The Spatial Pattern of Natural Selection When Selection Depends on Experience

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abstract: Apostatic (frequency- or density-dependent) selection, aposematic signals, and mate choice behavior generally require that the mean prey or potential mate density m value be high enough (above a threshold T) to result in sufficient encounter rates for the searcher to learn or retain the association between conspicuous signals and prey unprofitability, to forage apostatically, or to choose among mates. This assumes that all searchers experience $m > T$, which implicitly assumes an even dispersion of targets among searcher territories. Uneven dispersion generates new phenomena. If $m < T$, then only territories with local density x values that are greater than T favor experience-based behavior, leading to spatially variable frequency- or density-dependent selection intensity. As aggregation increases, the increase in percentage of targets in favorable territories ($x > T$) is greater than the increase in the percentage of territories that are favorable. The relationship is reversed when $m > T$. In both cases, because as few as 10% of the territories can contain 80% of the targets, only a few territory holders may account for most of the selection on most of the target population; accidents of experience in only a few searchers can have unexpectedly large effects on the target population. This also provides an explanation for high searcher behavior variation (personalities): individuals from favorable territories will behave differently in behavioral experiments than those from unfavorable territories, at least with respect to similar kinds of targets. These effects will generate spatial heterogeneity in natural and sexual selection in what are otherwise uniform environments.

Keywords: aposematism, apostatic selection, density dependence, dispersion, frequency dependence, mate choice, mate search, polymorphism, sexual selection.

Introduction

When predators search for prey or when individuals search for mates, experience can affect the outcome. The probability of taking or accepting a new individual may depend on the encounter rate with previous individuals of the same kind. Here we consider the effects of spatial variation on encounter rates and natural and sexual selection.

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Two phenomena usually depend on predator experience, aposematism and apostatic selection. Aposematism is an antipredator mechanism that depends on predators learning to associate a prey's color pattern or some other signal with unpalatability or unprofitability. Maintenance of aposematism depends on a sufficient density of aposematic prey from which naive predators can learn, and experienced predators can remember, the association between the signal and unprofitability (Speed 2000; Endler and Mappes 2004; Ruxton et al. 2004; Mappes et al. 2005). If prey density is too low, the association will not be learned or retained; learning and retention are more likely to occur and occur more quickly with higher density. This is one of the reasons why the fitness of aposematic phenotypes is likely to be positively frequency or density dependent (reviewed in Endler and Mappes 2004) and why aposematism is more likely to evolve and be maintained in prey species that aggregate (Gamberale and Tullberg 1998; Gamberale-Stille 2000; Lindström et al. 2001; Riipi et al. 2001; Ruxton et al. 2004): aggregation produces locally higher density. Aposematism favors population monomorphism within prey species and mimicry among species (Endler and Mappes 2004; Ruxton et al. 2004). Aposematism does not preclude some variation, however, and imperfect comimics still benefit from aposematism (Ham et al. 2006; Ihalainen et al. 2007; Ojala et al. 2007).

Apostatic selection occurs when predators take prey types in a manner that is disproportionate to the prey frequency or density; it refers to a collection of phenomena that includes density-dependent selection, frequency-dependent selection, and the functional response (Chesson 1984; Allen 1988; Endler 1991; Endler and Mappes 2004; Ruxton et al. 2004; Bond and Kamil 2006; Merilaita 2006). Explanations for the mechanisms that result in apostatic selection include the formation of a search image, limited attention, information-processing limits, context-mediated avoidance, and the results of optimum foraging processes (summaries in Endler 1991; Servedio 2000; Ruxton et al. 2004; Punzalan et al. 2005; Darst 2006; Merilaita 2006). In most cases, the fitness of a particular kind of

prey consequently declines with its frequency or density, and in contrast to aposematism, apostatic selection favors prey polymorphism (Allen 1988; Allen et al. 1998; Endler and Mappes 2004; Bond and Kamil 2006). In most forms of apostatic selection, the predator must encounter enough prey to select apostatically.

In some cases, frequency-dependent selection may occur even without experience, but this usually occurs at very high densities and leads to antiapostatic selection. In antiapostatic selection, fitness increases with frequency or density, favoring monomorphism. Antiapostatic selection may occur at very high prey densities because the more common forms become the visual background for themselves, making them individually hard to target, whereas the rare forms are relatively conspicuous and easier to pick out (Allen et al. 1998; Weale et al. 2000). This may be the reason that shoaling, herding, and other tightly aggregating species tend to be less variable than other species; we do not know of any tightly aggregating species that have polymorphic populations. The phenomena we describe below will probably not apply to high-density populations in which experience is not needed to induce the frequency dependence.

Note that selection for aposematic coloration is also antiapostatic, because the more common forms train and remind the predators about their noxiousness more effectively than the less common aposematic forms (Ruxton et al. 2004). In this case, antiapostatic selection can occur at low densities (Lindström et al. 2001), provided that the predator-prey encounter rate is high enough for predator training. However, training efficiency increases with density, and this is one reason that aggregation is favored in aposematic forms (Ruxton et al. 2004). In high-density aggregations of aposematic species, monomorphism is favored not only because of training but also because the rarer forms would be easier to target by naive predators against the visual background of the more common aposematic form. Thus, aggregation and monomorphism are mutually reinforcing in aposematic species. In this article, we will concentrate on situations in which prior experience is important, so our results will probably not apply to prey species that are dense enough such that many are simultaneously visible to predators.

Many animals do not mate randomly but instead select among potential mates using a variety of criteria. In order to find a mate meeting these criteria, many potential mates are sampled before mating actually occurs. For example, a survey of female choice of males in a variety of species found that the mean number of males visited by females before mating occurred ranged from 1.7 to 7.5 (Gibson and Langen 1996). Prior experience with potential mates can do more than provide assessment of the available distribution of potential mates. For example, the probability of choosing a given mate type may depend on prior experience with similar potential mates. This can result in a rare-male advantage (e.g., Farr 1977; Partridge 1988; Terzic et al. 1996; Eakley and Houde 2004; Croft et al. 2005; Kokko et al. 2007) or other experience-based effects on mating (Farr 1980; Rosenqvist and Houde 1997; Jirotkul 2000; Zajitschek et al. 2006) and also in experienced-based species recognition (Magurran and Ramnarine 2004). Frequency-dependent sexual selection can also occur in male-male interactions both within (Bleay et al. 2007) and between (Dijkstra et al. 2005) species. Choosiness itself may depend on potential mate densities; both empirical and theoretical studies suggest decreased choosiness with lower densities, particularly in species that compare mates sequentially rather than simultaneously (Kokko and Mappes 2005). In each case, a minimum number of individuals must be encountered before the process can work. As in the case of predators searching for prey, our conclusions may not apply in species that lek or otherwise provide potential mates with simultaneous choices. Our model assumes that choice is a function of experience or, more specifically, that the density of prey or mates must be high enough for a frequency-dependent choice to occur.

These three experience-based phenomena require that encounter rates be above a minimum value. For either aposematism or apostatic selection to work, the prey density must be high enough for sufficient prey encounter rates such that an individual predator can learn or retain the association between conspicuous signals and prey unprofitability or such that a search image, functional response, or other apostatic mechanism can be formed. Similarly, experience-based social effects require minimum encounter rates with potential mates or rivals. All three classes of models implicitly assume that all predators or mate searchers experience the same potential encounter rates and that these rates are above the thresholds required for the mechanisms. This is equivalent to assuming that prey or potential mates have even (or evenly spaced) dispersions among the searchers' territories or home ranges. This implicit assumption arose because previous articles were focused on what happens within a searcher's territory, and they did not consider variation among territories. Here we show how different patterns of dispersion among territories may affect selection by experience-based searchers, and we hope to promote more work on the effects of relative dispersion. For brevity, we will use the term "searcher" to mean either a predator searching for prey or an individual searching for a mate, "target" to mean either prey or potential mates, and "territory" to mean either a searcher's defended territory or its home range.

The Relevant Dispersion

Dispersion is a term that describes either the spatial distribution of animals or their distribution relative to a particular spatial reference such as quadrats or territories. We will refer to these definitions as spatial dispersion and relative dispersion, respectively. Dispersion can take various forms ranging from spaced dispersion, which is characteristic of territorial animals, to random dispersion, to aggregated dispersion, which is common in herbivores (Southwood 1978); examples of these forms are shown in figure 1. Spaced distributions are characterized by all areas having similar densities or a low variance in density. The mean (m) and variance (v) of density are similar in random distributions, whereas aggregated distributions display high variance. One measure of dispersion is the ratio of the variance to the mean (v/m); $v/m < 1$ for spaced dispersion, $v/m \approx 1$ for random dispersion, and $v/m > 1$ for aggregated dispersion (Southwood 1978). The dispersion index v/m can be used for both spatial and relative dispersion, but in this article we will restrict its use to relative dispersion; for our purposes, m and v, respectively, are the mean and variance of the number of targets per territory, regardless of the absolute spatial distributions of territory areas or targets.

