Does colour polymorphism enhance survival of prey populations?

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That colour polymorphism may protect prey populations from predation is an old but rarely tested hypothesis. We examine whether colour polymorphic populations of prey exposed to avian predators in an ecologically valid visual context were exposed to increased extinction risk compared with monomorphic populations. We made 2976 artificial pastry prey, resembling *Lepidoptera* larvae, in four different colours and presented them in 124 monomorphic and 124 tetramorphic populations on tree trunks and branches such that they would be exposed to predation by free-living birds, and monitored their 'survival'. Among monomorphic populations, there was a significant effect of prey coloration on survival, confirming that coloration influenced susceptibility to visually oriented predators. Survival of polymorphic populations was inferior to that of monomorphic green populations, but did not differ significantly from monomorphic brown, yellow or red populations. Differences in survival within polymorphic populations paralleled those seen among monomorphic populations; the red morph most frequently went extinct first and the green morph most frequently survived the longest. Our findings do not support the traditional protective polymorphism hypothesis and are in conflict with those of earlier studies. As a possible explanation to our findings, we offer a competing 'giveaway cue' hypothesis: that polymorphic populations may include one morph that attracts the attention of predators and that polymorphic populations therefore may suffer increased predation compared with some monomorphic populations.

Keywords: colour polymorphism; extinction risk; artificial prey populations; defensive coloration; predation

1. INTRODUCTION

The influence of differential selection imposed by visually guided predators on the evolution of animal colour patterns and dynamics of colour pattern polymorphisms remains a vivid line of research in evolutionary biology (Poulton 1890; Cott 1940; Ruxton *et al.* 2004; Bond 2007). Several authors have suggested that the coexistence within a population of two or more discrete phenotypic colour variants or morphs may contribute to reduced predation pressure and enhanced survival in polymorphic prey populations (Poulton 1890; Clarke 1962; Moment 1962; Croze 1970; Allen 1988; Knill & Allen 1995; Glanville & Allen 1997). Such a protective function of colour polymorphism, it has been argued, may arise if predators are conservative in their search and choice of prey, display perceptual switching and feed disproportionately for prey similar to well-known items (Allen 1984; Marples *et al.* 1998; Bond & Kamil 1999; Thomas *et al.* 2003), search for one type of prey at a time (Croze 1970; Allen 1988; Bond & Kamil 1998), or if predators that exploit polymorphic populations perceive prey densities as lower than they actually are (Croze 1970). Polymorphism may be protective also if predators that forage in polymorphic populations suffer from reduced efficiency, due to longer prey information processing time (Croze 1970; Allen 1988; Glanville & Allen 1997; Dukas & Kamil 2001; Punzalan *et al.* 2005).

The general opinion based on logical arguments, as outlined above, appears to be that groups of polymorphic

prey should be exposed to reduced risk of predation. Several mechanisms, such as frequency-dependent selection, may promote the maintenance within a population of several variants and polymorphisms can exist even if they do not slow the rate of predation. We are concerned here, however, with the possible influence of polymorphism on the survival of populations.

We are aware of only three studies that have tested the hypothesis of protective polymorphism. Two of them used an experimental protocol in which human predators were presented with digital prey on backgrounds displayed on computer screens (Knill & Allen 1995; Glanville & Allen 1997). Both these studies report a reduced rate of predation on individuals in polymorphic compared with monomorphic populations. In the third study, Croze (1970) presented groups of painted mussel shells that concealed a piece of meat reward to birds in the wild and found that mussel shells suffered less predation in trimorphic populations than in monomorphic populations. A single pair of carrion crows was used as predators in all replicates in Croze's study, and the results must therefore be interpreted with caution. The existing evidence in support of a protective role of polymorphism under ecologically natural conditions is thus weak, at best.

All three studies mentioned above (Croze 1970; Knill & Allen 1995; Glanville & Allen 1997) evaluate the hypothesis of protective polymorphism by comparing average fitness for individuals in polymorphic versus monomorphic populations. As far as we know, no previous study has tested whether polymorphism may lower susceptibility to predation to the extent that it may

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increase the survival prospects of groups. We do not adhere to naive group selection arguments, but agree with Wilson & Wilson (2007) that multilevel selection theory, including differential success of populations or groups of individuals, is necessary to fully account for the evolutionary process, and that traits that are selectively neutral or even disadvantageous within groups may theoretically increase the fitness of groups of individuals relative to other such groups.

