

PREY CONCEALMENT: VISUAL BACKGROUND COMPLEXITY AND PREY CONTRAST DISTRIBUTION

Marina Dimitrova^{a,*} & Sami Merilaita^{a,b}

^a Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden

^b Present address: Environmental and Marine Biology, Åbo Akademi University, FIN- 20500 Turku, Finland

* Corresponding author: Marina Dimitrova, marina.dimitrova@zoologi.su.se

Short title: Background complexity and prey camouflage

ABSTRACT

A prey may achieve camouflage through background matching and through disruptive coloration. Background matching is based on visual similarity between the prey and its background, whereas disruptive coloration emphasizes the use of highly contrasting pattern elements at the body outline to break up the body shape of the prey. Another factor that may influence prey detection, but has been little studied, is the appearance of the visual characteristics of the background. We taught blue tits (*Cyanistes caeruleus*) to search for artificial prey and manipulated the appearance of the prey and the background. We studied the effect of diversity of shapes in the background on prey detection time. We also studied the differing predictions from background matching and disruptive coloration with respect to contrast level and location of high-contrast elements in prey patterning. We found that visual background complexity did indeed increase prey detection time. We did not find differences in detection time among prey types. Hence, detection time was not affected by contrast within prey patterning, or whether the prey patterning matched only a sub-sample or all the shades present in the background. Also, we found no effect of the spatial distribution of shades (highest contrast placed marginally or centrally) on detection times. We conclude that background complexity is important for the evolution of prey coloration. We suggest that it may facilitate concealment and favor the evolution of camouflage over warning coloration. Preference for visually complex backgrounds might provide prey with a so far untested means to decrease predation risk.

Keywords: predation, crypsis, camouflage, background matching, disruptive coloration, aposematism.

INTRODUCTION

Natural selection imposed by predation has resulted in a variety of different adaptations aiming to decrease the predation risk of prey. One of these adaptations is cryptic coloration, which increases concealment and, thus, lessens the risk of visual detection (Poulton 1890). It is wide-spread in the animal kingdom and, for example, Caro (2005) proposed that such camouflage appears to be the single most important evolutionary force in explaining overall coloration in mammals. Two important principles of cryptic coloration are background matching and disruptive coloration (Cott 1940; Edmunds 1974; Ruxton *et al.* 2004).

According to the principle of background matching the more similar the color pattern of a prey is to the visual environment, the more difficult it will be for a predator to detect (e.g. Cott 1940; Norris and Lowe 1964; Endler 1978; Merilaita *et al.* 1999; Théry and Casas 2002). Thus, a prey is expected to be difficult to detect when its body coloration deviates little from the visual appearance (colors and patterns) of its environment. The principle of disruptive coloration, on the other hand, aims to reduce the detection or recognition of the characteristic shape or body outline of the prey (Thayer 1909; Cott 1940). Disruptive coloration uses pattern elements to create the appearance of false edges and boundaries and hinders the detection or recognition of an object's, or part of an object's, true outline and shape (Stevens & Merilaita 2009). This can be achieved if some parts of the prey outline blend in the background coloration and if high contrast between pattern elements by the outline creates edges that further distorts the appearance of the body shape (Thayer 1909; Cott 1940; Merilaita 1998; Cuthill *et al.* 2005; Schaefer and Stobbe 2006; Stevens and Cuthill 2006; Stevens *et al.* 2006; Fraser *et al.* 2007).

Evidently, although both these principles are at least to some extent dependent on how well the coloration of a prey blends into the background they emphasize different aspects of prey coloration. Disruptive coloration emphasizes the organization and relationship of elements within the animal color pattern, whereas the relationship between the appearances of an animal and its background is the core of background matching. These two principles thus focus on the animal color pattern *per se* as well as on how it interacts with the visual environment. Probably because the research on camouflage has mainly focused on these two principles, the effect of the appearance of the background *per se* on the evolution of camouflage has so far received very little attention. However, a recent study suggested that the appearance of the environment may influence natural selection on cryptic coloration: in a theoretical model visual complexity of the background hampered the detection of cryptic prey and facilitated evolution of camouflage (Merilaita 2003). This notion is also supported by some psychological experiments demonstrating the influence of background on search tasks (e.g. Gordon 1968; Farmer and Taylor 1980). Because of the huge visual variation that is found among natural habitats that different animals use, the effect of the appearance of the background on the evolution of camouflage clearly warrants further research.