Searchers and targets may have different spatial distributions. Figures 2 and 3 show examples of various combinations of spaced, random, and clumped spatial dispersions for both searcher territories and targets. The dispersion of targets per searcher territory, measured by v/m, is also shown for each case. Figures 2 and 3A–3C show the nine combinations of spaced, random, and clumped spatial dispersions when searchers and targets are spatially uncorrelated, and figure 3D–3F shows the effect of searchers locating their territories with respect to the target spatial distributions (spatially correlated). For example, if a given predator species uses a given prey species as its principal food, then the predators are likely to concentrate (form smaller territories) where prey density is higher, leading to spatial correlation between the predators' territories and the prey (fig. 3D–3F). Because predators eat a variety of prey species, they are more likely to aggregate where all of their prey species are locally most abundant. Spatial correlation between a given predator and a given prey species should be proportional to that prey's importance in that predator's diet, and it should be negligible if the prey is a minor part of the predator's diet. Correlation is particularly unlikely between predator territories and aposematic prey species because aposematic prey species are likely to be a negligible part of the predator's diet. Correlations may occur among home ranges of males and females, but they may not occur if there are different reasons for territory locations and sizes, such as
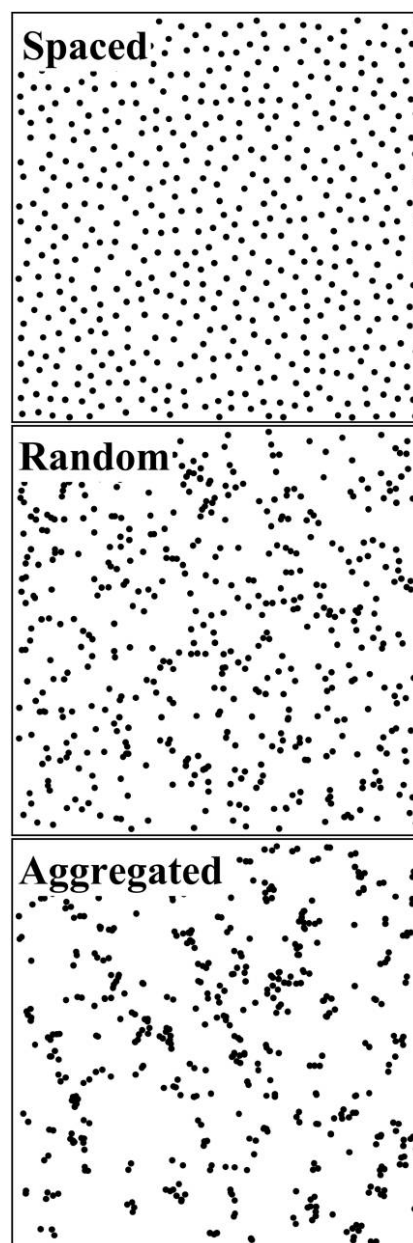

Figure 1: Examples of the three kinds of dispersion. These are examples of absolute dispersion, or relative dispersion with respect to equal-sized quadrats.

in male and female dendrobatid frogs (Pröhl and Berke 2001).

The v/m values in figures 2 and 3 illustrate how the spatial dispersions of searchers or targets do not necessarily predict their relative dispersions. For example, if every predator territory has the same number of prey, the relative dispersion is spaced, regardless of prey or predator dispersion; a small v/m value can arise if both are spaced (fig.
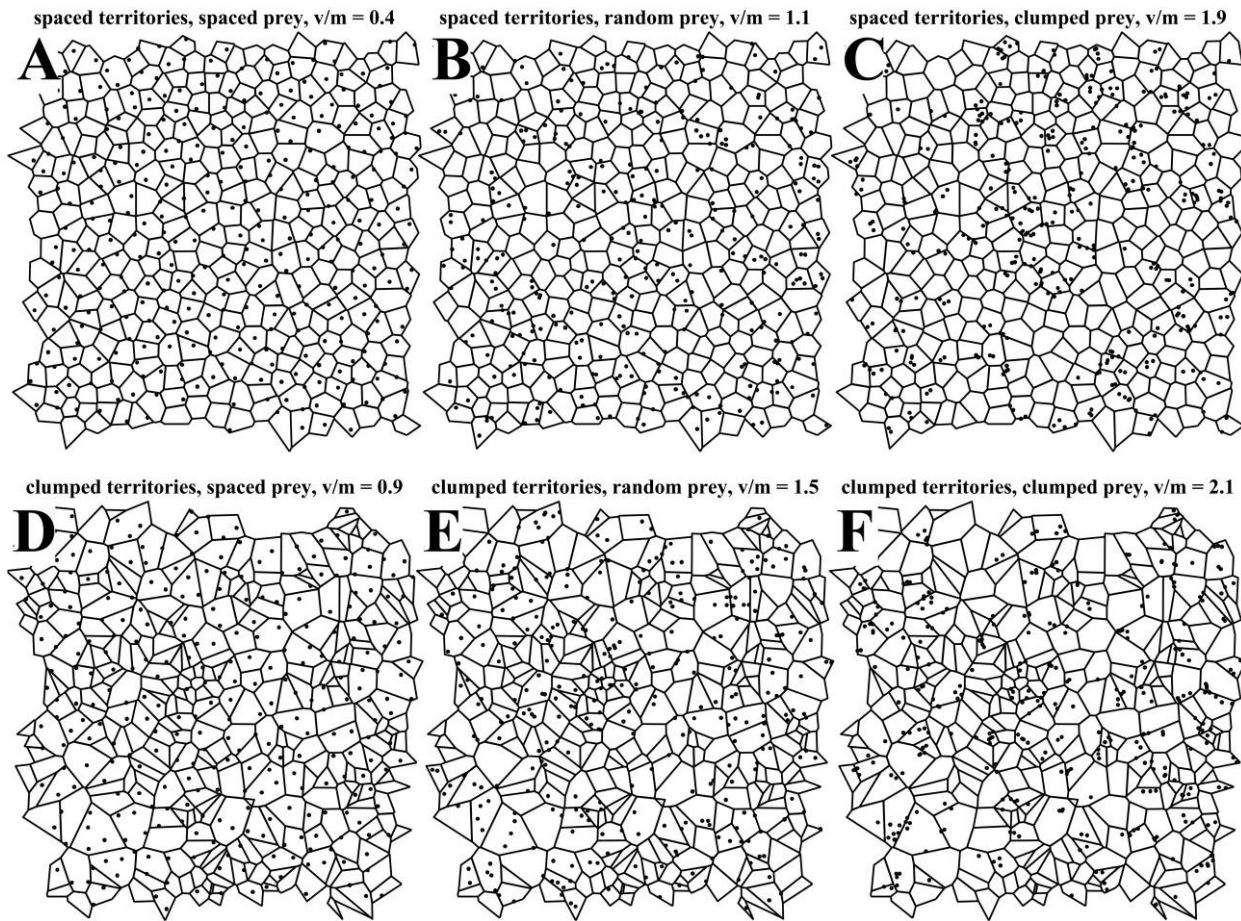
Figure 2: Examples of the spatial dispersion of targets (*dots*) and searcher's territories (*polygons*) when the targets and territories are not spatially correlated. The dispersion of targets per territory, which is the basis of our model, is indicated by the ratio of the variance of target number per territory (v) to the mean number of targets per territory (m); $v/m < 1$ if relative dispersion is spaced, $v/m \approx 1$ if relative dispersion is random, and $v/m > 1$ if relative dispersion is aggregated. Panel rows differ in territory dispersion and columns differ in target dispersion. Spaced (*A–C*) and clumped (*D–F*) territories are shown here, and randomly dispersed territories are shown in figure 3*A*–3*C*. These examples were made for low prey density for the sake of clarity. Random dispersion of targets was created by drawing pairs of Cartesian coordinates from a uniform distribution. Spaced dispersion was created by drawing random coordinates and using them only if they were greater than a critical distance from the closest existing point. Aggregated dispersion was created by drawing random coordinates for one-third of the points and then drawing additional random points and accepting them only if they were closer than a critical distance to the nearest existing point. Spaced, random, and aggregated territories were generated as random-set mosaics around points that were spaced, random, or aggregated.

2*A*), but it can also arise for any spatial dispersion of searchers and targets when they are spatially correlated (fig. 3*D*–3*F*). Also, note how clumped relative dispersion can arise even if only prey or only predators are clumped (fig. 2*C*, 2*E*; fig. 3*C*), and the v/m value can be large even if both are independently clumped (fig. 2*F*). In this article, we are not concerned with the causes of the spatial dispersion of predator and prey but instead with the effects of dispersion of prey relative to predators (v/m). The same applies to the dispersion of males, females, and females/male in a mate search context. It is relative dispersion,

rather than spatial dispersion, that will affect encounter rates.

