

Frequency-dependent predation and maintenance of prey polymorphism

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Abstract

In positive frequency-dependent predation, predation risk of an individual prey correlates positively with the frequency of that prey type. In a number of small-scale experiments individual predators have shown frequency-dependent behaviour, often leading to the conclusion that a population of such predators could maintain prey polymorphism. Using simulations, I studied the dynamics of frequency-dependent predation and prey polymorphism. The model suggests that persistence of prey polymorphism decreases with increasing number of predators that show frequency-dependent behaviour, questioning conclusions about polymorphism based on experiments with few predators. In addition, prey population size, prey crypsis, difference in crypsis between prey morphs and the way the behaviour was adjusted affected the persistence of polymorphism. Under some circumstances prey population remained polymorphic for a shorter time under frequency-dependent than under frequency-independent predation. This suggests that although positive frequency-dependent predator behaviour may maintain prey polymorphism, it is not a sufficient condition for persistent prey polymorphism.

Introduction

Frequency-dependent selection is both ecologically and evolutionarily an interesting phenomenon because it is one of the proposed mechanisms that may maintain species diversity and polymorphism (e.g. Ayala & Campbell, 1974; Gendron, 1987). Under frequency-dependent selection the fitness of an individual depends on the relative frequency of its phenotype. Here I will focus on positive frequency-dependent predation, also called apostatic selection (Clarke, 1962), which is frequency-dependent selection that is caused by predation, and in which predation risk of a prey individual correlates positively with the relative frequency of that prey type.

In several experimental studies with two prey types, predators have been shown to behave in a positive frequency-dependent manner (reviewed by Allen, 1988). This means that a predator consumes disproportionately more of the common than of the rare phenotype. The change of the preferred phenotype that may result from such frequency-dependent behaviour due to prey type

frequency variation has sometimes been referred to as switching (e.g. Murdoch *et al.*, 1975).

Suggested reasons for frequency-dependent adjustment of predator behaviour include learning to look for the common prey in the most likely parts of the habitat (Murdoch *et al.*, 1975; Greenwood, 1985), search image formation (e.g. Tinbergen, 1960; Pietrewicz & Kamil, 1979); selective attention (Langley, 1996; Dukas, 1998; Dukas & Kamil, 2001), and adjustment of search rate according to prey density and the difficulty of search task (Staddon & Gendron, 1983a,b; Gendron & Staddon, 1984). Limited attention, which is the constraint behind selective attention, has also been suggested to be the key feature explaining search image (Langley, 1996; Dukas & Kamil, 2001; Dukas, 2002). Studies by Dukas and colleagues provide explanations for the underlying mechanisms of and the relationship between selective attention, search image formation, and adjustment of search rate (Dukas & Ellner, 1993; Dukas & Clark, 1995; Dukas & Kamil, 2001; Dukas, 2002). Ultimately, frequency-dependent behaviour of predators can be explained in terms of optimal foraging. The predator increases its total food intake by improving its probability to catch the (apparently) most common prey type,

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although this decreases its probability to catch other prey types (Hubbard *et al.*, 1982; Staddon & Gendron, 1983b).

Results from controlled predator behaviour studies, in which predators have shown positive frequency-dependent predation, have often been interpreted as evidence for such behaviour resulting in maintenance of prey polymorphism (Manly *et al.*, 1972; Allen, 1988; Bond & Kamil, 1998, 2002). However, usually such experiments have used only few or just one predator in each trial. Thus, the conclusion about maintenance of polymorphism is based on the assumption that the behaviour of a predator population equals the behaviour of an individual predator. Yet the question of how frequency-dependent behaviour of individual predators translates into predation at the population level has received little, if any, attention. For example, considering the behaviour of a predator population equal to the behaviour of an individual predator assumes that all members of the population share the same information about prey type frequencies, an assumption that is not likely to be justified. The number of predator individuals is not the only factor that is interesting in this respect, but also other ecological factors as well as behavioural traits of the predator species may influence the frequency-dependent selection and the stability of prey polymorphism.

In this study I have used a simulation approach to investigate the dynamics of frequency-dependent processes underlying frequency-dependent predation. The behaviour of the model predators was determined by a set of simple rules, resulting in behaviour that is consistent with that of real predators observed in experiments. The changes of predation risks in the model correspond to search image formation or other adjustment of predator behaviour that similarly results in maximization of the detection of the more common morph. For one thing I wanted to find out whether the effect of frequency-dependent predation on prey polymorphism really is equal independently of whether it is one, few or several predator individuals that impose the selection. In addition to the number of predator individuals, I investigated other ecological and behavioural factors that may be important to the dynamics of frequency-dependent predation in terms of the stability of prey polymorphism (dimorphism). These factors are prey population size, and the adjustment rate as well as the adjustment range of frequency-dependent behaviour, variation in conspicuousness of the prey morphs, and difference in conspicuousness between the prey morphs.