An enhanced viability of polymorphic relative to monomorphic groups would have interesting evolutionary and ecological implications. For instance, superior survival of more diverse family groups might facilitate the evolutionary origin and establishment of novel phenotypes. This could provide a possible explanation for the initial evolution of conspicuous warning signals and aposematism, which is sometimes regarded as a paradox (Marples *et al.* 1998; Thomas *et al.* 2003). A survival advantage for small groups that have become polymorphic following the appearance of a novel phenotype may also facilitate evolutionary shifts of populations to alternative fitness peaks in the adaptive landscape (Wright 1988; Arnold *et al.* 2001). Finally, reduced predation on polymorphic groups may contribute to an enhanced colonization success and positively influence species range expansions and invasiveness (Agrawal 2001; Pigliucci 2001; Forsman *et al.* 2008).

Here, we address the issue of protective polymorphism by presenting artificial pastry prey, resembling *Lepidoptera* larvae, in monomorphic and tetramorphic populations on tree trunks and on upper surfaces of branches, such that they would be exposed to predation by free-living birds under natural conditions. We present prey in clusters of 12 individuals, resembling small families or groups of gregarious caterpillars. Because kinship increases genetic variation among groups, it may increase the importance of between-group selection compared with within-group selection (Wilson & Wilson 2007). We use a design that represents natural, ecologically diverse conditions and present artificial prey to predation by free-living avian predators against a range of visual backgrounds in different habitats, on different substrates, at different times of season and under a range of light conditions. Using many free-living avian predators is important because individual birds vary in their choice of prey (Marples *et al.* 1998), the predation pattern imposed by a single individual or species of predator may differ from that imposed by a community of predators (Merilaita 2006) and foraging behaviours of free-living wild birds may differ from those of captive birds in aviaries (Thomas *et al.* 2004).

The aim of the present study is to examine whether colour polymorphic populations of prey exposed to avian predators in the field are exposed to a lower extinction risk compared with monomorphic populations, as predicted by the 'protective polymorphism' hypothesis. We evaluate levels of selection using a nested series of comparisons: between groups within the population of groups and between individuals within groups.

2. MATERIAL AND METHODS

(a) Artificial pastry prey

We created pastry prey (Allen *et al.* 1998; Marples *et al.* 1998; Thomas *et al.* 2003; Rowland *et al.* 2008) formed into 20 mm

long and 5 mm thick cylinders, resembling caterpillars, in four different colours: red; yellow; green; and brown (figure 1). We mixed 200 g wheat flour, 120 g butter and 10 ml gelatin, dissolved in 30 ml water and melted in a hot water bath. The dough was divided into four parts, each coloured with 0.5 ml food colouring (Ekströms karamellfärg, red, yellow and green). We used a mixture of red, yellow and green in equal parts to obtain the brown colour. The four colours were distinctly different to the human eye. Evidence exists that colour vision, including the ultraviolet spectra, is important in behavioural decisions related to foraging in birds (Bennett & Cuthill 1994; Vorobyev & Osorio 1998; Church *et al.* 2001). We therefore examined our pastry bait colour treatments using a spectrometer (Ocean Optics USB 2000 with a PX-2 pulsed xenon light source) to measure reflectance spectra. All the four prey types showed very low reflectance within the UV range and none of them showed any reflectance peaks within the UV range (300–380 nm).

(b) Experimental design and presentation of artificial prey in the field

We used an experimental design with replicate blocks consisting of four polymorphic and four monomorphic populations. Each polymorphic population consisted of 12 pastry baits: three red; three yellow; three brown; and three green. Monomorphic populations consisted of 12 baits of the same colour. Within a replicate block, the eight populations were placed approximately 50 m from each other, in the same habitat (pastures or forests), on the same substrate and on the same day. Replicate blocks were separated by approximately 600 m to avoid that learning by birds during the experiment should influence our results.

We placed the pastry prey in splits in the barks of tree trunks (figure 1a) or needled them on the upper surfaces of twigs (figure 1b) on pine tree (*Pinus sylvestris*), oak (*Quercus robur*), birch (*Betula pendula*), alder (*Alnus glutinosa*) or aspen (*Populus tremula*). Pastry baits within each population were distributed on an area of 1–2 m². We always used the same tree species and substrate (trunk or twig) for all pastry baits within a given replicate block. Whether a monomorphic or polymorphic population should be placed in a particular place within a replicate block was decided using an eight-faced dice. We placed mono- and polymorphic treatments an equal number of times on both substrates (trunk or twig) and on different tree species.