The Model: Effects of Target Dispersion Relative to Searcher Territories

Let x be the number of target individuals (prey or potential mates) in a given territory. Let x be distributed among searcher territories, with mean per-territory m and variance v values and a relative dispersion that is measured by v/m. Our model makes no assumptions about the spatial
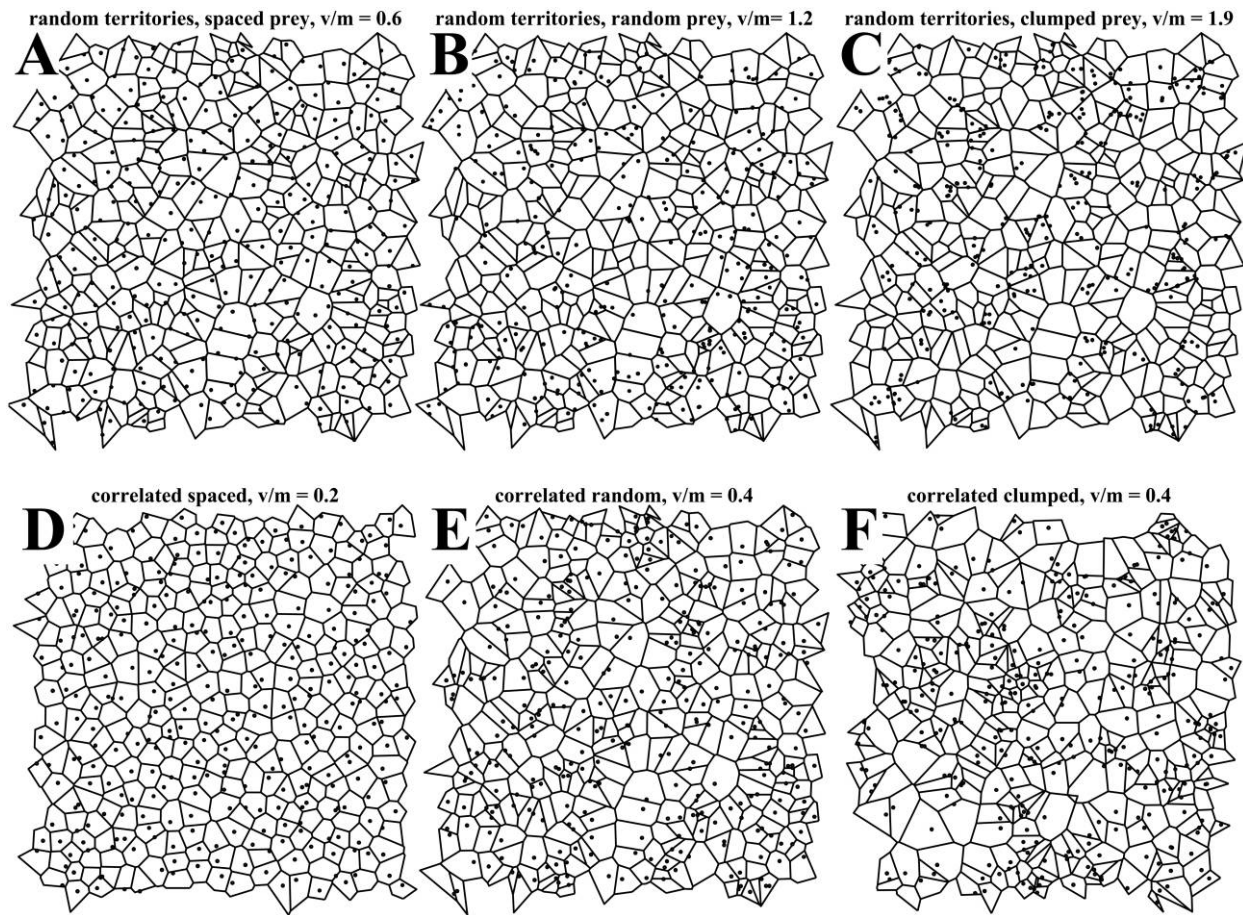
Figure 3: Examples of uncorrelated (*A*–*C*) and correlated (*D*–*F*) dispersion of targets and searchers; symbols are as they are in figure 2. When the searchers and targets are spatially correlated (*D*–*F*), the dispersion of prey per territory is spaced, no matter what their spatial (absolute) dispersions are.

dispersions of searchers and targets; it explicitly depends only on their relative dispersions: the distributions of targets among searcher territories. It also makes no assumptions about whether the territories overlap each other; we are concerned only with the *v/m* value that each territory holder (searcher) experiences. Overlap would be a problem only if one territory holder reduced the target density in the overlap areas of its neighbors during their learning period; this would be a good subject of future research. For brevity, we will use the term "dispersion" to refer to relative dispersion. Spaced, random, or aggregated dispersion will be associated with a characteristic distribution of targets per territory, $P(x)$, where $x = 0, 1, \ldots, \infty$ (in practical terms, ∞ is the maximum target number per territory). The expected distribution of numbers of targets per territory is $NP(x)$, where N is the total number of targets in the landscape or study area.

The form of $P(x)$ depends on the type of dispersion

(spaced, random, or aggregated). If targets are distributed at random (every territory is equally likely to contain a target individual), then

$$P_r(x) = \frac{e^{-m}m^x}{x!}. \tag{1}$$

This is the Poisson distribution (Southwood 1978).

If targets are aggregated, then

$$P_a(x) = \frac{\Gamma(k + x)}{x! \, \Gamma(k)} \left(\frac{m}{k + m}\right)^x \left(\frac{k}{k + m}\right)^k, \tag{2}$$

where k is related to the degree of aggregation, Γ is the gamma function, and $x!$ is x factorial ($x \times (x - 1) \times (x - 2) \ldots 3 \times 2 \times 1$). More tightly aggregated distributions have smaller k values (larger v/m values) and $P_a(x)$

is close to $P_r(x)$ when $k > 100$. This is the negative binomial distribution (Southwood 1978).

If prey are spaced, then one possible distribution is

$$P_s(x) = \frac{c}{s} e^{-(x-m)^2/2s^2}, \tag{3}$$

where c is a constant such that

$$\sum_{x=0}^{\infty} P_s(x) = 1 \tag{4}$$

for an integer x. More even spacing is associated with smaller s values (s^2 is the variance v mentioned at the beginning of this section). This is the discrete version of the normal distribution. Simulated prey distributions (as in the figures) closely match predictions from P_r, P_a, or P_s.

We will assume that a searcher does not adopt experience-based behavior unless the number of targets in its territory is above a threshold T. A predator cannot learn and/or retain the association between the prey signal and prey defenses or generate apostatic selection unless the prey density x in its territory or home range is at or above T ($x \geq T$). In other words, a predator needs at least T trials to learn, or at least T encounters with the aposematic prey to remember, the association between the prey signal and prey unprofitability or to generate apostatic selection (reviews in Endler and Mappes 2004; Ruxton et al. 2004; Mappes et al. 2005). The actual value of T depends on the rate of learning and memory of the predator species and may differ among predator species (Endler and Mappes 2004; Exnerová et al. 2007). It may also differ among individuals, but for our present models we assume that all predators have the same T values; effects should weaken as the among-individual variance in T increases. It is important to make the distinction between what happens when a predator (or mate searcher) forages within a territory and what happens between territories; we are concerned only with the latter, both for dispersion and for T. We are making no assumptions about the dispersion of prey within territories; it could be patchy, with the predator changing patches within its territory according to optimum foraging theory even if they are evenly dispersed among territories. Our model depends only on the dispersion of prey (or potential mates) among territories. Within a territory, the territory holder's T value may vary with its state (hunger or other physiological condition) and with time, but we are assuming that each individual has approximately the same average T value. Our model is unlikely to apply to those predator species that display innate avoidance ($T = 0$) or single-trial learning ($T =$

1, as is observed in some aposematic systems; Ruxton et al. 2004), and it may have limited applicability if there is innate neophobia (Exnerová et al. 2007); however, if neophobia or dietary conservatism is a function of early experience (Mappes et al. 2005; Marples et al. 2005), our models will apply. Note that we are not assuming that a searcher stops looking for targets when $x < T$ but only that frequency-dependent effects are weak and will become strong when $x > T$. The relationship between density and behavior of some species may be a slowly increasing function of the number of previous encounters, with a maximum slope at T rather than a threshold at T. Our models may not apply to nonthreshold behavior unless the slope of the relationship is steep (a threshold has a very high slope); however, if the slope is intermediate, some of the phenomena we describe may occur or will occur in a weaker form. There is virtually no information on these relationships in natural systems; this matter urgently requires study. However, for our purposes, we propose that, by taking T as a threshold, we will capture the essence of experience-based behavior found in most systems. The logic is identical for mate choice: T is the number of potential mates sampled before a mating decision can be made.