Methods

I used individual-based simulation modelling to study the dynamics of positive frequency-dependent predation. In the model, predators search for cryptic prey. There is one prey species with a population consisting of two cryptic but distinct morphs that only differ in coloration. The

predators behave according to simple rules (see below), resulting in behaviour that is consistent with that of real predators observed in experiments. The changes of detection probabilities in the model correspond to predator behaviour that aims to maximize the detection rate of the more common morph. The model was mainly inspired by changes in detection probabilities due to shifts of attention, but it is also applicable to memory and learning based changes with similar pattern of change. From studies on search image formation and shifts of attention with two cryptic prey types we know that (1) repeated detection of a prey type can successively increase a predator's ability to detect that prey type, (2) whereas it has an inverse effect on detection of the other, dissimilar prey type and (3) that these effect are reversible (Pietrewicz & Kamil, 1979; Langley, 1996).

I assume that there are n predator individuals and a prey population consisting of m individuals. There are two distinct prey morphs (or more generally, prey types), A and B . When the i th predator individual encounters a prey of the morph j (either A or B), the predator will detect it with the probability of $P(j,i)$. During each time step t all the predators search one at a time for a prey until detecting one.

I further assume that each predator can to a certain extent adjust its probabilities to detect the prey morphs in a manner that corresponds to search image formation. Thus, if a predator detects a prey of a given morph, then its probability of detecting that morph is increased by the amount of δ and its probability of detecting the other morph is decreased by the equal amount. However, this adjustment only happens within the limits of the extreme probabilities of detection, $P(j)_{\min}$ and $P(j)_{\max}$ ($P(j)_{\min} < P(j)_{\max}$ and $P(j)_{\min} > 0$ and $P(j)_{\max} < 1$), so that $P(j)_{\min} \leq P(j,i) \leq P(j)_{\max}$. Thus, the algorithm can be described by the following steps (1–4):

- (1) In the beginning of each simulation at time $t = 1$ the morph frequencies are unbiased and the probabilities of detection of the two morphs are assigned the unbiased, initial values $P(A,i)_1$ and $P(B,i)_1$.
- (2) For every following time step ($t > 1$) the probabilities of detection of each predator are adjusted the following way. The predators search prey in succession. Thus, on its turn, each predator is presented with prey individuals that are randomly drawn from the population, until it detects one. Detection of a prey affects the detection probabilities of the predator individual the following way:
 - (a) If the predator i detects a prey of morph A at time t , then $P(A,i)_{t+1} = P(A,i)_t + \delta$, given that $P(A,i)_t \leq P(A)_{\max} - \delta$, and $P(B,i)_{t+1} = P(B,i)_t - \delta$, given that $P(B,i)_t \geq P(B)_{\min} + \delta$.
 - (b) If, instead, the detected prey morph is B , (and $P(B,i)_t \leq P(B)_{\max} - \delta$ and $P(A,i)_t \geq P(A)_{\min} + \delta$), then $P(B,i)_{t+1} = P(B,i)_t + \delta$ and $P(A,i)_{t+1} = P(A,i)_t - \delta$.

Every detected prey is removed from the population. All the n predators continue hunting in succession until the prey population size has decreased to $m/2$ individuals.

- (3) A prey generation comes to its end when predation has decreased the size of the prey population to $m/2$ individuals. At that time reproduction takes place, and the next generation will consist of two copies of each of the individuals that have survived till the end of the previous generation. Thus, the prey population size will be restored to m individuals, but the proportions of the morphs are unaffected by the reproduction. After the shift of generation step (2) is resumed.
- (4) The simulation run ends when either the prey population becomes monomorphic or 100 000 prey generations have been completed.

Due to the adjustment of the probabilities of detection a predator improves its ability to detect the prey morph it finds more often, but this will simultaneously reduce its probability of detecting the other morph. Consequently, the predator increases its specialization to the morph it finds more often. Because there are limits to this adjustment ($P(j)_{\min}$ and $P(j)_{\max}$), the predator will never become perfect in detecting or fully lose its chance of finding either of the morphs. Therefore, the improvement in the probability of detection of one morph and the decrease the probability of detection of the other morph are not irreversible, but the direction of the adjustment may switch and a low probability of detection may start to increase.