Background matching and disruptive coloration also differ in their predictions about optimal colors and lightness (here defined as the measure of surface light reflection; Palmer 2002) for camouflage. Background matching emphasizes similarity in colors and lightness between prey and background pattern appearance. However, whether a prey pattern only matching a sub-sample is as good as a prey pattern matching all colors present in the background is not known (Merilaita and Lind 2005). In contrast to background matching, disruptive coloration suggests that high contrasts within prey color pattern are important. Previous experimental studies on disruptive coloration and prey contrasts have used artificial prey with two colors or lightness only and, furthermore, some of these have used natural backgrounds, for which it is difficult to control for variation in the level of background matching (Cuthill *et al.* 2005; Schaefer and Stobbe 2006; Stevens *et al.* 2006; Fraser *et al.* 2007, but see e.g. Kelman *et al.* 2007 for an experimental study using artificial backgrounds).

In this paper we have brought together the questions raised above. Thus, we have investigated how background appearance *per se* as well as the different predictions about optimization of prey coloration drawn from background matching and disruptive coloration influence prey detection. More specifically, we had the following aims. First, our main aim was to investigate the influence of background complexity on the risk of prey becoming detected, by comparing search times of avian predators that searched for artificial prey on artificial low and high pattern diversity backgrounds. Second, we investigated the optimization of lightness and contrast within prey patterning with respect to predictions from background matching and disruptive coloration. We did this by comparing the detection time of a high-contrast and a low-contrast pattern, both matching the background. We also tested whether it is better to match all the shades in the background than to match a sub-sample of shades. In addition, we investigated the

importance of spatial distribution of pattern contrasts (marginal vs. central), which could be expected to influence disruption of the outline.

MATERIAL AND METHODS

The predators

We used wild-caught blue tits (*Cyanistes caeruleus*) as predators in our study. Before the experiments the blue tits were trained to search for artificial prey items (hereafter prey item), covering a piece of peanut as a reward, on an artificial background (hereafter background). The prey items and the backgrounds were made of paper, allowing an easy manipulation of their patterning and also enabling us to control the appearance and lightness of both background and prey. Blue tits were selected because they represent a common omnivorous avian predator in the study area. Our prey items loosely resemble small insects, such as moths or butterflies, which constitute an important part of the diet of many passerine birds, such as the blue tit. We conducted our study between December-February, 2005-2006 (Experiment 1) and between November-January, 2006-2007 (Experiment 2) at Tovetorp Zoological Research Station (Stockholm University) in South-Eastern Sweden (58°56'N, 17°08'E). It was performed with permission from the Swedish ethical board in Linköping (Dnr: 56-06). We captured blue tits with mist nets and kept them indoors individually in cages (80 × 60 × 40 cm³). The room temperature was about 18°C and the light:dark rhythm (with dusk and dawn) was adjusted according to the prevailing day length. The birds were provided with suet, sunflower seeds, peanuts and water *ad libitum*. The birds were kept indoors for 7 days (median), before they were released in the area of capture.

The backgrounds and the prey items

We created the patterning of the backgrounds and the prey items with the software Corel Draw 11 (Corel Corporation) and reproduced them with a laser printer (HP LaserJet 4000 Series PS with 1200 dpi resolution) on white copying paper (Canon Office). The choice of the size, shape and density of the pattern elements of the backgrounds and the prey items were based on preliminary tests with blue tits that were trained as the experimental birds and excluded from the experiment. We wanted the prey items to be cryptic enough, so that any possible differences in search times would be detectable, but not too difficult so that the birds would lose their motivation to search for the prey items.

On the A4-sized (21 × 29 cm²) backgrounds there were equally many black and grey elements of every shape. The number of different background element shapes on the two backgrounds, hereafter referred to as simple and diverse, was five and eight, respectively, the five element shapes being common for both backgrounds. To control for the level of background matching of the prey items between the two backgrounds, we kept the density of the two element shapes that also constituted the prey item patterning (squares and triangles; Figure 1) equal in both backgrounds. In addition, the density of all background elements was equal in the prey and the two backgrounds. Further, the three other element shapes of the simple background were less abundant on the diverse background to keep the overall density of the elements as well as the total area they covered equal between the two backgrounds. Each printed background was glued on an equally-sized corrugated cardboard, using solvent free glue stick (Scotch, 3M), to form the experimental boards.