For our models, all that we assume is that the overall encounter rate within a given territory is x, the among-territory mean encounter rate is m, and there is a critical or threshold encounter rate T that will affect the behavior of the territory holder. Territories with $x \geq T$ are those that favor the maintenance of aposematism, apostatic selection, mate sampling, or other experience-based searching and decision making. For brevity, we will call territories where $x \geq T$ "favorable" territories. We can look at the distribution of favorable territories from the viewpoint of the searcher or the target; these have different properties and consequences.

Let $P(x)$ be $P_r(x)$, $P_a(x)$, or $P_s(x)$, depending on the type of dispersion (eqq. [1]–[4]). For each of these, the probability that a territory has T or more targets is

$$P_t(T) = \sum_{x=T}^{\infty} P(x), \tag{5}$$

where $P_t(T)$ is the probability that a given territory will be favorable ($x \geq T$). The probability that an individual target will be in a territory with $x \geq T$ is

$$P_i(T) = \frac{\sum_{x=T}^{\infty} x P(x)}{\sum_{x=0}^{\infty} x P(x)} = \frac{1}{m} \sum_{x=T}^{\infty} x P(x). \tag{6}$$

For searchers and targets, P_t and P_i have different meanings and implications. In terms of predators and prey, P_t is the
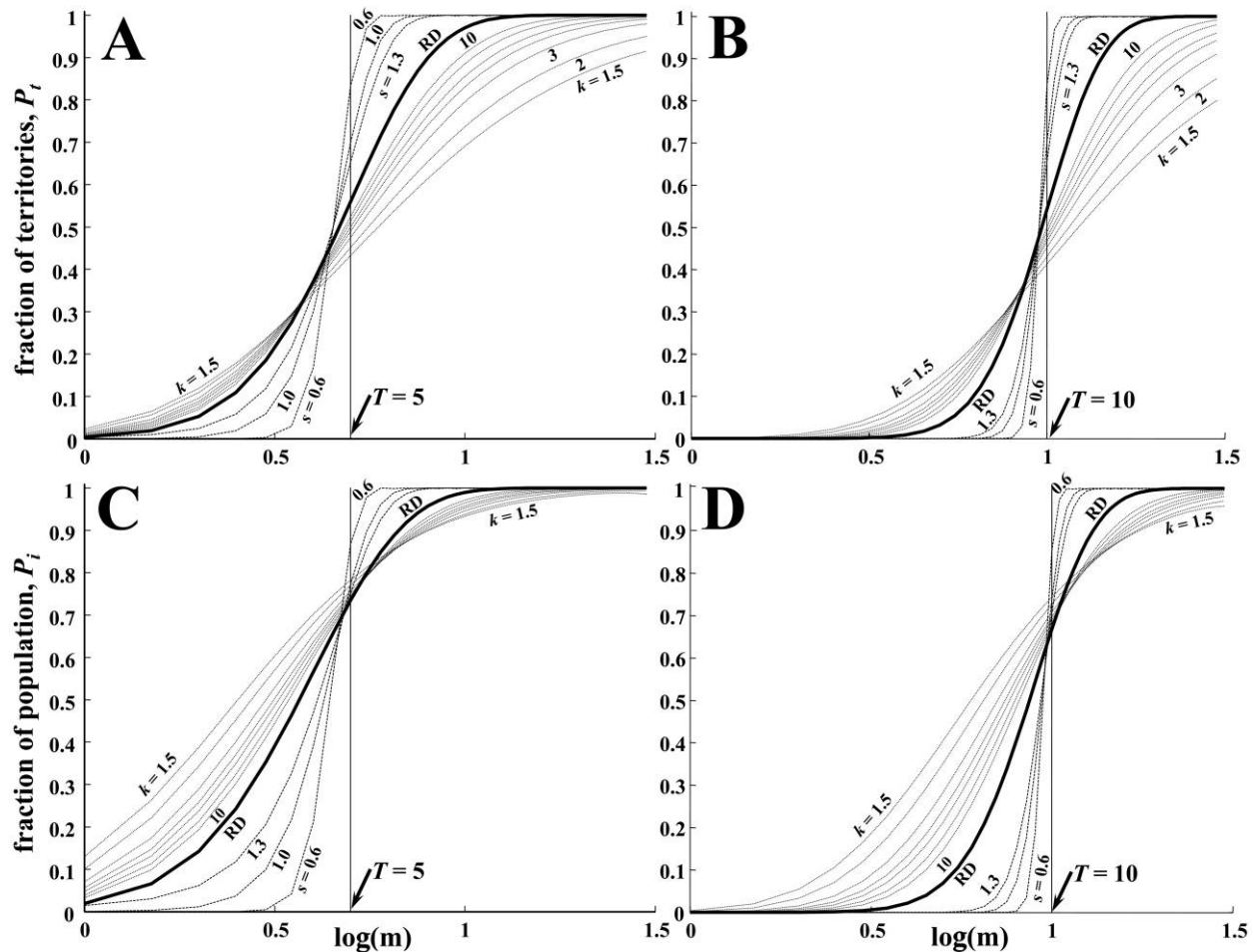
Figure 4: Relationship between the fraction of favorable territories (P_t) or the fraction of target individuals in favorable territories (P_i) and the mean prey density (m, plotted as $\log_{10}(m)$), for favorable threshold $T = 5$ (*A, C*) and $T = 10$ (*B, D*). For other values of *T*, the curves have qualitatively similar shapes and positions relative to *T*. Curves are shown for spaced (*s*), random (*RD*), and aggregated (*k*) dispersions with various *s* and *k* values, and the vertical line is at $m = T$. Note the more rapid transition for spaced distributions and the more gradual transition as aggregation increases (decreasing *k*); P_t and especially P_i are larger for clumped (small *k*) than for random or spaced (small *s*) dispersion when $m < T$, and the reverse is true when $m > T$. When *T* varies among individuals, the slopes of the curves in this figure are reduced in proportion to the variance, but the basic pattern remains unchanged.

probability that a given predator's territory will be favorable to aposematism or apostatic selection, whereas P_i is the probability that a prey individual will be in a favorable predator territory. Similarly, P_t is the probability that a female's home range will contain enough males for experience-based female choice ($x \geq T$), and P_i is the probability that a male will be in a female's home range with enough other males for the female to make a choice. Other experience-based mechanisms will have their own P_t and P_i values.

Results of the Model

As the mean density *m* increases, both the fraction of favorable territories P_t and the fraction of individual targets

in favorable territories P_i will increase, regardless of the dispersion mode, although the rate of increase depends on dispersion (fig. 4). Previous models of experience-based behavior assumed that either $m \gg T$ (all territories are favorable and all individuals are in favorable territories) or $m \ll T$ (no favorable territories). However, between these extremes, the favorable conditions ($x \geq T$) are spatially variable, with divergent effects on searchers (P_t) and targets (P_i) as aggregation increases (figs. 4–6).

