

The model allows to us to study the effects of 11 different parameters (numbers of the three prey types, number of predators, intensity of predation, conspicuousness of the aposematic prey, memorability and learning coefficients for both aposematic and cryptic defended prey, presence/absence of neophobia, and extinction rate of neophobia). Obviously, the number of different simulations that can be done is enormous. For simplicity, we only present results for selected parameter values to illustrate the most important general results emerging from the model. The results are presented graphically with the relative fitness of the aposematic morph (\( W \)) on the y-axis and either the frequency \( N_B(1)/[N_B(1) + N_D(1)] \) or abundance \( N_B(1) \) of the aposematic morph in the beginning of the season on the x-axis. The value \( W = 1 \) indicates equal fitness for the bright and dull defended prey. The default values for other parameters, unless otherwise stated, are number of palatable prey \( N_p(1) = 1000 \), number of defended prey \( N_B(1) + N_D(1) = 400 \), number of predators \( p = 1 \), predation intensity = 80%, conspicuousness of the bright morph \( c = 6 \), neophobia absent, distinctiveness of bright morph \( m_B = 0.98 \) and dull morph \( m_D = 0.5 \), learning coefficient of bright morph \( k_B = 0.25 \) and dull morph \( k_D = 0.1 \).

**Number- versus Frequency-Dependent Selection**

In the first set of simulations, we varied the number of individuals belonging to the defended prey species, \( N_B(1) + N_D(1) \). The simulations revealed that shape of frequency-dependent selection on the bright morph very strongly depends on the number of individuals belonging to the defended species. When abundance of the defended species is low, the threshold frequency for the spread of the aposematic morph is high, but when abundance of the species is high, the threshold is low (Fig. 2A). Thus, if we only know the relative frequency of the aposematic morph, but not the local abundance of defended prey, we cannot tell whether the aposematic morph is at a selective advantage or disadvantage.

We find that selection on the aposematic morph depends very strongly on the absolute number of aposematic individuals in a locality. There usually exists a threshold number of aposematic individuals below which aposematism is selected against and above which aposematism is selected for. Most important, this threshold number is largely independent of
the number of individuals belonging to the defended species. Only if the defended species is quite rare (and, consequently, learning of neither aposematic nor the dull morph is completed), does the threshold number shift to slightly lower values (Fig. 2B). If the defended species is very rare, it is also possible that aposematic morph is always selected against.

**The Effects of Signal Conspicuousness, Distinctiveness, and Rate of Learning**

In our model, signal conspicuousness \( (c) \), signal distinctiveness \( (m_i) \), and signal learning rate \( (k_i) \) can vary independently. Results of the simulations revealed that conspicuousness per se is not beneficial to the prey (unless there is innate avoidance against conspicuous prey, see below). If two signals differ only in conspicuousness, the less conspicuous signal is at a selective advantage because it is detected less often by predators (Fig. 3). Next, we study how signal distinctiveness and rate of avoidance learning affect evolution of aposematism.

We first focus on the relationship between signal conspicuousness and distinctiveness. Our simulations show that signal distinctiveness is the most important signal attribute for evolution of aposematism. In our model, a conspicuous warning signal cannot invade a population unless it reduces mistaken attacks by the predators. As discussed above, conspicuousness per se is detrimental to signal evolution. However, distinctive signals tend to be conspicuous, and it is interesting to ask how conspicuous can an aposematic signal can be. From the simulation results, a useful approximation for an upper limit of signal conspicuousness emerges:

\[
W = \frac{N_b(1)}{[N_b(1) + N_d(1)]}
\]