We visited the replicate blocks every 24 hours for one week and recorded each day the number of pastry baits remaining and non-attacked in each population. A pastry bait was regarded as attacked if it was completely or partly missing, or if it bore beak marks. We terminated the monitoring of a replicate block after one week if no predation had been noted during last 48 hours or after less than one week if there was only one population left. Thirteen of the 31 replicate blocks were monitored for less than one week. No replicate block was monitored for more than 12 days. The field study started on 23 April, before leafing, and was terminated on 7 July 2008. Study sites were located in the surroundings of Kalmar, in the southeast of Sweden. We chose habitats with a rich and variable bird fauna. Examples of bird species observed in several sites are: great spotted woodpecker (*Dendrocopos major*), chaffinch (*Fringilla coelebs*), blue tit (*Cyanistes caeruleus*), great tit (*Parus major*), willow warbler (*Phylloscopus trochilus*), nuthatch (*Sitta europaea*) and blackbird (*Turdus merula*).

(c) *Statistical analyses*

To test whether survival of prey populations was influenced by the colour of artificial pastry prey and by whether the population was monomorphic or polymorphic, we recorded each day the number of artificial prey subjects left in each population. The 12 pastry baits within a population cannot be considered independent, and our hypothesis concerns the differential survival of entire populations of monomorphic versus polymorphic prey. We therefore computed the survival time (in days) for each entire population of 12 pastry baits and used this as input data in our analyses. We estimate and compare survival curves, and test for the effects of experimental treatment on survival of experimental populations while controlling for effects of starting date, location and substrate, using the non-parametric procedure LIFETEST (SAS 2004).

An intrinsic characteristic of survival data that measure the time until an event (mortality, failure or disappearance) is the possibility for censoring of observations, i.e. when the time until the event is not observed (Hosmer *et al.* 2008). In our study, we sometimes terminated the monitoring of survival before all prey subjects had disappeared from each of the eight populations in a replicate block. Consequently, the actual survival time could not be ascertained and only a lower bound on their survival time is known for these populations. Such observations are said to be right censored. The method of analyses as implemented in the LIFETEST procedure takes censoring into account and uses information for both censored and uncensored observations (SAS 2004).

Our preliminary modelling of survival data suggested that survival differed among replicate blocks that were performed at different times of the season, at different locations and on different substrates (trunks or twigs of different species of trees). We chose an experimental design in which each replicate block contained all treatments (i.e. four polymorphic populations and four monomorphic populations representing each of the four colours) to ascertain that influences on survival of time and locality, etc., should not confound our comparisons between treatments. In addition, we assessed the effect of treatment (colour of artificial prey) on survival of populations while adjusting for confounding differences in survival among replicate blocks. To achieve this, we carried out a stratified test to test for treatment effects by specifying replicate block in the STRATA statement as a stratifying variable and by specifying colour treatment in the GROUP=option. The test statistics are then computed by pooling over STRATA defined by the values of replicate block and provide non-parametric *k*-sample tests based on weighted comparisons of the estimated hazard rate of the individual population under the null and alternative hypotheses (SAS 2004; Hosmer *et al.* 2008).

Following the recommendation of Hosmer *et al.* (2008), we report the statistical significance of explanatory variables (prognostic factors) as obtained for both the log-rank test (which places more weight on differences in survival at larger values of time) and the generalized Wilcoxon test (which places more weight on differences in survival at smaller values of time). To facilitate comparisons of survival between experimental treatments and visualize the survival functions, we provide plots of estimated mean survival times and associated standard error, and of the estimated survival probabilities (as obtained from the Kaplan–Meier estimator (also called the product-limit method) of the survival function) against survival time (Hosmer *et al.* 2008).

3. RESULTS

(a) *Summary statistics*

Throughout the study, we used 2976 pastry baits, organized in 31 replicate blocks of eight populations with 12 individual pastry baits in each population. The majority (79%) of pastry baits were 'killed' (i.e. disappeared or bore evident beak marks) during the study, and 180 of the 248 populations went extinct. The average time to extinction for populations was 2.54 days ($n=180$, range=0–11 days, s.d.=2.37). On average, 53 per cent (corresponding to 6.4 of the 12 pastry baits within a population) of pastry baits were killed after having been exposed to predation for 3 days, and 141 populations survived longer than 3 days. In 63 out of the 248 populations, all 12 individuals disappeared between two consecutive observation periods (within 24 hours). We therefore concluded that, in the majority of cases, the initial detection of one of the prey did not lead to immediate extinction of the entire population.