For spaced dispersion (small *s* in eq. [3]) and a given *T* value, as density *m* increases, there is a rapid transition from most territories being unfavorable ($x < T$) to most territories being favorable ($x \geq T$; see fig. 4). If dispersion is perfectly regular ($s = 0$), then there is a very sharp
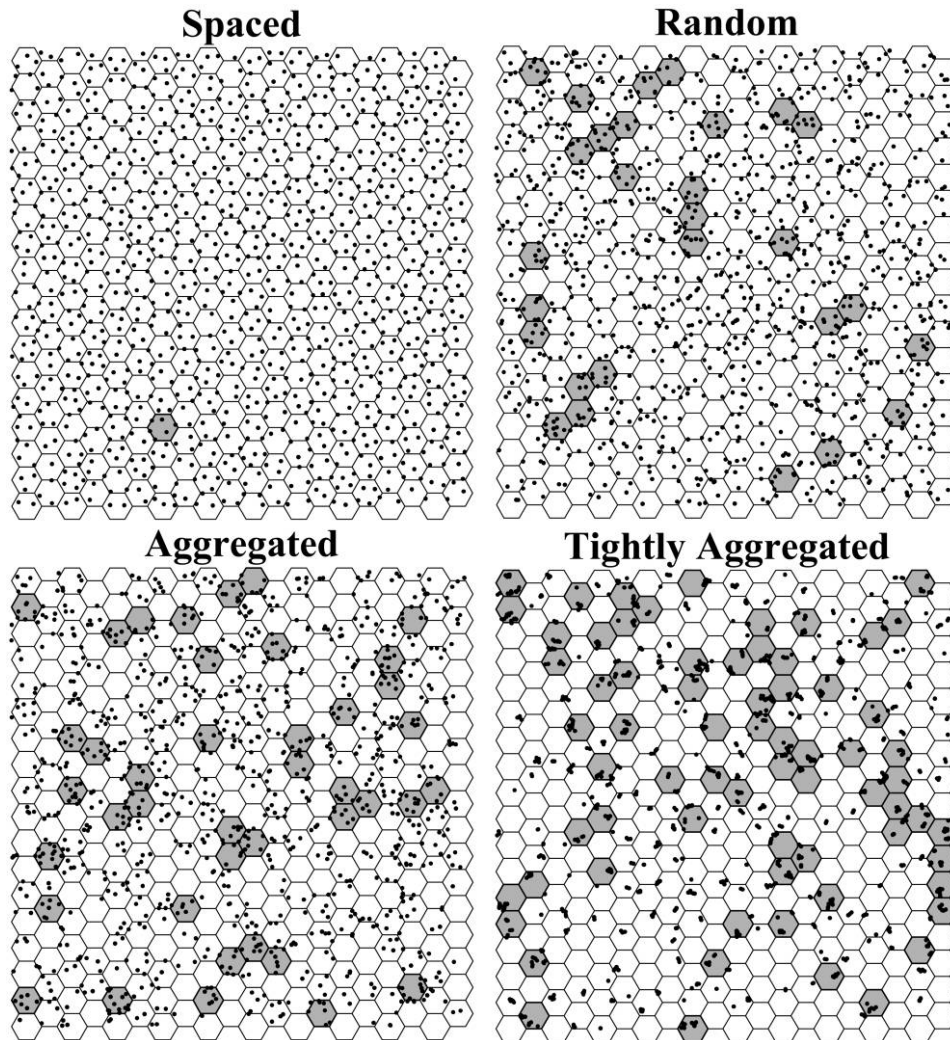
Figure 5: Examples of different target (*dots*) dispersions among territories (*hexagons*) but the same mean density per territory ($m = 3$). A spaced territory dispersion is shown for clarity, but the effects depend only on the relative dispersion (figs. 2, 3). Territories are shaded (favorable) when the prey density is greater than four individuals ($T = 5$); the figure shows the effects of relative dispersion when $m < T$. For the spaced distribution, 0.3% of the territories are above the critical prey density (favorable territories) and 0.5% of the prey population are in favorable territories. The corresponding percentages for the other dispersion examples are: for random dispersion, 8% of the territories contain 18% of the prey; for aggregated dispersion, 12% of the territories contain 28% of the prey; and for tightly aggregated dispersion, 20% of the territories contain 56% of the prey. As aggregation increases, the fraction of individuals in favorable territories increases faster than the fraction of favorable territories.

transition between territories being unfavorable and territories being favorable; this is the implicit assumption of previous models. As dispersion becomes more random (increasing s), the transition with m becomes more gradual. Moving past random, as dispersion becomes more aggregated (k in eq. [2] gets smaller), the transition with m becomes even more gradual (fig. 4). When the transition is gradual, P_t and P_i are neither 0 nor 1, resulting in a mosaic of favorable and unfavorable territories. Spatial heterogeneity arises for nonregular dispersion because, if $m < T$, any random or aggregation-induced increase of

local target density x can result in some territories where $x \geq T$ (fig. 5). Similarly, if $m > T$, any random or aggregation-induced local decrease in x (the territories in the spaces between the target aggregations) can result in some territories with $x < T$ (fig. 6). Consequently, as dispersion becomes less spaced and more random, spatial heterogeneity increases and the heterogeneity occurs over a larger range of m. As dispersion goes from random to aggregated, both the spatial heterogeneity and the range of m for heterogeneity increase even more.

The spatial heterogeneity in favorableness ($x \geq T$) re-

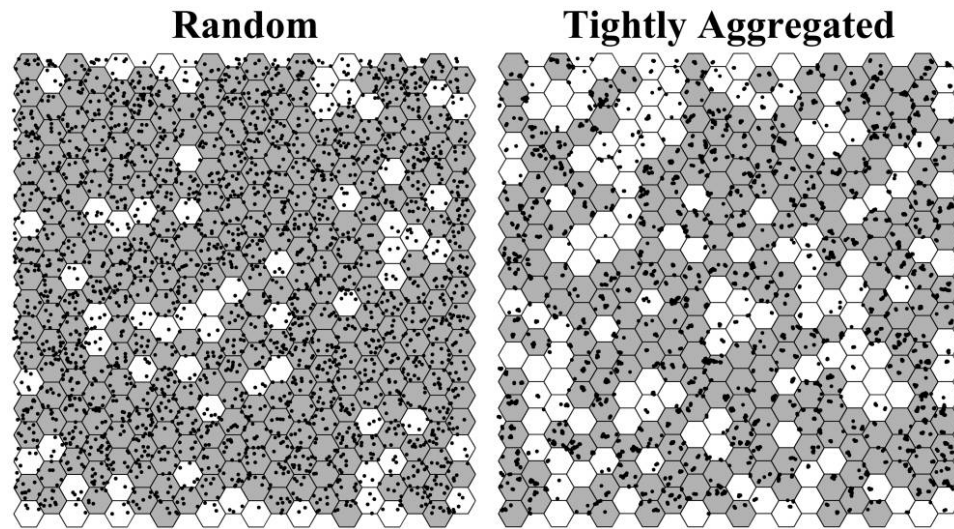**Random**   **Tightly Aggregated**

Figure 6: Distribution of predator territories and prey, as in figure 5, but with mean density ($m = 8.4$) greater than the threshold ($T = 5$). Because $m > T$, 100% of territories are favorable and 100% of the population are in favorable territories when the prey dispersion is spaced (not shown). In these examples, when prey are randomly dispersed, 82% of the territories are favorable and contain 92% of the population. When prey are tightly aggregated, 64% of the territories are favorable and contain 88% of the population. Note the reverse effects of aggregation when $m < T$ (figs. 4, 5); aggregation reduces the percentage of favorable sites when $m > T$.

sults in divergent effects on targets and searchers. First, consider conditions where the mean density m is less than the threshold T (figs. 4, 5). For a given $m < T$, as dispersion goes from spaced to random to aggregated, there is a small increase in the proportion of favorable territories P_t but a much larger increase in the proportion of individuals in favorable territories P_i (fig. 4, areas to the left of T; example in fig. 5). As aggregation increases, more and more territories have $x \geq T$, but because targets are aggregated, there are disproportionately more targets in these territories than in other territories; P_i increases faster with aggregation than P_t. It is possible for a few territories to contain most of the targets (figs. 4, 5), leading to significant behavior variation among searchers and disproportionate effects on the target population by relatively few searchers.

The divergent effects on predators and prey are reversed when $m > T$ (figs. 4, 6). For a given $m > T$, as dispersion goes from spaced to random to aggregated, there is a decrease in the fraction of favorable territories P_t and relatively little decrease in the fraction of targets in favorable territories P_i. As aggregation increases, even though $m > T$, the increase of low-density target areas results in a reduction in favorable territories, but the aggregation ensures that many of the targets remain in the favorable territories (fig. 6). Note that we are not saying that the targets explicitly aggregate in favorable territories but that the territories remain favorable with increased aggregation precisely because there is aggregation. Provided that $m >$

T but not that $m \gg T$, this will also generate variation in searcher experience and, hence, variation in searcher behavior. Over a range of m relative to T, the greater the aggregation, the greater the among-searcher variation in experience.

Figures 4, 7, and 8 illustrate the effects of varying mean prey density m relative to T for various values of T, and they show that the qualitative pattern is independent of T. When m is similar to T, changing dispersion has little effect on either the fraction of favorable territories P_t or the fraction of the prey in favorable territories P_i, except in cases of very high aggregation (very small k). However, P_i decreases with decreasing aggregation (increased spacing) when $m < T$, and it increases less strongly for $m > T$. A similar reversal of effects of decreasing aggregation occurs for P_t, but with larger changes with aggregation for $m > T$. Examples of both are shown in figures 5 and 6.