\[
W = \frac{N_b(1)}{[N_b(1) + N_d(1)]}
\]
This same expression was found by analytically Servedio (2000) to be a threshold for signal evolution when predators are assumed to have learned both morphs of defended prey. In our model, if signal conspicuousness $(c)$ exceeds the value given by equation (12), spread of the signal is unlikely (it can spread only if the dull morph is very rare, learning of the dull morph is extremely slow, or when there is neophobia). Equation (12) has a simple and intuitive interpretation: a conspicuous aposematic signal can invade a population only if it reduces mistaken attacks by a factor equal to or greater than the increase in conspicuousness. For example, a new morph that is twice as conspicuous as the old morph cannot invade a population unless the rate of mistaken attacks by experienced predators is reduced by 50% or more. Note, however, that it is not enough that a signal satisfies the condition expressed in equation (12), it also needs to cross the local abundance threshold where the per capita survival exceeds the survival of the dull morph (Fig. 2B). This is different from Servedio’s (2000) result where the effects of gradual learning were not taken into account.

From simulations with different learning coefficients, two results are apparent. First, for the spread of rare aposematic mutant, learning rate of the dull morph ($k_D$) is irrelevant (as long as $k_D > 0$). Second, the aposematic morph can invade a population more easily if the predator’s learning rate of the aposematic morph is high (high $k_B$).

It is often thought that if the aposematic morph is learned faster than the dull (or cryptic) morph, evolution of aposematism is not problematic. Our results suggest that this is not necessarily the case. If we keep the predator’s learning rate of the aposematic morph ($k_B$) constant and vary the learning rate of the dull morph ($k_D$), we see that the threshold number for the spread of the aposematic morph is not affected by learning of the dull morph (Fig. 4A). This result agrees with Servedio’s results, as she also found that the threshold is not affected by $k_D$ (eq. 12 in Servedio 2000; M. Servedio, pers. comm.). Thus, relative learning speed does not affect the threshold number. The reason for this counterintuitive result is that mortality during predator education has very little effect on the overall per capita mortality of abundant dull prey. Thus, when the dull morph is common and the aposematic morph is rare, $k_D$ has very little effect on the relative fitness of the aposematic morph.

The second result is that fast learning of the aposematic morph greatly facilitates evolution of aposematism (Fig. 4B). This is because the number of prey killed during predator education has a major effect on the per capita mortality of the rare aposematic morph. When both morphs have been learned, the aposematic morph has higher fitness because predators make fewer mistaken attacks toward the aposematic than the dull prey ($m_B > m_D$).

**Neophobia**

Neophobic aversion toward aposematic prey can facilitate the spread of a rare aposematic mutant to the population, and the facilitation is stronger the slower neophobic aversion...
fades (Fig. 5). An interesting finding is that when predators are neophobic, fitness of the aposematic morph is not a monotonically increasing function of morph abundance. The aposematic morph has minimum fitness when there are few aposematic individuals present in the population, but when there is only one aposematic individual, fitness can be high. This is because a single aposematic individual is sighted so rarely that it is effectively protected from predators. With several aposematic individuals, neophobic aversion is eroded more quickly, and predators start sampling the aposematic prey before the season is over. Thus, costs of predator education are being paid, but the aposematic morph does not enjoy the advantage of learned aversion of educated predators. When the aposematic morph is abundant, aposematic prey are protected by the learned aversion of educated predators for most of the season. The slight benefit from neophobia for abundant aposematic prey is a carry-over effect of low numbers of aposemes eaten in the beginning of the season.

**Escape Probability**

The possibility for defended prey to escape predator attack unharmed does not seem to provide an easy solution for the rare conspicuous mutant problem. If both aposematic and dull morph have equal probability of surviving a predator attack, high escape probability merely decreases the strength of selection, but it does not have a strong effect on the threshold number for the spread of aposematic morph (Fig. 6). High escape probability reduces selection intensity because the mortality of both aposematic and dull morph is reduced.