If the behaviour of a predator is positively frequency-dependent, then the more common prey type will be over-represented and the rarer prey type will be under-represented in its diet (Clarke, 1962; see also the experiments by Bond, 1983; Reid & Shettleworth, 1992; Bond & Kamil, 1998). Therefore, to demonstrate that the described algorithm results in frequency-dependent predation, I run the simulation with a series of prey morph frequencies. I set the prey population size $m = 100$, the initial and extreme probabilities of detection $P_1 = 0.5$, $P(A)_{\min} = P(B)_{\min} = 0.2$ and $P(A)_{\max} = P(B)_{\max} = 0.8$, and the adjustment rates $\delta = 0.025$. I run each simulation for 100 prey generations. Because my aim was to demonstrate the effect of prey morph frequencies on predator behaviour, every consecutive prey generation of a replicate began with the same morph frequencies, as an exception to all the other simulations presented in this study. I recorded the percentage of morph A of all caught prey in each replicate. For each prey morph frequency ratio (ranging from 0 : 100 to 100 : 0) I ran 50 replicates of the simulation. I did this both with one and with ten predators. In addition, as a control I ran this simulation with frequency-independent predation such that the probability of detection for both the prey morphs was constantly 0.5 (i.e. $\delta = 0$). The averages and extremes are

presented in Fig. 1. As expected, the proportions of the two prey morphs in the diet of the predator were directly related to the ratio of the morph frequencies, when the predation was frequency-independent. However, the adjustment of the probabilities of detection resulted in that the more common morph was over represented and the rarer morph was underrepresented in the predator's diet, indicating that the predator behaviour did indeed result in frequency-dependent predation. Interestingly, with frequency-dependent predation the one-predator case differed more from the response of the frequency-independent predation than did the 10-predator case, especially when the prey frequency was slightly below or above the 50 : 50 ratio. For example, at the 48 : 52 morph ratio the respective means for one frequency-dependent predator, ten frequency-dependent predators, and for frequency-independent predation were 35.1, 45.4 and 48.1%. The variation due to sampling error effects in the response of the frequency-dependent predators was largest at the middle of the range of the frequencies (Fig. 1) as has been proposed by Cook (1965).

With this model I studied maintenance of prey polymorphism (or, more generally, diversity) by positive frequency-dependent predation. For this purpose, in the following simulations I recorded the number of generations the prey population remained polymorphic for each replicate of a simulation, with the maximum number of generations set to 100 000. After 100 replications of a simulation I calculated the mean number of polymorphic generations and used it as the measure of persistence of

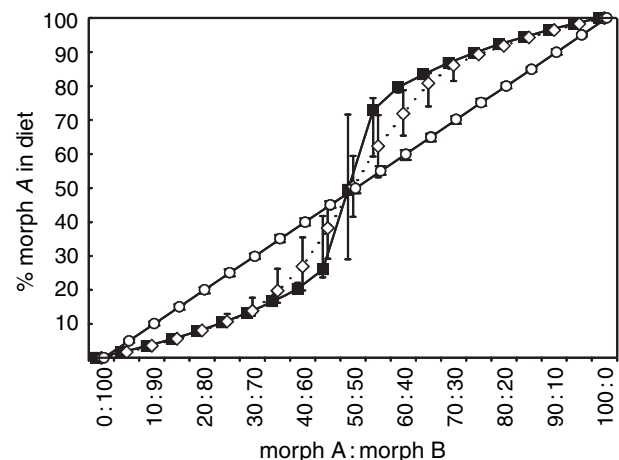


Fig. 1 Morph-specific predation risk (percentage of morph A in predator diet) in relation to proportions of the two morphs based on simulations, in which one predator preyed on 100 consecutive generations of 100-individual prey population. Every prey generation had initially the morph ratio given on the x-axis. The average and range of 50 replicates are shown for frequency-dependent predation with one (■) and with ten (◇) predators as well as for frequency-independent predation (○). See the text for more details.

polymorphism. (Note that in some cases the actual persistence of polymorphism would have exceeded the maximum of 100 000 generations and, consequently, in those cases the difference to simulations with less persistent polymorphism appears smaller than it really is.) The factors that I studied were the number of predators, n , the maximum size of the prey population, m , the spread of the adjustment range of the frequency-dependent predator behaviour, $P(j)_{\min}$ and $P(j)_{\max}$, as well as the adjustment rate of the behaviour, δ , the degree of conspicuousness or crypsis of the two prey morphs (by shifting $P(j,i)_1$, $P(j)_{\min}$, and $P(j)_{\max}$ equally much) and the difference in conspicuousness between the two prey morphs. My aim was not to make quantitative predictions about parameter values, but to qualitatively study the impact of these factors on maintenance of prey polymorphism by positive frequency-dependent predation.