Implications of Varying Dispersion

The effect of dispersion mode on the distribution of favorable territories ($x > T$) means that the prevalence of experience-based phenomena such as aposematism, apostatic selection, and active mate choice depends strongly on the joint distribution of searchers and targets. A major consequence of noneven relative dispersion is spatial heterogeneity in behavior among territory holders, hence spatial variation in natural or sexual selection on the targets.
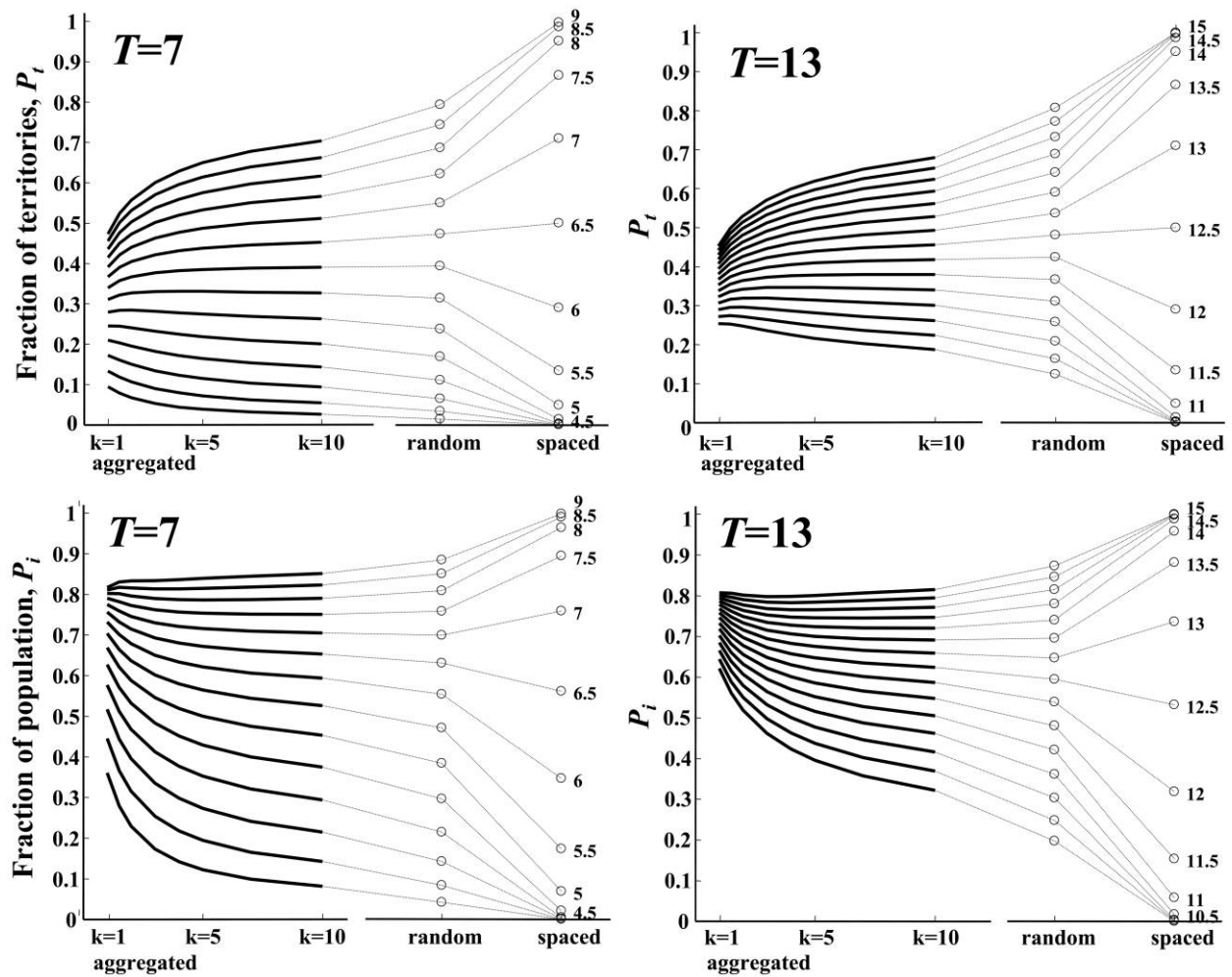
Figure 7: Effect of dispersion on P_t and P_i for various mean densities (m, indicated by numbers on the right side of each graph) and thresholds (T). The broad pattern is similar for various T; P_t and P_i change little when T is similar to m. When $m < T$, the fraction of the population in favorable conditions increases with aggregation (see also fig. 5), but it decreases with aggregation when $m > T$ (see also fig. 6).

For example, even when every predator is capable of learning the association between signal and defense, it is possible for many individual predators not to have learned this relationship (figs. 5, 6, *unshaded areas*).

Variation in searcher experience may make searching behavior highly variable and experiments with wild-caught searchers difficult. For example, experiments with wild-caught birds do not take into account the prey density in each bird's natural home territory. This is one explanation for the large variation observed among individuals and populations in experiments of wild-caught predators (Church et al. 1997; Allen et al. 1998; Endler and Mappes 2004; Exnerová et al. 2007) and the extensive variation in mating preferences observed among females within each of a variety of species (Jennions and Petrie 1997). This explanation contrasts with the more usual assumptions of randomly different encounter histories or genetically determined variation in behavior. We suggest that the variation in searcher behavior can be a deterministic effect of the dispersion of targets among searcher territories, even if the cause of target dispersion is random. The model leads to the obvious prediction that spatial variation in behavior among searchers should be smallest for searcher populations with high target density and/or even dispersion. Spatial variation in territory favorableness ($x > T$), and hence searcher experience and behavior, may contribute to the origin or maintenance of personalities and behavioral syndromes (Sih et al. 2004). For predator-prey systems, different prey species are likely to be dispersed differently. Therefore, spatial variation in predator expe-
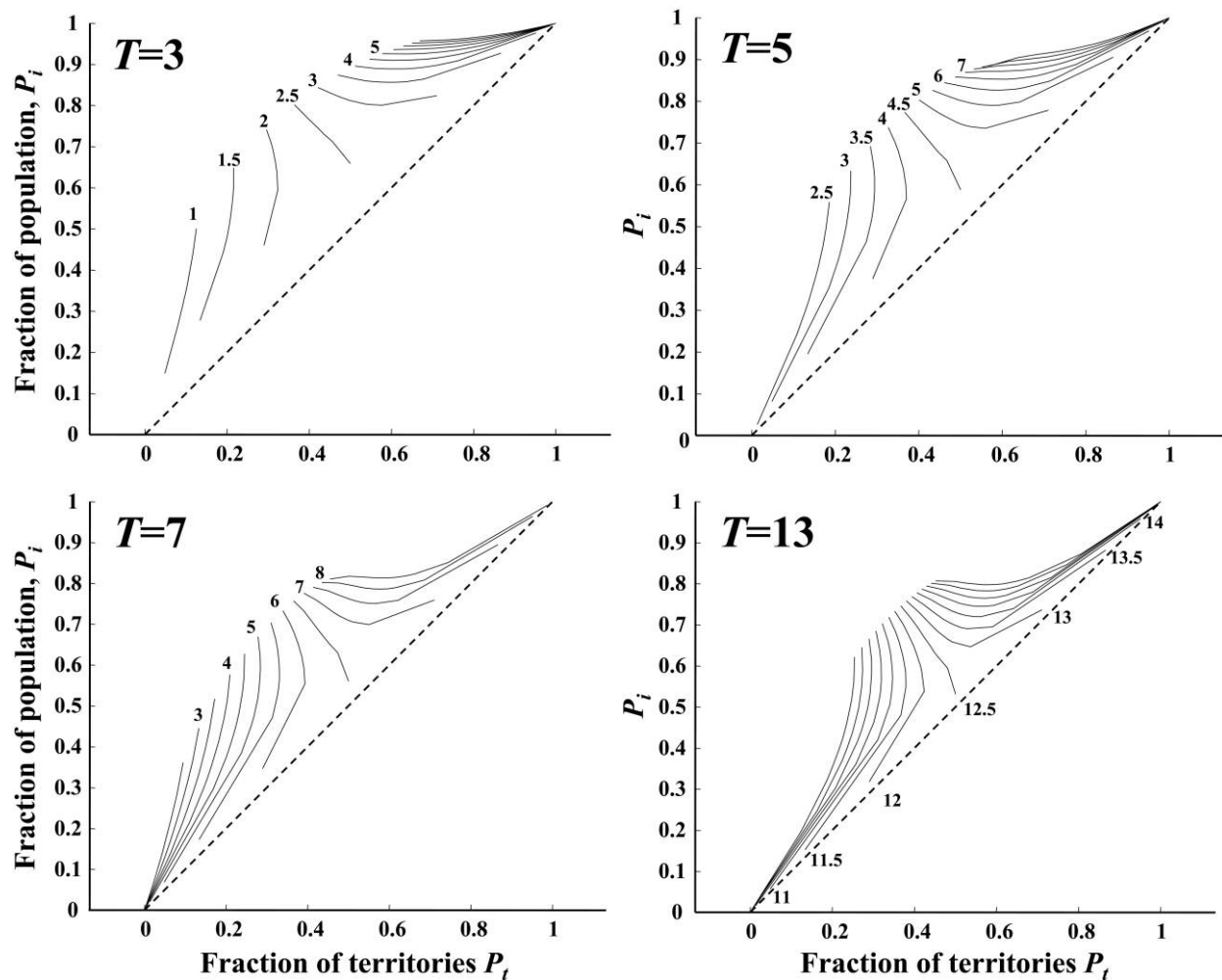
Figure 8: Relationship between P_t and P_i for various mean densities (m, indicated by numbers within graphs) and density thresholds (T), showing a qualitatively similar pattern for various values of T. The dashed lines are for $P_t = P_i$, and the degree of aggregation increases along each solid line going away from the dashed line (distal tips at $k = 1$, proximal tips at $s = 1$); P_i increases faster than P_t as aggregation increases when $m < T$, but when $m > T$, it changes little and can actually decrease for P_t if m is just larger than T.

rience is likely to be high, producing little consistency or variation without predator personalities. Distinct or classifiable predator personalities should emerge only if members of suites of prey species display spatially correlated dispersion, although predator personalities may emerge if single or very few prey species are a major part of a predator's diet. Similarly, mating personalities should be strong only if male and female territories are spatially correlated during the mate choice season (fig. 3D–3F); however, this is not necessarily the case (e.g., Pröhl and Berke 2001). Generally, over a range of values of m relative to T, the more aggregated the relative dispersion, the greater the among-searcher variation in experience and the more variable the behavior among individuals.