**Predation Intensity**

Predation intensity has a strong impact on the evolution of aposematism. With low predation intensity, the rare aposematic morph is at a slight selective disadvantage, but the selective advantage for common aposematic morph is also low. More intense predation makes selection against rare aposematic morph stronger. However, intense predation also decreases the threshold number of aposematic individuals and increases the fitness benefit of common aposematic morph (Fig. 7). Thus, we would expect aposematism to be more common in environments where predation is intense than in environments where predation is weak, provided that the aposematic morph can somehow overstep the abundance threshold.

**Number of Predators**

The effect of the number of predators on evolution of aposematism depends on whether predation intensity is constant or not. If predation intensity is constant (i.e., the total proportion of palatable prey eaten by predators stays the same), increasing the number of predators makes aposematism less likely to evolve (Fig. 8). This is because the cost of educating many predators increases the per capita mortality of the aposematic prey, thus raising the threshold number of aposematic individuals. Based on this result, we would expect aposematism to be more common in environments with one or few predators per locality than in environments where the same predation intensity is caused by many individual predators. However, if the number of prey eaten per predator is constant, increasing the number of predators makes selection more intense, but does not affect the threshold number of apose-
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FIG. 7. Fitness of the aposematic morph as a function of its abundance for different levels of predation intensity (proportion of palatable prey eaten by predators during the course of the season).

FIG. 8. Fitness of the aposematic morph as a function of its abundance for different numbers of predators in a locality. Here, predation intensity (proportion of palatable prey eaten by predators) is constant (80%). When there are many predators, each predator attacks a smaller number of prey than when there are fewer predators.

FIG. 9. Fitness of the aposematic morph as a function of its abundance for different numbers of predators in a locality. Here, predation intensity increases linearly with the number of predators in a locality.

DISCUSSION

Our numerical simulation model helps to resolve several ambiguities in the current understanding of evolution of aposematism. Specifically, we clarify questions about frequency- versus number-dependent selection, the role of predator learning and recognition errors, the effects of neophobia and prey escape, and the effect of predation intensity on evolution of aposematism.

Frequency- or Number-Dependent Selection?

Strong selection against rare conspicuous morphs of defended prey is often thought to be the main obstacle for the evolution of novel warning signals. But rarity has two meanings, and in most discussions, no distinction is made between rarity as low relative numbers and rarity as low absolute numbers of the aposematic morph (e.g., Endler 1988; Servedio 2000; Speed 2001; Lindström et al. 2001b; Endler and Mappes 2004). Our results show that it is important to distinguish between relative and absolute numbers. Rarity as low relative frequency does not tell us whether aposematism can spread. If the defended species is very abundant, apo-
sematism can be favored even if the relative frequency of the aposematic morph is very low. Conversely, if the species is very rare, a conspicuous aposematic morph will not be able to invade the population even if it was to initially emerge at a very high relative frequency (see also Edmunds 1974).

Our results show that it is the absolute number of aposematic individuals in a locality that determines whether the aposematic morph will invade the population and that this threshold number is largely independent of the numbers of individuals in the defended species. Further, assuming constant predation intensity (i.e., that the proportion of palatable individuals eaten over the season is same), the threshold number is not affected by the abundance of the palatable species either. Thus, the threshold number of aposematic individuals can be derived from predator cognitive abilities and predation intensity only, without a need to explicitly consider the abundance of the palatable species.

The phenotypically plastic density-dependent warning coloration of Schistocerca locusts (Sword 1999; Sword et al. 2000) is a prime example for the importance of local abundance in warning color evolution. Normally these species occur at low densities and are cryptic, but when population densities increase, locusts feeding on toxic host plants change from cryptic to highly conspicuous aposematic coloration. Indeed, our model could be used to predict the critical density where warning coloration becomes beneficial, provided that relevant parameters relating to predator learning and predation intensity can be obtained for the specific system.