I varied the number of predators, n , such that I ran every simulation with 1, 2, 5 and 10 predators (and, additionally, with 20 predators in the case of the simulation in which the prey population size was varied). I set the prey population size $m = 100$, the initial probability of detection of both of the morphs and all predators $P(j,i)_1 = 0.5$, the minimum probability of detection $P(A)_{\min} = P(B)_{\min} = 0.2$, the maximum probability of detection $P(A)_{\max} = P(B)_{\max} = 0.8$, and the adjustment rates $\delta = 0.025$. (These are the parameter values used, if not otherwise told.) I then varied one parameter at a time, keeping the other ones unchanged. For comparison, I also ran equivalent simulations with frequency-independent predation, such that the probabilities of detection were constantly 0.5.

Results

Prey population size and predator population size

First, I varied the prey population size, m , using the values of 40, 80, 120, 160, 200 and 240 prey individuals. Figure 2 shows that prey polymorphism was strongly stabilized by an increase in prey population size. Moreover, prey population size had a much stronger impact on the maintenance of polymorphism under frequency-dependent predation than under frequency-independent predation.

The number of predators, n , in contrast, had the opposite effect than prey population size (Fig. 2). Thus, increasing the number of predators strongly decreased the probability of prey polymorphism being maintained by frequency-dependent predation. Interestingly, for small prey populations and large numbers of predators the persistence of polymorphism was actually shorter under frequency-dependent than under frequency-independent predation. Figure 2 also suggests that keeping the ratio of predators to prey constant but increasing the numbers (e.g. from 5 : 120 to 10 : 240) may increase the

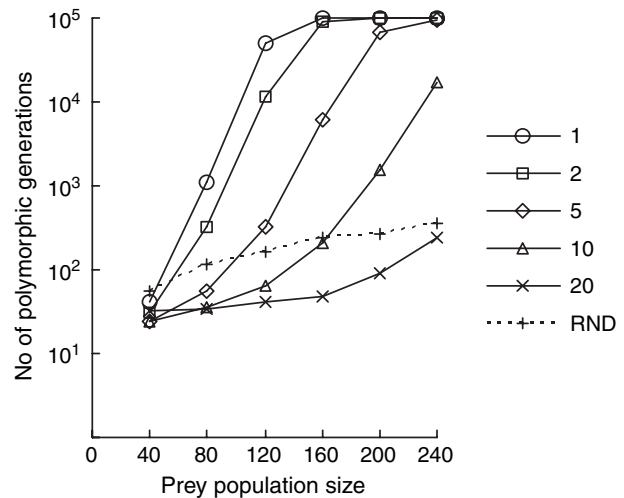


Fig. 2 The number of polymorphic prey generations out of 100 000 generations, when prey population size was varied. The simulation was run with 1, 2, 5, 10 and 20 frequency-dependent predators and with frequency-independent predation (RND). The other parameters were set to $P(j,i)_1 = 0.5$, $P(j)_{\min} = 0.2$, $P(j)_{\max} = 0.8$ and $\delta = 0.025$. Each data point is based on the average of 100 replicates.

persistence of polymorphism. This indicates that with the parameter values used in Fig. 2 the opposite effects of prey and predator population sizes were not equally strong, but the persistence of prey polymorphism increased with a higher rate with increasing prey population size than it decreased with increasing predator population size.

Variation in the detection probabilities of the morphs

Next, I shifted simultaneously and equally the detection probabilities of both the morphs from the values $P(j,i)_1 = 0.5$, $P_{\min} = 0.2$ and $P_{\max} = 0.8$. This shift ranged from -0.1 to 0.1 . Increasing the detection probabilities increased the stability of polymorphism (Fig. 3).

Difference in the detection probabilities between the morphs

So far the variation in the probability of detection has been similar for both the prey morphs. In the next simulations I relaxed this assumption and studied the effect of difference in crypsis between the morphs. For morph A I set $P(A,i)_1 = 0.5$, $P_{\min} = 0.3$ and $P_{\max} = 0.7$, but for morph B I simultaneously and to equal extent varied the values of the corresponding parameters. The difference between morphs A and B in these three parameter values ranged from -0.2 to 0.2 .