Overall, our analyses uncovered large, statistically significant and consistent differences in survival both among and within populations of artificial pastry baits of different colours, as outlined in greater detail below.

(b) *Differences in survival among monomorphic populations*

To facilitate comparisons of survival between experimental colour treatments, we provide plots of estimated survival functions (figure 2) and of estimated mean survival times and associated standard error (figure 3). We report the statistical significance of experimental colour treatments as obtained using the non-parametric procedure LIFETEST in SAS for both the log-rank test and the generalized Wilcoxon test in table 1.

When artificial pastry prey were presented in monomorphic populations, there was a significant effect of prey coloration on estimated survival (table 1; figures 2 and 3), confirming that the coloration of artificial prey influenced their susceptibility to visually oriented predators. The monomorphic green populations had the longest mean estimated survival, followed by brown, yellow and red (figure 3).

(c) *Comparing survival of monomorphic and polymorphic populations*

The prediction that polymorphic populations would be protected from predation and therefore experience higher survival and lower extinction rates compared with monomorphic populations was not supported. Significant effects of experimental colour treatment on survival were evident among populations when data for the polymorphic populations were included in the analyses (table 1). Bonferroni corrected pairwise tests (four comparisons, test-wise *p*-value for significance=0.0125) showed that polymorphic populations survived worse than monomorphic green populations (log-rank test, $\chi^2=10.6$, $p=0.0011$; Wilcoxon test, $\chi^2=10.9$, $p=0.001$), but did not differ significantly from monomorphic brown, yellow or red populations (all $p>0.016$; figures 2 and 3).

(d) *Effects of coloration on survival within polymorphic populations*

The pattern of variation in survival among artificial pastry baits that we found in our comparisons among monomorphic populations of different colours (figure 3) was

Figure 1. (a) Part of polymorphic population of green, brown, yellow and red artificial pastry prey affixed in crevices on oak (*Quercus robur*) trunk and (b) one red pastry prey presented on the upper surface of a twig of birch (*Betula pendula*). Photographs L. Wennersten.

Figure 2. Estimated survival probability (product-limit survivor function estimates) as a function of survival time in days for artificial pastry prey subjects presented in monomorphic brown (solid curve), green (dotted curve), red (dot-dashed curve) or yellow (long-dashed curve) and in polymorphic (medium dashed curve, tetramorphic) populations. (Artificial prey subjects were presented on the upper surface of branches or in crevices on tree trunks where they were exposed to predation by free-ranging avian predators.)

paralleled by patterns seen in comparisons within polymorphic populations (figure 4). We were able to determine which of the four colours that disappeared first in 21 out of the 124 polymorphic populations. Among these 21 replicates, the distribution of prey items that first went extinct was dependent on coloration ($\chi^2_3 = 17.67$, $p = 0.0005$); with red prey most frequently going extinct first, followed by yellow and brown (in no case did green prey go extinct first; figure 4). Similarly, we were able to determine which of the four colours that remained last in 14 out of the 124 polymorphic populations. The distribution of prey items that survived the longest was dependent on coloration ($\chi^2_3 = 16.29$, $p = 0.001$), with green prey being the last survivors in nearly all (10 out of 14) cases (figure 4).

Figure 3. Comparisons of estimated mean survival times (mean days $\pm$ s.e.) and associated standard errors for red, yellow, brown or green monomorphic populations and for polymorphic (mix of all four colours) populations of artificial prey subjects exposed to predation by free-ranging avian predators.

Table 1. Results from a stratified test of experimental colour treatment effects (monomorphic green, brown, yellow or red or tetramorphic (=mixed colours)) on survival of artificial pastry prey populations exposed to predation by free-ranging avian predators. (Statistical significance of differences in survival as obtained for both the log-rank test (which places more weight on differences in survival at larger values of time) and the generalized Wilcoxon test (which places more weight on differences in survival at smaller values of time) while controlling for confounding effects of starting date, location and substrate, using the non-parametric procedure LIFETEST in SAS (2004).)

statistic	value	d.f.	p-value
<i>comparison restricted to the four monomorphic colour treatments</i>			
log-rank test	12.88	3	0.0049
Wilcoxon test	12.50	3	0.0058
<i>comparison among four different monomorphic and one polymorphic colour treatment</i>			
log-rank test	12.12	4	0.0165
Wilcoxon test	15.04	4	0.0046

Figure 4. Comparison of distribution of prey colours that (a) first went extinct and (b) those that survived the longest within polymorphic groups of artificial pastry bait subjects exposed to predation by free-ranging avian predators.

