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Original article

Adaptive colour polymorphism of *Acrida ungarica* H. (Orthoptera: Acrididae) in a spatially heterogeneous environment

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ABSTRACT

Intra-specific colour polymorphism provides a cryptic camouflage from predators in heterogeneous habitats. The orthoptera species, *Acrida ungarica* (Herbst, 1786) possess two well-distinguished colour morphs: brown and green and displays several disruptive colouration patterns within each morph to improve the crypsis. This study focused on how the features of the background environment relate to the proportion of the two morphs and to the intensity of disruptive colouration patterns in *A. ungarica*. As the two sexes are very distinct with respect to mass and length, we also distinctively tested the relationship for each sex. In accordance with the background matching hypothesis, we found that, for both sexes, the brown morph was in higher proportion at sites with a brown-dominant environment, and green morphs were in higher proportion in green-dominant environments. Globally, individuals in drier sites and in the drier year also had more intense disruptive colouration patterns, and brown morphs and females were also more striped. Colour patterns differed largely between populations and were significantly correlated with relevant environmental features. Even if *A. ungarica* is a polymorphic specialist, disruptive colouration still appears to provide strong benefits, particularly in some habitats. Moreover, because females are larger, they are less able to flee, which might explain the difference between sexes.

1. Introduction

Prey species have evolved a large diversity of strategies to limit predation, among which the most common are active escape and cryptic colouration (Forsman and Appelqvist, 1998). Which strategy evolves in a specific context will depend on the habitat background as well as on the biological constraints of the organism (e.g., mass, body shape, flight organs). The various evolved strategies, however, are not mutually exclusive alternatives: many grasshopper species, for instance, have developed in parallel both an efficient crypsis and the ability to escape by jump or flight once discovered.

Crypsis, i.e., resemblance to the background environment, can be achieved either by general background matching (Ahnesjo and Forsman, 2006; Stevens and Merilaita, 2009) or by disruptive colouration (Silberglied et al., 1980; Stevens and Merilaita, 2009). In the case of background matching, individuals evade predation by mimicking the colour or other features of the environment they inhabit. As a consequence, predators that hunt by sight have greater difficulty distinguishing prey from the background. Hence, the efficiency of crypsis should depend on the degree of resemblance of the prey's colouration to the background features. For example, Fuller and Joern (1996) showed experimentally that grasshopper species tend to be less susceptible to predation in areas that are most similar to their naturally chosen microhabitats, and Ahnesjo and Forsman (2006) found that different genetic colour morphs of the pygmy grasshopper, *Tetrix undulata*, select substrates that reduce predation risks.

Apart from background matching, a large number of grasshopper species display variation in points and stripes along the body, called disruptive colouration, which improves their camouflage by breaking up the body into a series of apparently unrelated objects (Cott, 1940; Silberglied et al., 1980; Sandoval, 1994; Stevens and Cuthill, 2006; Stevens and Merilaita, 2009). Because the combination of disruptive colouration and crypsis works better than either one alone, disruptive colouration is an efficient improvement to the crypsis by background matching (Cuthill et al., 2005; Stevens et al., 2006). Additionally, a disruptive pattern alone can have a significant effect independently from colour morph (Schaefer and Stobbe, 2006).

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Disruptive colouration works on a higher diversity of visual backgrounds than background matching, and, thus, it might allow greater survival in heterogeneous habitats and enable individuals to forage in more diverse places (Ruxton et al., 2004; Sherratt et al., 2005). This is highly advantageous compared to developing a unique strong crypsis which reduces the risk of predation but constrains the prey species to a very few specialized habitats (Merilaita et al., 1999; Ruxton et al., 2004). Crypsis in a heterogeneous habitat may be achieved by compromising the degree of crypsis between diverse microhabitats and alternatively improving it in one of the microhabitats at the expense of the others (Merilaita et al., 1999). Or it may be achieved more efficiently by developing intra-specific, locally adapted polymorphisms (Eterovick et al., 1997). Colour polymorphism, however, may also be maintained by predation through aposematism. Predators may build a search image of the most common prey, which should provide frequency-dependent benefits for rare morphs (Rand, 1967). This selective attention leads to frequency-dependent selection, favouring rarer forms and, thus, maintaining polymorphism (Bond, 2007).

These two mechanisms differ in several aspects. Apostatic selection relies crucially on genetic polymorphism, and it maintains diversity at a within-habitat scale through frequency-dependent selection (independently of the habitat background). In contrast, the polymorphism maintained by spatial heterogeneity may also rely on phenotypic plasticity. In this case, polymorphism will mostly accrue among habitats, such that colour patterns are expected to co-vary with environmental features. Patterns of covariance, however, should be modulated with specific behaviours, particularly by patterns of dispersal among populations, as well as by the active search of cryptic microhabitats. In particular, prey should favour areas in which their colouration confers strong crypsis (Ergene, 1952; Sandoval, 1994; Eterovick et al., 1997; Ahnesjo and Forsman, 2006) while avoiding habitats where they have low performance. For example, the larvae of *Acrida turrita* have been shown to prefer habitats matching their body colour (Ergene, 1952).

The current study investigates the colour-morph and disruptive-pattern polymorphisms in *Acrida ungarica* (Herbst, 1786) in a heterogeneous habitat. This species presents two distinct colour morphs (green and brown), both showing a continuous variance in disruptive colouration levels. We tested whether to proportions of the two colour morphs varies with environments (expressed in terms of vegetation composition, aspect and cover) and with sex. We also investigated the variation of the intensity of disruptive colouration according to the environment as well as to the sexes and morphs of the individuals. From the background matching hypothesis, we expected

1) The variance in colouration would take place among, rather than within, populations.
2) The among-population variance would be correlated with environmental features, and, in particular, the proportion of brown morphs would increase with the dominance of brown grasses and bare soil.
3) The relationship in females would be greater than in males because owing to their larger size, they are more profitable to predators, less cryptic, and less able to escape by flight.

2. Methods

2.1. Target species

Acrida ungarica (Acrididae, Orthoptera) is a large grasshopper living in open grasslands of Southern Europe and two subspecies are actually recognized: *Acrida u. ungarica* from south-eastern Europe and *Acrida u. mediterranea* in south-western Europe (Harz, 1975). With a total length of 65–75 mm from the head to the end of the wings, females are much larger than males (35–45 mm). Two colour morphs, green and brown, are distinguished, and the wings and the body of individuals have varying levels of disruptive colouration, which mainly comprises stripes and dots of different intensities of black, pink and white (Fig. 1).

2.2. Study area and field sampling

Our study sites are situated on the Bulgarian shore of the Black Sea in south-eastern Europe. Several types of grassland occur there, and the type of grassland varies according to the soil properties and the availability of water to the vegetation. We classified grasslands into three categories: 1) *sand meadows*, vegetation associations on drained sand dunes and beaches characterised by the presence of

Fig. 1. Pictures of two females of *Acrida ungarica* in their habitats where they are most cryptic: the brown morph (a.) and the green (b.). The patterns of disruptive colouration are also distinguishable along the body of the two individuals (Pictures credit: Nicolas Perrin) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).