The four prey pattern categories with white ground color were (i) high internal contrast (all elements black), (ii) low internal contrast (all elements grey), (iii) average contrast with high marginal contrast (half of the elements black and marginally located) and (iv) average contrast with low marginal contrast (half of the elements black and placed away from the margin; Figure 1c). With these four categories we investigated the optimization of internal contrast (shades of the patterning) within the contrast range of the background, and with categories (iii) and (iv) we, specifically, tested the effect of the spatial distribution of the highly contrasting elements.

We established that the lightness of the grey elements was about half of the lightness of the white areas: the lightness of the grey was 56.1% and the lightness of the black was 3.2% in relationship to the white areas. These values were calculated between 300 and 700 nm by using blue tit double-cone sensitivity (measured by Hart *et al.* 2000) and spectrometry (Ocean Optics USB 2000 spectrometer with a PX-2 pulsed xenon light source) following Vorobyev and Osorio (1998) and Siddiqi *et al.* (2004).

As mentioned above, the density of the non-white elements (both in terms of number and relative area covered) was equal in the backgrounds and in the prey items. Thus, because the proportion of white was equal in all prey categories (and the background), the difference in average lightness was only influenced by the black and grey elements. The three-shaded prey (iii and iv) had three black and three grey

elements, whereas the two-shaded prey had either six black (i) or six grey (ii) elements. The averaged lightness of the prey categories were 85.1% for the black prey, 89.2% for the three-shaded prey and 93.3% for the grey prey. Consequently, the mean of the average lightness of the two two-shaded prey categories equals the average lightness of the two three-shaded prey. For this reason, the average lightness of the three-shaded prey and the background were equal, and the prey with six black elements and the prey with six grey elements deviated from the three-shaded pattern equally much (but to opposite directions).

To increase the generality of our results, we made two different series of these four categories (i-iv), prey series A and B (Figure 1c). We created these two series somewhat differently. In series A one side of each of the three marginal element touches the outline, increasing the probability that some parts of the marginal area of the prey will blend in the multi-shaded background. In contrast, in series B only a corner of the three marginal elements touches the outline, and they can be considered to give the appearance of 'cutting out' a corner of the prey body and thus distorting the shape. Within a series all prey patterns were geometrically identical, but for both prey series the four categories differed only in lightness and in distribution of lightness of the pattern. For presentation of prey items in the experiment, one prey item was lightly glued at three points on each experimental board. The prey item covered a randomly placed hole, in which there was a piece (about $2 \times 2 \times 2 \text{ mm}^3$) of an organically grown peanut as a reward for a bird that found the prey item and tore it off the background.

Training of the birds

Prior to the experiment, we individually trained the blue tits to search for the prey items by associating the prey items with the pieces of peanut they covered. The training of a bird began the day after its capture. Each bird was assigned to one background (simple or diverse) and one prey series (A or B). Each training session took place in an experimental cage with water *ad libitum*.

In the first training step six prey items were glued directly on a brown, $10 \times 15 \text{ cm}^2$ corrugated cardboard and were thus easy to detect: (a) two white prey items had a piece of peanut glued on them so that it was fully visible; (b) two patterned prey items were glued on the cardboard from one point, with a piece of peanut glued to their underside, but not sunk in a hole so that it was partly visible; and (c) two patterned prey items were glued from one point to cover a hole with a piece of peanut in it. One prey item from each of the four categories (i-iv) was used as the four prey items with a visible pattern. In the second training step the cardboard was covered with the experimental background, thus making the prey items cryptic. Four prey items, one from each category (i-iv), were lightly glued from three points on four randomly placed holes with pieces of peanut. A tip of one of the prey items was slightly bent up to initiate searching.

Every training session and the experiment were preceded by 45-60 minutes without food in the experimental cage. A bird advanced to the next step if it found all the prey items on the preceding training step within one hour. Otherwise, it had to redo that step in the next training session.

The experiment

The experimental cages were made of plywood ($W \times H \times D: 55 \times 90 \times 70 \text{ cm}^3$) and were lit from the ceiling with two fluorescent lamps (9W, Philips). An observation window ($10 \times 12 \text{ cm}^2$) was covered with a one-way see-through plastic sheet and the experimental room was always kept dark when a bird was in an experimental cage to hinder the blue tits from seeing the observer. There was water *ad libitum* in the cage and the temperature was about 16°C . There was a perch 20 cm below the ceiling and on the opposite side, near to the floor an opening, through which the experimental boards could be inserted.