The prey population remained polymorphic for longer the less the range of the detection probabilities differed between the two morphs (Fig. 4). Increasing the

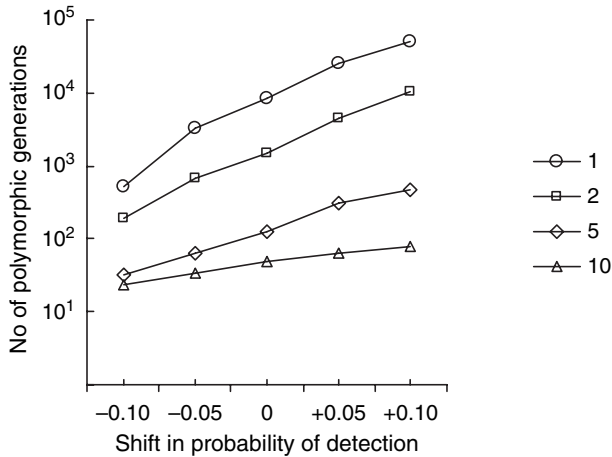


Fig. 3 The number of polymorphic prey generations out of 100 000 generations, when the initial and extreme probabilities of detection of both the prey morphs ($P(j,i)_1$, $P(j)_{\min}$, and $P(j)_{\max}$) were varied equally much. The x-axis shows the deviation from values $P(j,i)_1 = 0.5$, $P_{\min} = 0.2$ and $P_{\max} = 0.8$. The simulation was run with 1, 2, 5 and 10 frequency-dependent predators. The other parameters were set to $m = 100$ and $\delta = 0.025$. Each data point is based on the average of 100 replicates.

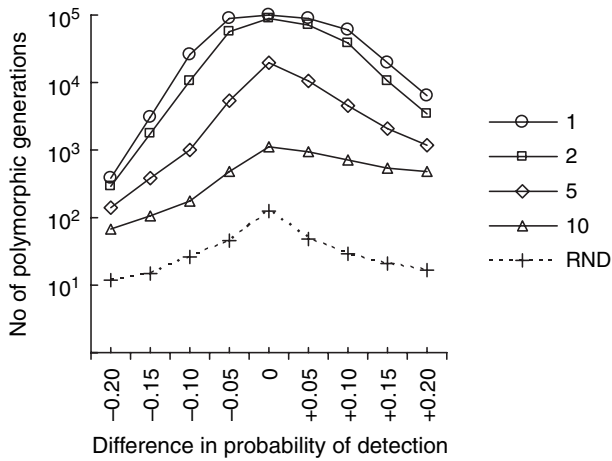


Fig. 4 The number of polymorphic prey generations out of 100 000 generations, when the difference in probability of detection between the two morphs is varied. For morph A, $P(A,i)_1 = 0.5$, $P(A)_{\min} = 0.30$, and $P(A)_{\max} = 0.70$, and for morph B the corresponding parameter values were varied. On the x-axis is the difference between the morphs (morph B–morph A) in these parameter values. The other parameters were set to $m = 100$ and $\delta = 0.025$. The simulation was run with 1, 2, 5 and 10 frequency-dependent predators and with frequency-independent predation (RND). Each data point is based on the average of 100 replicates.

difference in crypsis between the morphs had a negative effect on prey polymorphism both under frequency-dependent and under frequency-independent predation. This effect was somewhat more pronounced when the

parameters of morph B were decreased in comparison to the parameters of morph A than when they were increased. Again, increasing the number of frequency-dependent predators destabilized prey polymorphism (Fig. 4).

Adjustment range of predator behaviour

Next, I varied the spread of the adjustment range of predator behaviour from $P_{\min} = P_{\max} = 0.5$ to $P_{\min} = 0.1$ and $P_{\max} = 0.9$ (Fig. 5). The case with $P_{\min} = P_{\max} = 0.5$ (i.e. no adjustment) is obviously equivalent to frequency-independent predation. Introducing the frequency-dependent adjustment of predator behaviour by increasing the spread of the adjustment range at first steeply increased the number of generations the prey population maintains polymorphism. However, after passing $P_{\min} = 0.4$ and $P_{\max} = 0.6$ the trend changed, such that the larger the number of predators, the earlier started the stability of polymorphism decrease with increasing spread of the adjustment range. Thus, after that point the number of predators had a considerable effect on the stability of prey polymorphism. When the spread of the adjustment range was large, the polymorphism was less stable under frequency-dependent than under frequency-independent predation.

