Size variability effects on visual detection are influenced by colour pattern and perceived size

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Most animals including humans use vision to detect, identify, evaluate and respond to potential prey items in complex environments. Theories predict that predators' visual search performance is better when targets are similar than when targets are dissimilar and require divided attention, and this may contribute to colour pattern polymorphism in prey. Most prey also vary in size, but how size variation influences detectability and search performance of predators that utilize polymorphic prey has received little attention. To evaluate the effect of size variability on prey detection we asked human subjects to search for images of black, grey and striped pygmy grasshoppers presented on computer screens in size-variable (large, medium and small) or in size-invariable (all medium) sequences (populations) against photographs of natural grasshopper habitat. Results showed that size variability either increased or reduced detection of medium-sized targets depending on colour morph. To evaluate whether bias in perceived size varies depending on colour pattern, subjects were asked to discriminate between two grasshopper images of identical size that were presented in pairs against a monochromatic background. Subjects more often incorrectly classified one of the two identical-sized targets as being larger than the other in colour-dimorphic than in monomorphic presentations. The distinctly patterned (striped) morph elicited stronger size perception biases than the dorsally grey or black morphs, and striped grasshoppers were incorrectly classified more often as smaller than grey grasshoppers. The direction of the effect of size variability on detection changed across colour patterns as the bias in perceived size increased. Such joint effects of variation in size and colour pattern on detection and perception can impact the outcome of behavioural and evolutionary interactions between visually oriented predators and their camouflaged prey. This may have consequences for population dynamics, evolution of polymorphisms, community species composition and ecosystem functioning.

For individuals in search of mates or food, the ability to detect and recognize objects and compare among them is of utmost importance. For instance, within the context of mate choice, females and males must be able to recognize individuals that belong to the same species, discriminate between potential mates, and evaluate the quality of potential mates and competitors. Discrimination is often based on visual cues such as variation in size, coloration, shape and minor deviations from bilateral symmetry of ornaments (Andersson, 1994). Within the context of foraging, predators commonly search visually for preferred prey that are similar in size but differ in appearance from nonpreferred prey and inedible objects, or for prey that are similar in appearance but of

variable sizes owing to sexual size dimorphism and age differences. This is likely to have favoured recognition and detection strategies that rely on multiple visual features that are diagnostic of object identity (Rosselli, Alemi, Ansuini, & Zoccolan, 2015).

Visual perception concerns both sensory stimulation elicited by the target's physical properties ('bottom-up' processes) and cognitive processes such as expectations or specific knowledge about the target ('top-down' processes; Corbetta & Shulman, 2002; Rosselli et al., 2015; Wolfe, Oliva, Horowitz, Butcher, & Bompas, 2002). For example, detection of salient targets is little influenced by the observer's previous knowledge (Wolfe, Butcher, Lee, & Hyle, 2003). On the other hand, when the search task is difficult, for example due to camouflage, top-down processes including previous knowledge and experience with targets and backgrounds may become more important (Chen & Hegdé, 2012). Because the amount of information that can be processed at any given time is limited, search efficiency for a target category is expected to be

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negatively affected both by diversity within the target category (Karpestam, Merilaita, & Forsman, 2014b, 2016; Langley, Riley, Bond, & Goel, 1996; Pietrewicz & Kamil, 1979; Plaisted, 1997; Schmidt, Sebastian, Wilder, & Rypstra, 2012; Werner & Hall, 1974) and by the degree to which targets differ from the visual background (Karpestam, Merilaita, & Forsman, 2012, 2013). Accordingly, it can be predicted that target variability weakens the performance of searchers.

It can further be hypothesized that variability in some target features (e.g. coloration, shape, orientation, size or movement) may be more important than others, depending on the utility of the selection criteria used by searchers (Duncan & Humphreys, 1989; Zelinsky, 2005). For example, Kazemi, Gamberale-Stille, Tullberg, and Leimar (2014) investigated the role of stimulus salience for predator learning, and found that prey colour had a stronger influence on the rate of predator learning than the pattern and the shape of colour pattern elements. However, little is known about whether, and how, phenotypic diversity among potential prey may affect the visual search performance of predators. Yet, illuminating this issue is important because any effects of variation in size and colour pattern on detection and perception can impact behavioural and evolutionary interactions between visually oriented predators and their camouflaged prey.