During the experiment, each blue tit was presented three times one prey series (A or B) on one background pattern (simple or diverse). This resulted in 12 successive presentations for a bird. For each bird, we randomized the order of the four prey categories (repeating the order three times), but made sure that equal numbers of birds started the experiment with each prey category. In total (across all treatments) we used 86 blue tits. We used 21 blue tits for each series-background combination in the experiment except for prey series A on the diverse background, in which 23 birds were used.

For each presentation the observer recorded the effective search time, i.e. the time during which the bird actively searched for the prey item on the experimental board. The timing was stopped when the bird had found the prey item and pecked at it to tear it off. The bird was then allowed to eat the reward, before the experimental board was replaced. In rare cases the bird did not manage to find the prey item within 20 minutes time or 2 minutes of effective search time on an experimental board. To prevent loss of motivation due to long, unsuccessful search, the experimental board was taken out in such cases and

presented again after the rest of the series had been presented, and the active search time of the second presentation was used in the analysis.

Finally, because an aversion towards any of the prey patterns would have confounded our estimates of camouflage based on the effective search times, we wanted to establish that the blue tits were equally willing to attack all eight prey types. Therefore, we randomly chose 20 birds that had completed the experiment (ten from series A and B, respectively) and presented them two times with all eight prey types (16 boards in total) on plain brown corrugated cardboard, thus making the prey items easy to detect. The blue tits were presented prey items in the same way as in the experiment (i.e. one prey item per experimental board) and the effective search time was recorded. To familiarize the birds with this new background, we began each presentation with a white, non-patterned prey item that was excluded from the analysis. To confirm that the prey items were conspicuous to the blue tits when presented on the brown background, we estimated the chromatic contrast between the background and the white color covering main part of the prey items, using spectrometry according to the protocol described above. We measured chromatic contrast in JNDs (Just Noticeable Difference; Vorobyev and Osorio 1998, Vorobyev *et al.* 1998), values smaller than or equal to 1 JND indicating that the chromatic difference between two samples is not discriminable by the blue tits. The mean (\pm SD) chromatic contrast was 24.7 (\pm 6.4) JND, and thus, unsurprisingly, the prey items were conspicuous when presented on the brown background.

Statistical analyses

When analyzing the data, we used for each bird the means of the effective search times of each prey category and background combination, thus resulting in four values per bird. To achieve normal distribution and homoscedasticity we applied ln-transformation, suggested by the Box-Cox analysis, on the effective search times. We analyzed the transformed search times with repeated measurements ANOVA, using the Mixed procedure in SAS 9.0. We used prey category as a within-subject factor and background and prey series as a between-subject factor.

RESULTS

We found that there was no significant difference in effective search time between prey series A and B (series $F_{(1,82)}=0.99$; $p=0.32$; Figure 2). Also, all interactions with factor prey series were non-significant (series \times background $F_{(1,82)}=0.06$, $p=0.80$; series \times prey category $F_{(3,82)}=0.76$, $p=0.52$; series \times prey category \times background $F_{(3,82)}=0.67$, $p=0.57$). Therefore, we conducted a pooled analysis of the effective search times for prey series A and B, with prey category as a within-subject factor and background as between-subject factor.

The pooled analysis showed that there was a difference in search time between the two backgrounds ($F_{(1,84)}=20.84$, $p<0.0001$; Figure 2). Search times were consistently longer on the complex background compared to the simple background. There was no difference in search time between the four prey categories ($F_{(3,84)}=1.47$, $p=0.23$), suggesting that prey items with high-contrast patterns, prey items matching all shades or a sub-sample of the shades present in the background and also prey items with the highest pattern contrast placed marginally or centrally were all equally difficult to detect. The interaction between background and prey category was also not significant ($F_{(3,84)}=1.28$, $p=0.29$).

Finally, we investigated if there was a different prevalence for the blue tits to attack any prey of the four categories and two prey series when presented on plain brown backgrounds. The results showed that the birds were equally willing to attack both prey series ($F_{(1,38)}=0.41$, $p=0.53$), as well as all prey categories ($F_{(3,38)}=1.56$, $p=0.22$). Also the interaction between prey series and prey category was not significant ($F_{(3,38)}=1.89$, $p=0.15$). The birds attacked all prey items immediately without hesitation: for prey series A the mean effective search times ranged between 1.5-1.9 seconds and for prey series B they ranged between 1.7-2.0 seconds.