Adjustment rate of predator behaviour

I studied the effect of adjustment rate of predator behaviour, δ , by assigning it the values of 0, 0.005, 0.01, 0.025, 0.05 and 0.1 (Fig. 6). The case with $\delta = 0$

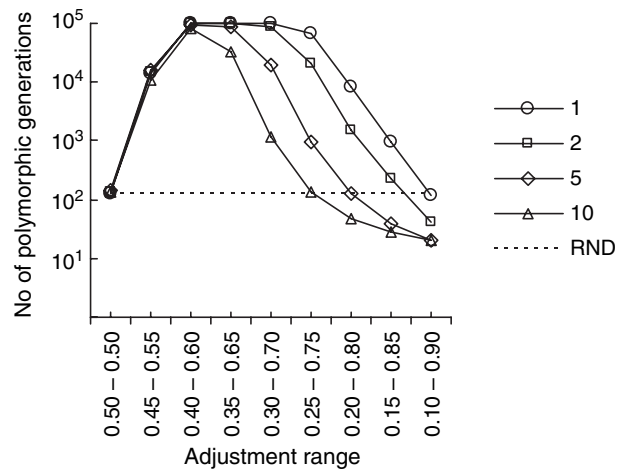


Fig. 5 The number of polymorphic prey generations out of 100 000 generations, when the adjustment range of predator behaviour ($P(j)_{\min}-P(j)_{\max}$) was varied. The simulation was run with 1, 2, 5 and 10 frequency-dependent predators and with frequency-independent predation (RND). The other parameters were set to $m = 100$, $P(j,i)_1 = 0.5$ and $\delta = 0.025$. Each data point is based on the average of 100 replicates.

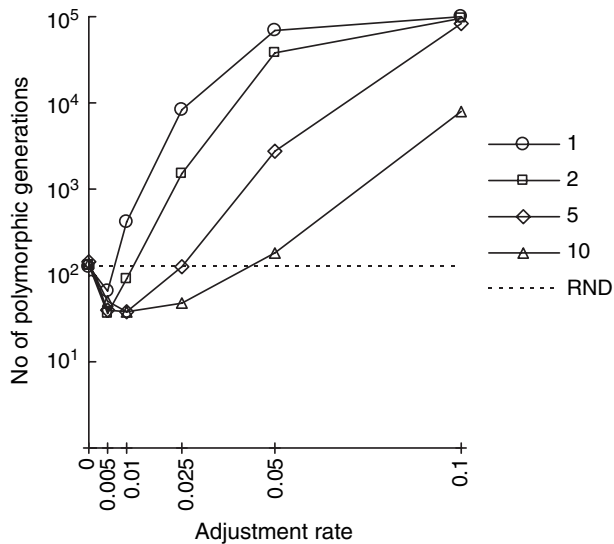


Fig. 6 The number of polymorphic prey generations out of 100 000 generations, when the adjustment rate of predator behaviour (δ) was varied. The simulation was run with 1, 2, 5 and 10 frequency-dependent predators and with frequency-independent predation (RND). The other parameters were set to $P(j,i)_1 = 0.5$, $P(j)_{\min} = 0.2$, $P(j)_{\max} = 0.8$, and $m = 100$. Each data point is based on the average of 100 replicates.

(no adjustment) is equivalent to frequency-independent predation. A small increase in the adjustment rate rapidly dropped the probability of polymorphism for all the four numbers of frequency-dependent predators below the persistence of polymorphism under frequency-independent predation. A further increase in the adjustment rate made the stability of polymorphism rise. This rise was the steeper the smaller the number of predators was.

Discussion

To better understand the dynamics of the frequency-dependent processes that underlie frequency-dependent predation, I simulated predation caused by various numbers of predators that showed positive frequency-dependent behaviour. I studied the effect of ecological factors (number of predators, prey population size, probability of detection of the prey types and the difference between the prey types in probability of detection) and behavioural factors (the spread of adjustment range and the rate of adjustment of the frequency-dependent response of the predator) on the probability that frequency-dependent predation maintains prey polymorphism. The present model allows several ecological and evolutionary conclusions about apostatic selection and prey polymorphism.

The effects of the ecological factors can be summarized as follows. It was evident from all simulations where the number of predator individuals was varied that the effect

of an increase in the number of predators on maintenance of the prey polymorphism was negative and often strong. On the other hand, increasing the prey population size strongly increased the persistence of the polymorphism. Further, increasing the probability of detection of both prey morphs increased the persistence of the polymorphism. In contrast, increasing the difference in the probability of detection between the two prey morphs decreased the persistence of the polymorphism.