In a slightly different context, Mallet and Joron (1999) suggested a numerical model for evolution of alternative warning signals in a defended species. In their model, the numbers of different prey morphs predefined during a season are entered as model parameters, whereas our model uses a mechanistic model of predation to derive the number of different prey morphs killed. The model of Mallet and Joron (1999) suggests that there exists a relative frequency threshold above which a novel alternative signal is selected for, and that this relative frequency threshold is independent of the abundance of the defended species. Our model produces qualitatively identical results to those of Mallet and Joron (1999) if the two morphs have equal conspicuousness ($c = 1$) and equal distinctiveness ($m_B = m_D$, results not shown). The position of the relative frequency threshold is then determined by the predator’s learning rates of the two morphs ($k_B$ and $k_D$). Note, however, that if the two signals differ in conspicuousness and/or distinctiveness (as when a conspicuous signal arises in previously cryptic population), the threshold for spread of the novel morph depends on the abundance of the morph rather than on its relative frequency (Fig. 2).

**Predator Learning and Recognition Errors**

What is it about aposematic signals that make them effective in reducing predation on defended prey species? Here we have focused on two aspects that have been most intensively studied, namely the rate of avoidance learning and the accuracy of species recognition. Experimental studies show that predators learn to avoid conspicuous unpalatable prey more quickly than cryptic unpalatable prey (Gittleman and Harvey 1980; Sillén-Tullberg 1985; Roper and Redston 1987; Alatalo and Mappes 1996; Lindström et al. 1999; Riipi et al. 2001), and it is often implicitly assumed that faster learning of the aposematic morph is sufficient to explain its evolution (but see Mallet and Singer 1987; Speed 2001; Sherratt and Beatty 2003). However, our results show that it is not important that the aposematic morph is learned faster than the dull morph. Even though the relative learning rate does not matter for evolution of aposematism, learning rate is nevertheless important: evolution of aposematism is much easier if the aposematic morph is learned quickly than if it is learned slowly.

Our results support the view that the main advantage of warning signals is to allow educated predators to distinguish the defended species from undefended species. The idea that aposematic displays have evolved to allow easy and correct identification of defended prey stems back to the work of A. R. Wallace, “it would be highly advantageous to a caterpillar to be instantaneously and certainly recognised as unpalatable by all birds and other animals. Thus the most gaudy colours would be serviceable, and might have been gained by variation and the survival of the most easily-recognised individuals” (Darwin 1882, referring to correspondence with Wallace). The idea that conspicuousness reduces recognition errors has gained support from empirical studies (Guilford 1986). Our results, however, suggest that we should not expect warning signals to be exceedingly conspicuous, because conspicuousness comes with the cost of increased detection rate. If the new, more conspicuous signal increases detection rate more than it decreases mistaken attacks, the signal is not expected to spread to the population. Conspicuousness of many warning signals could thus be best understood as a means of achieving distinctiveness, and the increased rate of predator detection is an unfortunate side effect of signal design (for a thorough discussion of this topic see Guilford 1990). Indeed, not all efficient warning signals are conspicuous (e.g., Wüster et al. 2004). In experiments with humans predating on computer-generated prey, more cryptic warning signals evolved if they made the defended prey distinct from undefended prey (Sherratt and Beatty 2003). More cryptic warning signals can also be favored if prey defenses are not efficient against all predators, and/or if there is variation in predator cognitive abilities (Endler and Mappes 2004; Mappes et al. 2005).

**Neophobia**

Our model shows that neophobic aversion toward conspicuous prey could protect rare aposematic individuals, allowing the aposematic morph to increase in abundance to a level where learned predator avoidance favors aposematism. Whether neophobic aversion has been an important factor contributing to the initial evolution of novel warning signals or whether it has evolved after the emergence of aposematic prey is a more difficult question (Sherratt 2002; Marples et al. 2005).