In a series of previous studies, we have used computer-based detection experiments with human subjects acting as 'predators' searching for 'prey' in the form of photographs of colour polymorphic *Tetrix subulata* grasshoppers inserted into images of their natural background. In brief, these previous experiments have demonstrated that (1) probability of detection depends on target colour pattern (Karpestam et al., 2014b, 2013), (2) the relative protective value of colour patterns changes with the visual background (Karpestam et al., 2012) and with target size (Karpestam, Merilaita, & Forsman, 2014a) and (3) variation in colour pattern among targets (colour polymorphism) impairs search performance and decreases detection rate (Karpestam et al., 2014b, 2016). Because *T. subulata* males are larger than females and colour morph frequencies differ between the sexes (Forsman, 2018), we investigated in a recent study the effect of body size on detection risk of colour morphs and on colour morph frequencies. We found that prey size can differently influence detection of different colour patterns (Karpestam et al., 2014a). It is known that shapes of a specific size presented during a learning phase are more easily remembered and recognized if they remain the same size during the test phase (Jolicoeur, 1987; Milliken & Jolicoeur, 1992). Therefore, in the present study we focused on the effect of variation in size: the question of whether variation in size per se among different prey (as often exists in prey populations) impairs detection (as does variation in colour pattern, reviewed in Karpestam, Merilaita, & Forsman, 2016) has not been previously addressed.

Accurate assessment of prey body size allows predators to evaluate both the rewards and the costs associated with initiating an attack. Larger prey contain more nutrients and energy, but may also be more likely to inflict costs associated with a more difficult capture or greater risk of injury (e.g. Cooper & Stankowich, 2010; Forsman, 1996). The size of a prey and whether it deviates from the size of other potential prey individuals in a group may also influence predation risk through the oddity effect (i.e. a deviating prey being singled out in a group and targeted by a predator, Landeau & Terborgh, 1986; Morse, 1970; Rodgers, Ward, Askwith, & Morrell, 2011; Theodorakis, 1989). Correct assessment of prey size is therefore important for predators' decision making and foraging success. Conversely, biased decisions due to incorrect assessment of size may favour the prey by decreasing probability of attack. Psychological experiments have shown that colour and pattern can influence perception of the size of visual targets (Gundlach &

Macoubrey, 1931; Ling & Hurlbert, 2004; McClain et al., 2014). This raises the possibility that biases in perceived size have the potential to modify the degree to which detection of prey is impaired by true size variability. If such moderating effects on perception depend on colour pattern, this can be of importance for ecological and evolutionary interactions and processes. Yet, it has not been established whether natural colour patterns of prey differently influence size perception.

The knowledge gap regarding the interactive effect of body size and colour pattern on perception is unsatisfying, because natural predators commonly encounter prey of various sizes owing to sexual size dimorphism, age differences and feeding history (Forsman, 1995; Forsman & Appelqvist, 1999; King, 1987). On a more general note, improved knowledge of how variation in different phenotypic dimensions impacts the perception of and interactions between different individuals can further the understanding of the evolution of biodiversity. Here, we present two experiments addressing these questions.

Our first aim in the present study was to test the hypothesis that size variability reduces detection of otherwise similar prey in serial encounters. To achieve this, we compared the performances of human subjects that searched for images of pygmy grasshoppers presented on computer screens, in size-variable (large, medium and small) sequences or in size-invariable (all medium) sequences. Our second aim was to test whether and how the colour patterns of pygmy grasshoppers influenced perception of size. To that end, we conducted a second experiment in which human subjects were presented with cards showing pairs of grasshoppers that were of identical size and either belonged to the same or to different colour morphs. Our third aim was to explore whether the effects of size variability on detection were influenced by biases in perceived size. To that end, the outcomes of experiment 1 and 2 were considered together.

METHODS

Equidistant presentation of the prey patterns was crucial for the testing of our hypotheses concerning detectability of prey (experiment 1) and perception of prey size (experiment 2). Further, it was essential that estimates of detectability or size differences were not confounded by differences between predators in motivation, hunger levels, experience, or any acquired preferences or aversions that might influence the decision to attack or ability to successfully capture the prey. For the evaluation of how colour pattern influences perceived size it was also crucial that different prey could be presented simultaneously (experiment 2). We therefore used two-dimensional images to represent the prey and we presented the images to human subjects that represented the 'predators', in two separate experiments.

Experiment 1: Effect of Size Variability on Detection

Methods

To examine whether size variability reduces search efficiency of visually oriented predators and thereby improves the survival prospects of prey individuals that are members of size-variable populations we asked human subjects to search for images of grasshoppers inserted into photographs of their natural habitat. The approach used for the computer-based experiment was similar to what we have used in our previous studies designed to address related questions (Karpestam et al., 2012, 2013, 2014a, 2014b, 2016).

Using humans as substitutes for real predators in detection experiments is an increasingly common approach to studying the function and evolution of protective coloration (see Fig. 1 in Karpestam, Merilaita, & Forsman, 2013). One reason for this is that direct observations of natural predation events are typically rare.