DISCUSSION

Our results show that there is a strong effect of visual diversity of the background on the probability of prey detection. We found no difference in prey camouflage depending on contrast within prey pattern, number of prey pattern shades, or spatial distribution of pattern shades.

The high degree of background matching with respect to pattern element shape and shade resulted in relatively good concealment of all the prey categories on both backgrounds (cf. the prey categories presented on the plain brown background). Because color and lightness deviation provided little information, it seems likely that the birds needed to use edge detection in the search for the matching prey items to find the physical discontinuities between the prey items and the background patterning as well as the slightly visible shadow.

While the relationship between the appearance of prey and its background (i.e. how to optimally resemble the background: e.g. Endler 1978; Merilaita *et al.* 1999, 2001; Merilaita and Lind 2005; Houston *et al.* 2007; Sherratt *et al.* 2007) as well as the appearance of prey color pattern *per se* (e.g. Cuthill *et al.* 2005, 2006; Merilaita and Lind 2006; Fraser *et al.* 2007) have been recognized as central factors in the evolution of cryptic coloration, the role of the appearance of the background *per se* has so far received little attention. However, a recent model, which simulated the evolution of cryptic prey coloration, suggested that visual fine-scale complexity of the environment affects prey camouflage (Merilaita 2003). (Note that this fine-scale complexity should not be confused with larger scale spatial heterogeneity due to difference between patches or microhabitats (cf. Merilaita *et al.* 1999; Bond and Kamil 2006; Houston *et al.* 2007)). In this simulation it was less demanding both to produce an effective cryptic pattern and to gain a given level of protection through camouflage in a visually complex than in a visually simple habitat (Merilaita 2003). Our present study demonstrates the biological plausibility of this idea by experimentally showing that background pattern diversity, an aspect of visual complexity, facilitates camouflage of the prey items of natural predators. This is further supported by psychological studies showing that a test subject needs longer time to find a target among distractors, when the diversity of the distractors is increased (e.g. Duncan and Humphreys 1989). There is psychological evidence for other aspects of background complexity, such as color diversity (Farmer and Taylor 1980) and density of distractors (Gordon 1968), that may influence search tasks and thus should also be investigated in a biological context.

Ideally, we would have included several different variants of simple and complex backgrounds in our study. Currently, it is possible that in addition to pattern diversity of the backgrounds, the specific shape of some elements present only on the complex background could also have contributed to some extent in the difference in search times. However, we note that all the shapes missing from the simple background (i.e., the two star-like shapes in Fig. 1b) had actually a more complex shape than the other elements. Thus, even this additional effect would be attributable to geometric complexity of the background. Further, these two backgrounds unarguably demonstrate that two backgrounds with equal element density and equal number of exactly matching elements can result in different detection probabilities. In any case, in future studies it would be important to investigate prey detectability on a range of different backgrounds, including various natural backgrounds, to increase our understanding of the importance of background appearance *per se* on prey detection.

We note that natural habitats can be highly variable. This is also supported by studies on natural scene statistics which have shown that there is a substantial variation in the different visual aspects of natural environments (e.g. contrast, lightness, spatiochromatic properties) even within short distances (Parraga *et al.* 2002; Frazor and Geisler 2006; Geisler 2008). We consider it likely that many prey species can potentially move between patches that differ substantially in their degree of visual complexity. Rocks or tree trunks covered by lichens to different degrees, bark that differs in complexity among different species of trees or sand or gravel that varies in diversity of grain size are just some examples. Therefore, our result of the effect of background diversity on prey camouflage has several interesting implications about the evolution of prey coloration and behavior. For one thing high visual habitat complexity may favor the use and evolution of camouflage due to the decrease in risk of becoming detected that is mediated by such environments. On the other hand, if a prey animal lives in a visually simple habitat there may be two different evolutionary implications. One is that in order to achieve a given probability of escaping detection animals living in the simple habitat should develop cryptic coloration with higher level of matching than animals living in a visually complex habitat. Another implication is that animals living in visually simple habitat will be less likely to escape predation with a given level of background matching and it will be more demanding to evolve a good cryptic coloration. Hence, evolution of defenses other than camouflage, such as aposematism, may be more likely to evolve in simple than in complex habitats. This is in accordance with the more general idea that the initial evolution of aposematism may be promoted by costs or constraints related to camouflage (Hagman and Forsman 2003; Merilaita and Tullberg 2005; Speed and Ruxton 2005).