Figure 5. Consequences of belonging to a polymorphic prey population for prey of different colours. (Figure shows the difference (mean $\pm$ s.e.) between the mean percentage of artificial pastry prey subjects of four different colours presented in polymorphic and monomorphic populations that survived for at least 3 days when exposed to predation by free-ranging avian predators.)

(e) Comparisons of relative survival of each colour in polymorphic versus monomorphic populations

Our experiment shows that the consequences of belonging to a polymorphic population, in terms of individual survival, depend on coloration. A comparison of the proportion of pastry baits of a given colour that survived for at least 3 days shows that red and yellow prey were more likely to survive if they were presented in polymorphic than in monomorphic populations. The survival prospects of brown and green prey were instead higher in monomorphic than in polymorphic populations (figure 5). Relative survival in polymorphic versus monomorphic populations varied significantly among pastry baits of different colours (two-factor ANOVA on mean difference in survival, effect of prey colour: $F_{3,90}=4.09$, $p=0.0091$; effect of replicate group: $F_{30,90}=1.99$, $p=0.0068$). These findings show that the ‘fitness’ of an individual depends not only upon its own phenotype, but also upon the phenotypes of other members of the group.

4. DISCUSSION

Does colour polymorphism enhance survival of prey populations, as predicted by the protective polymorphism hypothesis (Clarke 1962; Moment 1962; Croze 1970;

Allen 1988; Knill & Allen 1995; Glanville & Allen 1997)? To address this issue, we presented artificial pastry prey resembling *Lepidoptera* larvae in monomorphic and tetramorphic populations on tree trunks and on upper surfaces of branches such that they would be exposed to predation by free-living birds under a range of natural visual backgrounds, in different habitats, substrates, light conditions and times of season. Our analyses clearly show that colour matters: we found large, statistically significant and consistent differences in survival among monomorphic populations and within polymorphic populations of artificial pastry baits of different colours (figures 2–4).

(a) No support for the protective polymorphism hypothesis

The survival of polymorphic populations of pastry baits of four different colours was inferior to that of monomorphic green populations, but did not differ significantly from survival of monomorphic red, yellow and brown populations (figures 2 and 3; table 1). These results are not consistent with the hypothesis of a general protective effect of colour polymorphism. Our results also differ from those of the earlier studies that report findings interpreted as evidence in support of a protective effect of polymorphism (Croze 1970; Knill & Allen 1995; Glanville & Allen 1997). Both Knill & Allen (1995) and Glanville & Allen (1997) found that polymorphic digital prey on backgrounds displayed on computer screens were attacked at a lower rate by human predators, as compared with digital prey in monomorphic populations. Our present study differs from these investigations not only in terms of results and conclusions, but also in that we compared survival rates of entire populations, rather than the survival rate of individuals within populations, and in that we used an ecologically natural and more relevant experimental set-up. Another difference is that we recorded the combined predation by many individual predators of different species, whereas the other studies examined the behaviours of individual crows and humans. We therefore conclude that, to our knowledge, there exists as yet no indisputable evidence that prey populations that are polymorphic for colour pattern are less susceptible to predation under natural conditions, compared with monomorphic populations. Admittedly, we cannot dismiss the possibility that polymorphism does have a protective effect under natural conditions but that we have failed to detect it, for reasons discussed below.

(b) Perhaps polymorphism is protective only if all prey colour variants are cryptic?

It has been argued that polymorphism may be less protective if prey are conspicuous (Knill & Allen 1995). However, Knill & Allen (1995) and Glanville & Allen (1997) report a reduced rate of predation on individuals in polymorphic compared with monomorphic prey populations that were independent of population density and the level of crypsis. These results argue against the suggestion that the protective effect of polymorphism is dependent on the degree of camouflage.

(c) The protective effect of polymorphism may have gone undetected because artificial pastry prey do not behave

Artificial pastry prey have been used in a number of experimental studies that seek to investigate the role of selective predation for the evolution of animal colour patterns (Allen *et al.* 1998; Marples *et al.* 1998; Thomas *et al.* 2003; Rowland *et al.* 2008). An intrinsic drawback of artificial prey, however, is that they do not behave, or, rather, they all behave in a fixed manner. Selection imposed by visually oriented predators does not necessarily act on prey coloration *per se*; the protective value of a colour pattern is instead determined interactively with other traits (Brodie 1992; Forsman 1995; Forsman & Appelqvist 1998). Such correlational selection favours the evolution of complex phenotypes and integration of colour pattern with other traits (Brodie 1989; Forsman *et al.* 2002). We propose a hypothesis that a protective effect of colour polymorphism may be manifest more strongly in systems where alternative morphs represent such different co-adapted trait-value combinations. To investigate this, we can see no other way than using natural polymorphic prey populations in an experiment.