**Prey Escape Probability**

Observations that aposematic insects can survive attacks by predators (Järvi et al. 1981; Wiklund and Järvi 1982)
spurred the idea that aposematism could evolve via individual selection if predators learn to avoid the aposematic morph without causing mortality on aposematic individuals. However, models assessing this possibility (Sillén-Tullberg and Bryant 1983; Engen et al. 1986) did not consider selection in frequency- or number-dependent context, and plausibility of the idea was subsequently put into question (Mallet and Singer 1987; Mallet and Joron 1999; Ruxton et al. 2004, p. 110). Our model shows that the possibility of prey escaping unharmed does not provide an easy solution for the evolution of conspicuous warning coloration. If the aposematic and the dull morph have the same probability of escaping predator attack unharmed, there still exists an abundance threshold for the spread of aposematic morph. High prey escape probability for both morphs, however, makes selection on prey appearance weak, possibly permitting nearly neutral evolution of prey appearance. However, in an intriguing study with two color forms of a distasteful bug as prey and hand-reared great grey shrikes as predators, Sillén-Tullberg (1985) showed that the escape probability of aposematic individuals can be substantially higher than the escape probability of otherwise similar but dull individuals. If the probability of surviving predator attacks is higher for aposematic than cryptic defended prey, it is conceivable that novel aposematic signals could evolve via individual selection.

**Predation Intensity and Number of Predators**

Our model shows that predation intensity (defined as the proportion of palatable prey consumed by predators) and predator numbers can have strong effects on the evolution of aposematism. We would expect aposematic coloration to be most common in environments where predation intensity is very high and where there are few (specialist) predators in each locality. Such conditions provide the highest relative fitness for aposematic individuals when the aposematic morph is reasonably common. In contrast, if predation is less intense and/or there are many (generalist) predators in a locality, evolution of aposematism is more difficult (see also Endler and Mappes 2004). Perhaps the abundance of aposematic and mimetic species in the tropics and the relative lack thereof in temperate and boreal regions reflect differences in predation intensity among these environments (L. Lindström and J. Mappes, pers. comm.). According to our model, intense predation in the tropics should favor the evolution of efficient warning signals. Conversely, in seasonal environments where insects abound and predation is weak, there is very little selection to favor the evolution of eye-catching aposematic displays.

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**LITERATURE CITED**


Riipi, M., R. V. Alatalo, L. Lindström, and J. Mappes. 2001. Mul-
tiple benefits of gregariousness cover detectability costs in apo-
prey affects the strength and durability of one-trial learning.
Anim. Behav. 35:739–747.
Roper, T. J., and R. Wistow. 1986. Aposematic colouration and
avoidance learning in chicks. Q. J. Exp. Psychol. 38:141–149.
attack: the evolutionary ecology of crypsis, warning signals, and
Servedio, M. R. 2000. The effects of predator learning, forgetting,
and recognition errors on the evolution of warning coloration.
signals as reliable indicators of prey defense. Am. Nat. 162:
377–389.
Sillén-Tullberg, B. 1985. Higher survival of an aposematic than of
Sillén-Tullberg, B., and E. H. Bryant. 1983. The evolution of apo-
sematic coloration in distasteful prey: an individual selection
Speed, M. P. 2001. Can receiver psychology explain the evolution
397:217.
Density-dependent aposematism in the desert locust. Proc. R.
Thomas, R. J., N. M. Marples, I. C. Cuthill, M. Takahashi, and E.
A. Gibson. 2003. Dietary conservatism may facilitate the initial
Thomas, R. J., L. A. Bartlett, N. M. Marples, D. J. Kelly, and I. C.
Cuthill. 2004. Prey selection by wild birds can allow novel and
conspicuous colour morphs to spread in prey populations. Oikos
being attacked by naïve birds: a reappraisal of the theory of
aposematic coloration evolving through individual selection.
Evolution 36:998–1002.
Wüster, W., C. S. E. Allum, B. Bjargardóttir, K. L. Bailey, K. J.
Dawson, J. Guenioui, J. Lewis, J. McGurk, A. G. Moore, M.
Niskanen, and C. P. Pollard. 2004. Do aposematism and Batesian
mimicry require bright colours? A test, using European viper