Another implication of this result has to do with habitat choice. It has often been suggested that cryptic prey could minimize predation risk by preferring those parts of their environment that maximize their

level of background matching (e.g. Kettlewell 1955; Edmunds 1974; Gillis 1982; Morey 1990; Merilaita *et al.* 1999). Our results suggest an intriguing alternative way to increase camouflage, namely through the preference for visually complex parts of the habitat. Whether and how commonly real prey use preference for visually complex backgrounds to decrease their predation risk remains for future empirical studies to reveal.

The next question that our study addressed was the optimal choice of contrast and lightness for camouflage. We found no effect of contrast within prey pattern on camouflage. This differs from results of studies on disruptive coloration, in which high pattern contrast has been found to enhance prey camouflage (Cuthill *et al.* 2005; Schaefer and Stobbe 2006; Stevens *et al.* 2006). On the other hand, in another study by Stevens *et al.* (2009) with artificial prey pinned on tree trunks, prey with high-contrast markings survived no better than prey with low-contrast markings, which supports our findings. These contradictory results hint that the effect of high-contrast markings are context dependent and that further studies are needed to be able to fully understand the function of prey pattern contrast and its effect on prey camouflage.

Our two-shaded prey was equally hard to detect as the three-shaded prey. Considering camouflage through background matching, this suggests that a fully representative sample of shades (colors or lightness) is not always necessary, but an equally high level of background matching may be achieved by a sub-sample of the shades in the background. This may help to understand why so many patterns used for concealment by prey animals can be characterized as being dull rather than intensely patterned. Clearly this warrants further research.

We also investigated the effect of spatial distribution of shades in three-shaded prey items. It has been suggested that highly contrasting coloration at the prey margin is especially effective in disrupting the body outline (Cott 1940; Merilaita 1998; Cuthill *et al.* 2005). However, we did not find a significant increase in prey camouflage due to the marginal placement of high-contrast elements in comparison to the non-marginal placement of high-contrast elements. Our result thus implies either that high-contrast limited to the margin does not provide much more effective camouflage than high-contrast limited to the central area (but see Stevens *et al.* 2009 for a different result) or that any variant of the prey patterns we produced did not markedly benefit from disruptive effect. Real insects that are considered to be camouflaged, such as many moths, often have several “dull” colors and elements on their wings and body. Thus such animals are clearly more than two-shaded. Therefore, it is noteworthy that in addition to this study, more than two-shaded prey has only been used in one other experiment investigating disruptive coloration (Stevens *et al.* 2009). Interestingly, in Stevens *et al.* (2009) a three-shaded prey with low-contrast markings at the prey body margin and high-contrast markings centrally located survived better than all other tested disruptive treatments. Therefore it seems worthwhile to further investigate such multi-shaded prey, either artificial or natural, in combination with other backgrounds or prey patterning (cf. Cuthill *et al.* 2005; Schaefer and Stobbe 2006; Stevens *et al.* 2006; Fraser *et al.* 2007).

To summarize, the use of artificial prey items and backgrounds allowed us to specifically investigate the effect of background diversity and prey contrast on prey camouflage against avian predators. Birds are important visually hunting predators that affect the natural selection of the appearance of many prey animals, such as small insects. Our results show that, because the effect of prey contrast was different depending on background diversity, there is a complex coupling between background diversity and prey appearance. Moreover, the effect of background geometrical diversity *per se* on prey camouflage seems to be far more important in the evolution of camouflage than previously thought, and in the future it would be interesting to further investigate the effect of other visual aspects of background on the evolution of prey camouflage as well as on anti-predator warning signals.