The number of predators was varied between simulations, but all the predators were identical so that they obeyed exactly similar behavioural rules, and therefore differed only in the information that they acquired on the prey type frequencies through prey detection. Varying the number of predators in the model had the following effects on the acquirement of information: first, when only one predator was preying on the prey population, all the information collected was channelled to that individual. In contrast, when there were, for example, ten predators, the behaviour of each individual predator was formed by only one tenth of the information about prey type frequencies in relation to the total number of consumed prey, compared to the one-predator case. Thus, to achieve a given average change in the detection probabilities of the predators, more prey needs to be consumed when there are several predators than when there is one predator only. Therefore, for a prey population with given size, the fewer predators there are, the quicker the predators will respond to a change of prey morph frequencies by adjusting the detection probabilities and the more persistent the polymorphism will be. Second, from the point of view of an individual predator, the more predators there are, the more volatile the morph frequencies will be. This is because the total prey consumption rate in relation to the individual predator's sampling rate increases with increasing number of predators. Third, predator's sample information about prey morph frequencies by detecting prey, and when there is more than one predator, it is likely that the predators' samples will differ. This variation, which increases with the number of predators, is reflected in the predators' detection probabilities. These three points suggest that the lower the number of predators is, the quicker and more accurate the predators' frequency-dependent response will be. This is in accordance with the difference in frequency-dependent predation between the one-predator and the ten-predator cases (see Methods), indicating that a slight deviation from the even morph ratio will result in a much stronger frequency-dependent adjustment in the one-predator case than in the multi-predator case. In sum, the lower the number of predators is, the better the predation risk of the morphs will correlate with biases in the relative morph frequencies.

The persistence of prey polymorphism increased with increasing prey population size both under frequency-independent and frequency-dependent predation. The

effect of prey population size on the persistence of polymorphism was not completely unexpected. It is well known that small populations are more susceptible to random effects, such as genetic drift than are large populations, and therefore also the risk of losing diversity is higher for small than for large populations. This is because a removal or addition of one individual has a larger impact on the proportion of morphs in a small than in a large population. Even though an increase in prey population size had a positive effect on the persistence of polymorphism both under frequency-independent and under frequency-dependent predation, this effect was markedly different between these two modes of predation. In particular for the smaller numbers of predators the persistence of polymorphism increased much more steeply under frequency-dependent predation compared to frequency-independent predation. This interaction between prey population size and the mode of predation suggests that there was an additional effect of prey population size at play when predation was frequency-dependent. This additional effect can be explained, again, in terms of acquisition of information. Thus, for a given average amount of information (i.e. for a given accuracy of frequency-dependency), the members of a predator population of a certain size will have to consume proportionally more of a small than a large prey population. Therefore, a small prey population will either be closer to the critical minimum population size for maintenance of polymorphism, or the frequency-dependency of predators will be less accurate when compared to a larger prey population.

The marked impact of prey population size on persistence of polymorphism required that the maximum and minimum prey population sizes (m and $m/2$) be kept constant in comparisons between different numbers of predators. The unavoidable side effect of this was that the number of prey that one predator ate *per* prey generation decreased with increasing number of predators, and one can ask how this affected the comparisons. The only way to keep both the prey population size and the capture rate of individual predators *per* prey generation constant would be to accelerate prey generation time with increasing number of predators. This would simply correspond to accelerating the sequence of events in the multi-predator cases, hastening the loss of polymorphism and, consequently, increasing the differences between simulations with different numbers of predators. This suggests that the results presented here are conservative. Moreover, even if the predation rate of individual predators changed, it would not change individual predator's capture rate in relation to the total capture rate, meaning that an individual predator's gain of information in relation to changes in prey morph frequencies remains constant.

The result that increasing the probabilities of detection of both the prey morphs increased the persistence of the polymorphism suggests that frequency-dependent pre-

dition may be less likely to maintain polymorphism in cryptic prey than in conspicuous prey. Also, this result demonstrates the importance of the correlation between prey morph frequencies and predation risks of the morphs for maintenance of prey polymorphism. An increase in the probability of detection decreased the random factor in prey detection. Consequently, it allowed the predators to acquire more accurate information on prey morph frequencies and, thus, the predator behaviour adjustment better tracked changes in prey morph frequencies. Interestingly, results from studies about search image formation and selective attention suggest that a certain level of perceptual load is required before it is beneficial to selectively attend the prey types (Bond, 1983; Langley *et al.*, 1996; Dukas & Kamil, 2001; Dukas, 2002). Thus, if both prey types are conspicuous a predator is likely to detect them without narrowing its attention. In concert, these results suggest that the range of prey conspicuousness (or crypsis), for which search image formation may contribute to maintenance of polymorphism, is limited.