(d) A modified hypothesis: perhaps polymorphism is protective compared with some, but not all, monomorphic populations?

The original hypothesis that colour polymorphism in general should reduce susceptibility of prey populations to predation may be an oversimplification. We propose as a possible explanation to our findings (figures 2 and 3) that populations of prey with a colour pattern that is well camouflaged or otherwise provides good protection against predation (such as the monomorphic green ones in our study) may be exposed to increased predation following the appearance (by means of immigration, novel mutation or developmental plasticity) of an additional morph(s) that is more conspicuous and acts as a 'giveaway cue'. Conversely, moderately well-camouflaged prey phenotypes may be better off in polymorphic populations where they are surrounded by alternative colour variants. Polymorphism may thus reduce susceptibility to predation compared with some, but not all, monomorphic populations. Our study showed that survival prospects of red and yellow prey were higher in polymorphic than in monomorphic populations, while the opposite was true for brown and green prey (figure 5). Because we did not record the behaviour of predators, we cannot identify the mechanism(s) responsible for this result, but the differential fates within polymorphic groups (figure 4) argue against an important role of aversions to red or yellow and

preferences for green and brown. If the cost (or benefit) to the population in terms of increased (or decreased) predation following an evolutionary transitions from mono- to polymorphism depends on how well camouflaged the colour pattern in the original monomorphic population is, one would expect polymorphism to evolve more frequently from some ancestral monomorphic states (e.g. monomorphic red) than from other such states (e.g. monomorphic green). This prediction is amenable to empirical testing using a phylogenetically based comparative approach.

(e) Implications of our findings for the initial spread of conspicuous morphs via protective polymorphism

Red artificial prey survived the worst, both among monomorphic populations and within polymorphic populations. This result is difficult to reconcile with the notion that red is commonly considered a warning signal that may deter attacks by potential predators (Ruxton *et al.* 2004). There are, however, additional exceptions (Marples *et al.* 1998; Forsman & Herrström 2004), supporting the view that red colour is a context-dependent stimulus that sometimes functions as an avoidance inducing signal, and sometimes attracts the attention of predators by signalling palatability in ripe fruits and berries (Schmidt & Schaefer 2004).

We found no general advantage of polymorphic over monomorphic populations. Our results suggest, however, that certain morphs (such as red ones) that perform poorly within a polymorphic group do even worse in monomorphic groups (figure 5). In other words, the fitness of an individual may depend not only upon its own phenotype, but also upon the phenotypes of other members of the group. This raises the possibility that benefits accruing to relatively poorly protected phenotypes that belong to polymorphic groups, such as sibships, may enhance evolutionary transitions between alternative adaptive fitness peaks, and thereby promote the initial evolution and spread of conspicuous warning signals.

(f) Conclusions

Tetramorphic populations survived less well than green populations, and slightly (but not significantly) better than the other three monochromatic populations. These findings do not support the traditional prediction from theory that polymorphic populations should be less susceptible to predation. It appears instead that polymorphic populations are more vulnerable than the most well-protected monomorphic populations because the existence in polymorphic populations of prey phenotypes with imperfect camouflage functions as 'giveaway cues' that attract the attention of predators, and that revealing phenotypes may benefit from being members of polymorphic groups (figure 5). The protective polymorphism hypothesis, or a modified version thereof, in combination with multilevel selection theory (Wilson & Wilson 2007) deserves further attention when it comes to explaining evolutionary transitions between alternative fitness peaks in the adaptive landscape, such as the evolution of conspicuous coloration, and associations across species of variable coloration with niche breadth, range expansions and

conservation status that suggest that species that are polymorphic for colour pattern enjoy greater ecological success (Forsman & Åberg 2008; Forsman *et al.* 2008). Our present results are in conflict with those of earlier studies that report superior survival of individuals in polymorphic populations, and further investigations under ecologically realistic circumstances are required to properly evaluate the hypothesis that colour polymorphism may enhance the survival of prey populations.

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