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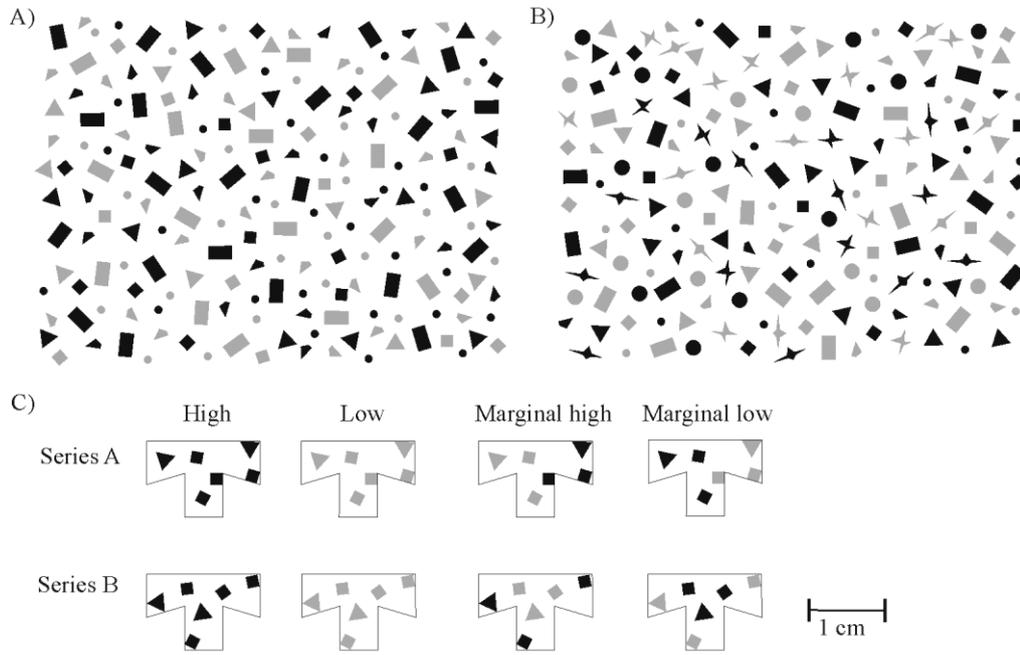


Figure 1. The two backgrounds, **A)** simple and **B)** diverse, differed only in the number of differently shaped pattern elements, five and eight, respectively. **C)** The two prey series A and B, and the four prey categories: high internal contrast (High); low internal contrast (Low); average contrast with high marginal contrast (Marginal high); and average contrast with low marginal contrast (Marginal low). The borderlines around the prey items are included for illustratory reasons only.

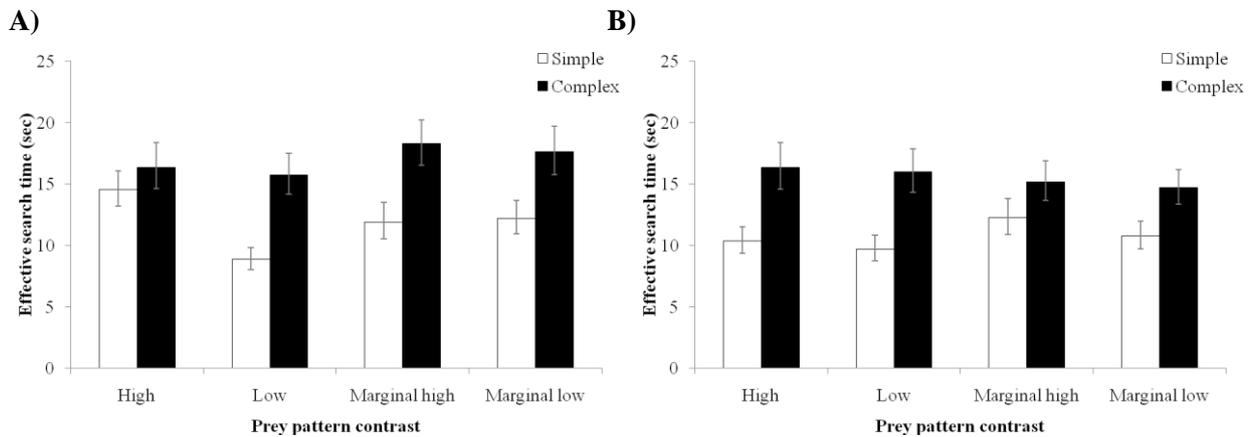


Figure 2. The effective search time (seconds) on the simple and the complex background for **A)** prey series A and **B)** prey series B. The four prey categories are high internal contrast (High); low internal contrast (Low); average contrast with high marginal contrast (Marginal high); and average contrast with low marginal contrast (Marginal low). Error bars show back-transformed standard errors.