Not unexpectedly, assigning the morphs different probabilities of detection decreased the persistence of prey polymorphism. The obvious result of such a difference in conspicuousness of the morphs is a directional, frequency-independent selection against the more conspicuous morph. Directional selection, which favours one of the morphs at the cost of the other, acts against maintenance of the polymorphism by frequency-dependent selection (see also Endler, 1988). Combined with frequency-dependent predation this effect was asymmetric, such that the polymorphism was more persistent when the probability of detection of one of the morphs was increased than when it was decreased for the same amount. This is in accordance with the conclusion above, stating that increased level of prey conspicuousness allows the predator behaviour better track changes in prey morph frequencies.

Also the behavioural factors of the predators had a strong impact on the prey polymorphism. The results suggest that predators that show frequency-dependent behaviour with a wide adjustment range may actually destabilize prey polymorphism. This is because the more the extreme probabilities deviate from the median, the more steps are needed to switch the probabilities from favouring one morph to favour the other and the slower the response is. Note that the values used in the simulations fall within the adjustment ranges of behaviour reported by Manly *et al.* (1972). In their experiment with pairs of Japanese quail (*Coturnix coturnix japonica*) as predators and coloured pastry pellets as prey, 0.12 was the lowest probability of a prey morph to be taken when it was as rarest (with the relative frequency of 10%), and 1.00 was the highest probability when it was as most common (80%).

For low adjustment rates it was unlikely that prey polymorphism was maintained, whereas a rapid adjustment

of behaviour resulted in long persistence of prey polymorphism. Thus, also these results suggest, in accordance to the results about the adjustment range, that the persistence of polymorphism is increased if the delay in predator's response is decreased such that a predator's behaviour can rapidly switch from favouring one prey type to favouring the other.

It is worth bearing in mind that knowledge about frequency-dependent adjustment of predator behaviour is quite scarce. In this model I have striven for parsimony rather than elaborate assumptions based on guesses. For example, it is not known whether adjustment rates are symmetric (i.e. increase equals decrease) and constant as has been assumed in this study. These issues warrant further empirical and theoretical studies.

This study identifies some ecological and behavioural factors that have an impact on maintenance of prey polymorphism by frequency-dependent predation, and it makes qualitative predictions about those impacts. Further, the study suggests that although positive frequency-dependent selection by predators may maintain prey polymorphism in some conditions, it is not a sufficient condition for persistent polymorphism. Instead, under some conditions prey polymorphism was actually less persistent when predators showed frequency-dependent behaviour than under frequency-independent selection. Thus, even though positive frequency-dependent predator behaviour may be common, positive frequency-dependent predation favouring prey diversity need not be equally common. The results of this study further indicate that the relationship between frequency-dependent predator behaviour and prey diversity is not as simple as previously thought and that more studies about the population level consequences of frequency-dependent predator behaviour are therefore needed. The results also indicate that it is too simplistic to assume that the dynamics of frequency-dependent predation would be equal at the individual level and at the population level. This suggests that it is premature to argue for predators' frequency-dependent behaviour being able to maintain prey polymorphism in natural populations on the basis of trials with only few predator individuals (cf. Manly *et al.*, 1972; Allen, 1988; Bond & Kamil, 1998, 2002).

By and large, decreasing the gap in our knowledge about the dynamics of frequency-dependent processes appears to be helpful for understanding frequency-dependent predation, maintenance of prey polymorphism and diversity in general. The present study points out several questions for future studies in this area. For example, several experimental studies have reported considerable variation among predator individuals in their frequency-dependent behaviour (e.g. Manly *et al.*, 1972; Murdoch *et al.*, 1975), and whether such variation plays any role to the stability of prey polymorphism is a question worth addressing in future studies. Further, frequency-dependent predation is interesting from the population ecological point of view, too. Models on

predator-prey systems in which the predator shows positive frequency-dependent predation suggest that the switching behaviour affects the dynamics of the system (Abrams, 1999; Abrams & Matsuda, 2004). The importance of the number of predators and prey for maintenance of prey polymorphism by frequency-dependent predation shown in this study suggests that it would be worthwhile to investigate the effect of prey and predator population dynamics on the persistence of polymorphism. In the present study the variation in experiences among predators had an effect on polymorphism and therefore also the effect of spatial heterogeneity in the distribution of prey types might turn out to be important, as it may induce additional variation in the experiences of the predators. Finally, the importance of the behavioural parameters in this study suggests that more detailed knowledge about the adjustment of frequency-dependent prey detection is needed.

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