When the relative dispersion of targets per searcher is not spaced, experience and experience-based behavior of searchers will vary (figs. 5, 6), and this will lead to spatial variation in the selection that they induce on the targets. For example, when $m < T$ and there is aggregated dispersion, aposematism may be favored only in a few places (fig. 5, *shaded*). Even when $m > T$, not all territories will be favorable (fig. 6). Although a large fraction of the prey population may be in favorable territories (where aposematism is favored), most of the predator distribution may cover areas where the prey density is insufficient for $x > T$, which means that many or most predator individuals would be naive or untrained or prey densities would be too low for individuals to retain the memory of prey de-

fense capabilities. This means that selection and maintenance of aposematism may occur in only some of the predator territories ($x > T$); selection for aposematism is spatially variable. The same conclusion applies to apostatic selection: many predators may not have experienced a long enough run of one prey type to take it disproportionately, and prey in the unfavorable territories should be less polymorphic. The same applies to mate search: noneven dispersion means that many females may not have sampled enough males to make a mating decision and will be less choosy. Frequency-dependent (apostatic) mating or male-male interaction favors polymorphism (Partridge 1988; Punzalan et al. 2005; Bleay et al. 2007; Kokko et al. 2007), so we also predict spatial variation in the degree of polymorphism in secondary sexual traits when relative dispersion of the sexes is not even. This is one way of getting out of the lek paradox (Kirkpatrick and Ryan 1991). In addition, uncorrelated male and female home ranges (as in fig. 2) will result in spatial variation in the sex ratio, creating spatial variation in x relative to T and further increasing spatial variation in preferences, the degree of choosiness, and the intensity of sexual selection.

Predator-prey systems yield more predictions. Because the proportion of prey in favorable territories (P_i) increases faster with aggregation than the proportion of favorable territories (P_t), it is possible for few territories to contain most of the prey. Only those individual predators whose territories have $x \geq T$ can reinforce aposematism or apostatic selection of the prey species as a whole. This is likely to generate geographic variation in the occurrence of aposematism in protected prey and polymorphism in unprotected prey because the conditions vary in space. For unprotected prey, this would generate higher levels of polymorphism within the aggregations than outside of them, beyond what is expected from sample-size effects alone. This is an explanation for spatial variation in polymorphism that is in addition to the usual assumptions of spatial variable visual backgrounds, random selection, or simple genetic drift (e.g., Davison and Clarke 2000). For protected prey species, this would generate geographic variation in the degree of aposematism. It also means that there can be strong selection for aposematism in the prey species as a whole, even though only a small fraction of the predators learn the association between the signal and unprofitability; most predator individuals may be untrained, even though most prey are in the territory of an experienced predator. If most predators are naive, it may be difficult for natural selection to favor innate avoidance by prey for particular aposematic color patterns unless the prey density is high enough for $m > T$ or at least most $x > T$; widespread selection of predator traits is more likely to occur if the prey are spaced. These conditions will also make it more difficult for predator-prey coevolution be-

cause only a fraction of predators may be involved. Coevolution would be even less likely if a given territory holder is replaced by one that originated in a territory where its experiences were different from those in its new territory. Selection on predators is mediated through P_t, whereas selection on prey is mediated through P_i, and the two are not necessarily positively correlated (fig. 8). A further asymmetry in selection arises because T is a property of the predator's sensory and cognitive abilities and m is a property of the prey ecology, including the regulation of m by the predators. All of these factors promote divergent selection of predators and prey, promote spatial variation in selection, and limit coevolution between searchers and targets.

Because the patterns switch as m approaches T, we predict that, at a lower density, prey populations are more likely to evolve and/or maintain aposematism if they are aggregated and the aposematism is more likely to occur in high-density populations that are spaced or random. Similarly, polymorphism of unprotected prey due to apostatic selection is more likely for aggregated low-density populations or in random or spaced high-density populations, provided that the density is not too high. The aggregation-aposematism prediction for low m is also expected from classical kin selection theory (Ruxton et al. 2004), but our results indicate that aggregated lower densities are favorable even if the prey are unrelated simply because learning and reinforcement are higher in the aggregations than in the "holes." This means that kin selection is not needed to maintain aposematism, even if it helps in the origin of aposematism (see also Servedio 2000 for the equivalent of a single-territory or even-dispersion model). The high-density random or spaced prediction appears to be new and opposite to the classical model, but it could be interpreted as a result of the classical model that also assumes sufficient density everywhere for aposematism to be maintained (as in Sherratt 2006).

If $m < T$ and if the prey evolves territoriality, prey absolute dispersion will probably change from aggregated dispersion to random and spaced dispersion; resource competition selects against aggregation and frequently results in spaced distributions. This can result in a widespread decrease of predator training over the entire predator population, leading to a loss of aposematism of protected species or a loss of polymorphism of palatable species; this would be equivalent to going from aggregated to spaced dispersion, as in figure 5. On the other hand, if $m > T$, evolving territory (less aggregation) will ensure that there are fewer "holes" in the distribution (fig. 6), and support for aposematism or polymorphism is likely to increase as territoriality gets stronger. This suggests that, although conspicuous signals can be used for both territorial defense and aposematism, territorial prey species

should not be aposematic unless they are abundant enough so that most $x > T$; the average condition $m > T$ is not sufficient except for in situations of spaced dispersion and/or very high density.

Dispersion patterns may effect the dynamics and evolution of mimicry, which includes several forms of aposematism in which groups of species share the same signal. Mimicry rings are groups of both unpalatable (Müllerian) and palatable (Batesian) mimic species that share the same aposematic signals even if they belong to different genera and families (review in Mallet and Gilbert 1995). The color pattern of a given mimicry ring can change from place to place. Geographic variation within rings is puzzling because if one aposematic form has a greater total fitness, it is expected to invade adjacent areas even though the rate of cline movement can be slower as the number of species increases and the similarity in color patterns increases (Sasaki et al. 2002; Kawaguchi and Sasaki 2006). However, in spatially heterogeneous habitats, the clines between color patterns, and hence geographic variation, can be stable because cline movement slows or stops at low-density locations (Sasaki et al. 2002; Kawaguchi and Sasaki 2006). Our results suggest that spatial heterogeneity in predator experience and learning (e.g., fig. 1) would generate heterogeneity in predator-based natural selection (see also Sherratt 2006). This would have the same effect as habitat heterogeneity and would act in addition to this heterogeneity to maintain geographic variation in mimicry complexes. Of course, habitat heterogeneity for prey would enhance the difference between $x > T$ and $m > T$ as well as generating it directly. Consequently, we predict that, while holding the predator community constant (T), the size of zones with particular color patterns should be smaller, and mimicry rings should be more common, among species that are at lower density. We also expect fewer mimicry rings in territorial species than in nonterritorial species (at the same m) because there would be fewer unfavorable territories if $m > T$.

Dispersion and Dispersal

We have assumed static distributions of predators and prey or negligible dispersal of targets among searcher territories. This is not the same as assuming no dispersal of targets, because if territory size is many times larger than target home ranges, local dispersal by targets would lead to only slight dispersal among searcher territories. For example, predators are known to concentrate in places where locally there is more prey, but if these clumps occur within each predator's territory, they will affect only predator movement within territories, which is irrelevant to our model. However, in the long term for most relative scales, over many relative expansions and contractions of territories,

predator generations, and territory takeovers, it is likely that predator territories will tend to concentrate in areas of highest prey density. The resulting correlated predator and prey distributions will make the dispersion of prey per territory relatively more spaced (fig. 3D–3F) and will mitigate the effects arising from the assumptions of our model. However, one has to be careful about assumptions about the prey species with which the predator territories aggregate. In fact, predator territories should aggregate in areas where the predator's most important food species are most abundant, and there should be little or no spatial correlation with these aggregations and prey species that are small or minor parts of the predator's diet. There is no reason why minor prey species should affect the distribution of predator territories, and thus the relative dispersion can take any form (figs. 2, 3). This is particularly obvious for aposematic species, which are unlikely to be the targets of predator aggregation because they are poor food items, but this applies to any minor prey species. This predicts that the relative dispersion should go from spaced for major prey items (fig. 3D–3F), to random, to aggregated (figs. 2, 3A–3C) as species become less and less important in a predator's diet. The presence of sympatric multiple predator species will further mitigate the spatial correlation of predators and prey, reducing the tendency for spaced dispersion and making the effects of our model more likely than in a single-predator/palatable-prey system. For mating, only one target species is relevant, so spaced dispersion is more likely than in predator-prey systems. However, variation in mate and territory quality may lead to spaced relative dispersion in the "best" mates and random or even clumped relative dispersion among the poorer individuals. For these reasons, correlated distributions and spaced relative dispersion may be rare or have weak effects on the generality of our model.

Dispersal of targets among territories has another effect, even if it has little or no effect on relative dispersion. If some territories are associated with experience-based phenomena and others are not, and if these territories are randomly interspersed (as in figs. 5 and 6), natural selection will be spatially variable at the same microgeographic scale as the distribution of favorable territories. The result of spatial variation in natural selection depends on the relative strength of natural selection and the gene flow scale (Endler 1977). Dispersal of targets among these patches will both reduce the degree of spatial differentiation among areas and increase the size of the differentiated areas, with an intermediate level of selection/gene flow leading to a joint maximum degree of local differentiation and differentiated zone size (Endler 1977). In a very interesting series of simulations of the origins of geographic variation in Müllerian mimicry, Sherratt (2006) observed this pattern. He also showed the second conse-

quence of local dispersal, that the locally favored form was present even in adjacent territories without predators (equivalent of unfavorable territories in our terminology). Even when only 80% of the territories were favorable, the favorable form spread to most territories. Dispersal leads to beneficial forms in places where they are not necessarily actively favored, allowing widespread dispersal of beneficial genes (Sherratt 2006). This might also serve to train naive predators in what would otherwise be unfavorable sites. Basically, gene flow and dispersal blur the edges of spatially differentiated patches caused by selection.

Sherratt (2006) also found that the form that arrived in a territory first often determined which form predominated in that territory and in adjacent territories, suggesting that accidents of initial establishment can be important. Random starting points that influence subsequent spatial patterns of evolution may also be induced by the distributions of unique predator experiences with prey in each territory. In cases where only a few territory holders are responsible for most of the selection, gene flow will spread the territory holders' effects much farther than neighboring territories, and interesting things may happen when the experienced territory holders die or are superseded. All of these effects favor spatial variation in response to selection in what are otherwise spatially uniform selective environments.

A Dearth of Data

Although the relative densities and dispersions of predators and prey are critical to the maintenance of aposematism and visual polymorphism and can produce heterogeneity in predator behavior, there does not seem to be any spatially explicit data; no one has recorded dispersion for both predator and prey in the same study area. However, there are some suggestive studies. Territory sizes of insectivorous birds in tropical and temperate habitats range from 6 to 25 ha (Terborgh et al. 1990; Stouffer 2007). Densities in a Neotropical rainforest of birds that do or might eat frogs range from 1 to 6 pairs ha^{-1} (Terborgh et al. 1990). Densities of *Dendrobates pumilio* (a strongly aposematic frog) range from 170 to 310 individuals ha^{-1} in primary forest and from 610 to 850 individuals ha^{-1} in secondary forest (Pröhl and Berke 2001; Pröhl 2002). For frog-eating birds with territory sizes of 1–6 pairs ha^{-1}, this means that each bird would encounter, at a minimum, 15–85 frogs in its territory in primary forest and a minimum of 50–300 frogs in its territory in secondary forest. This conservatively assumes that the male and female birds encounter half the frogs located in a territory; more realistically, however, both birds would encounter all frogs, so the minimum values would be 30 and 100 frogs, respectively. Unfortunately, the major potential predators of dendrobatids are unknown, so we cannot even guess the value of T, although for many vertebrate species, $T = 1$–10 (references in Servedio 2000). This suggests that $m > T$ (as one would expect, given that the frogs are aposematic). These frogs are territorial, and males are dispersed at random whereas females are aggregated near breeding sites (Pröhl and Berke 2001; Pröhl 2002). Because birds would not distinguish gender, the combined absolute dispersion is somewhere between random and aggregated. The dispersal of frogs relative to birds is unlikely to be spaced because the birds have no reason to concentrate their territories with respect to the frogs (fig. 3E, 3F); the frogs are aposematic and are likely to be a very minor part of the birds' diet. Given that birds may not see all the frogs in their territory in one day, the spatial heterogeneity effects we discussed may be observed in primary forest but seem to be somewhat less likely to occur in secondary forest, where frog density is higher. Explicit studies of the dispersion of both aposematic prey and predators are needed. It would be interesting to know whether less conspicuous dendrobatid frog species are less territorial or have lower densities. It would also be interesting to know the relative dispersions for other possible predators such as snakes or land crabs.

Willmott and Mallet (2004) found that members of mimicry rings tended to share the same host plants more frequently than just by chance. They also pointed out that spatial patterns in host-plant dispersion and limited dispersal of butterflies between host plants will lead to limited dispersal between predator territories, as in our model. Both phenomena are likely to favor aposematism and mimicry in territories containing the host plants (Willmott and Mallet 2004), whereas aposematism would not be favored in territories containing few host plants (as in fig. 5). Pinheiro (2003) found that birds avoided attacking mimetic butterflies only in sites in which they co-occurred with the mimics. It would have been interesting to relate the behavior of each bird with the density of mimics on its own territory, but this was a between-population study. In this situation, the host-plant dispersion significantly affects the prey dispersion (plant and insect prey dispersions are correlated as in fig. 3D–3F). Although host specificity may not necessarily affect the prey (insect) dispersion relative to the predators, it may provide predators with cues about where to search within their territories. On the other hand, if newly dispersing young predators use the host plant as a cue to new territory quality, then the host-specific prey may be spatially correlated with the predator territories (fig. 3D–3F) and the relative dispersion will be spaced. There is much to be learned about the spatial relationships between predator and prey.

There are also some suggestive experimental studies on apostatic selection. Church et al. (1997) examined the effects of random and aggregated baits, but within a small

area. They observed no effect of local dispersion on frequency- or density-dependent selection, but this may have been because the dispersion treatments were within the same predator home ranges. However, the densities they used were all very high (25 or 50 m^{-2}) and the selection that they did find was all antiapostatic (common form favored). In our terms, this is equivalent to both $m \gg T$ and $x \gg T$, so the effects of density and dispersion should have been negligible (fig. 4). High densities like these are usually associated with antiapostatic selection; in a variety of studies, antiapostatic selection is generally found to be >10–25 baits m^{-2}, whereas apostatic selection is generally found to be at or below 2–10 baits m^{-2} (Church et al. 1997; Allen et al. 1998). Experimentally, and with two prey densities, Fernández-Juricic et al. (2001) looked at selection by birds on polymorphic baits at a forest edge (more predators) and a forest interior (fewer predators). They expected less apostatic selection where there were more predators, as suggested by Church et al. (1997) and modeled by Merilaita (2006). They did find less apostatic selection, but it was actually a reduction in the amount of antiapostatic selection, as we would expect given that their experimental densities were 30 and 50 baits m^{-2}, which is well within the density range favoring antiapostatic selection. These studies used palatable prey or baits, but Lindström et al. (2001) observed antiapostatic selection at about 3.5 baits m^{-2}. However, unlike other apostatic experiments, some of the baits were distasteful, and the birds had already experienced palatable baits in the training period before the experiment. There is an interesting interaction between encounter rate and degree of prey defense that affects whether selection is apostatic or antiapostatic; this would merit further empirical and theoretical investigation. However, it is at least clear that encounter rates must be high enough for apostatic selection to work.

There is a significant lack of data that are needed to test the predictions of the effects of dispersion on the spatial distribution, and hence the specieswide effects, of predation and sexual selection. Experiments with natural predation or predators have not noted dispersion or have used inappropriate densities. We need studies that simultaneously assess the dispersion of both predators and prey, experiments that are performed under natural conditions and with natural parameters, and estimates of the densities required to produce aposematic and apostatic behavior (T). We also need more studies relating behavior to prey density to see how realistic a T threshold model is and how and why T values may vary among individuals and with territory quality. We are not denigrating the otherwise excellent pioneering studies on aposematism or apostatic selection, but we are merely pointing out that those studies do not currently allow us to explore the effects of dispersion of prey among predator territories. Such data would greatly increase our understanding of the evolution of aposematism and polymorphism. Similarly, studies of sexual selection have not considered the effects of variable choosiness that can depend on local density (Kokko and Mappes 2005); spatial data on male and female home-range dispersion would increase our understanding of the evolution of mate choice.

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