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Indirect effects of prey coloration on predation risk: pygmy grasshoppers versus lizards

Emilio Civantos,[1]* Jonas Ahnesjö,[2] Anders Forsman,[2] José Martín[1]
and Pilar López[1]

[1]*Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC),*
c/ José Gutiérrez Abascal 2, 28006 Madrid, Spain and
[2]*Department of Biology and Environmental Science,*
Kalmar University, 391 82 Kalmar, Sweden

ABSTRACT

Because body temperature influences the physiology, behaviour and performance of ectothermic organisms, thermal conditions might influence the frequency and outcome of predator–prey interactions. Furthermore, differences in colour pattern among prey individuals may *indirectly* influence predation risk, through effects of coloration on body temperature. We performed staged encounters between lizards (*Psammodromus algirus*) and grasshoppers (*Tetrix subulata*). We painted the dorsal surface of grasshoppers either black or grey to manipulate their body temperature and behaviour, and exposed them to predation under two different thermal conditions (sun and shade). Grasshoppers were less active in the presence of a lizard, suggesting that they modified their behaviour to avoid detection. Lizards were more active and attacked the grasshoppers more frequently in the sun than in the shade. However, the proportion of unsuccessful attacks did not differ between sun and shade, suggesting that thermal environment did not influence the relative performance of predators and prey. In the sun, black grasshoppers were more active and tended to be attacked more frequently than grey ones, albeit not significantly so. However, mortality did not differ between black and grey individuals. This suggests that an elevated activity need not translate into increased predation if accompanied by enhanced escape performance. Conversely, individuals may compensate for a poor escape performance associated with low body temperatures by reducing activity. Our findings suggest that selection imposed by predators may favour certain combinations of prey coloration and behaviour, and that colour polymorphism in ectotherms may be influenced also by indirect effects of coloration on predation risk. Counter to intuition, the existence of such indirect effects raises the possibility that the evolution of prey coloration may be governed by selection imposed also by colour-blind or even totally blind predators.

Keywords: activity, coloration, grasshoppers, lizards, predation, prey, temperature.

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* Author to whom all correspondence should be addressed. e-mail: e.civantos@mncn.csic.es

INTRODUCTION

Predation may have pervasive effects on several traits in prey animals, influencing morphology, physiology, life-history characteristics, colour patterns and behaviours, such as the level and temporal patterning of activity (e.g. Cott, 1940; Edmunds, 1974; Curio, 1976; Endler, 1986, 1991, 1995; Lima and Dill, 1990; Skelly and Werner, 1990; Anholt and Werner, 1995; Lima, 1998). Activity is generally associated with an elevated risk of predation, mainly because moving individuals are more likely to be encountered and detected by visually oriented predators, compared with motionless individuals (Wassersug and Sperry, 1977; Ramcharan and Sprules, 1991; Martel and Dill, 1993; Skelly, 1994; Anholt and Werner, 1995; Brown, 1999, but see Houtman and Dill, 1994). There also is ample evidence to suggest that the risk of detection and predation is influenced directly by prey coloration. Whether a certain colour pattern will increase or decrease probability of detection is dependent upon the properties of the visual background against which the prey is viewed, and the perceptual and cognitive abilities of the viewer (Isley, 1938; Cott, 1940; Endler, 1986, 1991; Merilä *et al.*, 2001). The relative protective value of alternative colour patterns may therefore also vary depending on prey behaviours, such as microhabitat selection, movement patterns and body orientation (Isley, 1938; Schultz, 1981; Endler, 1991; Brodie, 1992; Sandoval, 1994; Forsman, 1995; Forsman and Appelqvist, 1998; Cuadrado *et al.*, 2001). Theory posits that if prey coloration and a behavioural or morphological trait interactively influence risk of detection and susceptibility to predation, then selection will promote functional integration and the evolution of genetic correlations between loci influencing the two traits (e.g. Cheverud, 1982; Lande and Arnold, 1983; Lande, 1984).

In addition to directly and interactively influencing the risk of being detected by predators, one might expect prey colour pattern to have *indirect* effects on predation risk. Such indirect effects should be particularly important in ectothermic organisms (such as insects and reptiles). The reason is that the body temperature of ectothermic organisms typically is highly variable and affects many important aspects of the physiological and behavioural repertoire of individuals, including locomotion and predator avoidance behaviours (e.g. Bennett, 1980, 1984; Christian and Tracy, 1981; Avery *et al.*, 1982; Huey and Hertz, 1984; Huey and Kingsolver, 1989; Forsman and Appelqvist, 1998; Forsman, 1999a,b). Moreover, ectotherms rely upon external radiant energy to achieve body heating (e.g. Casey, 1981; Heinrich, 1993; Peterson *et al.*, 1993), and individuals belonging to different colour variants differ in their ability to attain and maintain body temperature within a range yielding optimal performance (e.g. Watt, 1968; Kingsolver and Watt, 1983; DeJong *et al.*, 1996; Forsman, 1997). Differences in thermal properties mediated via coloration are therefore predicted to translate into differential performance (e.g. Digby, 1955; Willmer, 1991; Adolph and Porter, 1993; DeJong *et al.*, 1996; Forsman, 1999a; Forsman *et al.*, 2002).

Here we report on an experimental test of the hypothesis that the coloration of prey animals may indirectly influence susceptibility to predation, through effects of colour pattern on body temperature, behaviour and performance. In the experiments, pygmy grasshoppers were used as prey and lizards as predators. To induce a difference in coloration (and hence in body temperature and behaviour) between prey individuals, we experimentally manipulated the phenotypes of grasshoppers by painting the dorsal surface of their pronotum either black or grey (see also Forsman and Appelqvist, 1998, 1999). We have previously shown that individuals painted black and grey experience differences in warming up rates and asymptotic body temperatures that are similar to those observed between naturally black and grey colour morphs (Forsman *et al.*, 2002). We then compared the relative susceptibility of black and grey grasshopper individuals when exposed simultaneously to predation by lizards. To separate the *direct* influence of coloration on detectability from the *indirect* effects of prey coloration mediated via differential body temperature, behaviour and escape capability, trials were performed both in the sun (where individuals painted black and grey experienced different body temperatures) and in the shade (where body temperature was lower than in the sun treatment but similar in black and grey individuals; see Forsman, 2001). Under this experimental set-up, any difference in predation on black and grey individuals in the shade treatment can be attributed to differences in relative crypsis, whereas differences in the sun treatment will reflect the combined effect of relative crypsis and behavioural differences between black and grey individuals. Consequently, indirect effects of coloration (if present) will be manifested as a difference in outcome between trials performed in the sun and shade.

It has previously been shown that pygmy grasshoppers subjected to predation from domestic chicks experienced significantly greater escape rates at high than at low ambient and body temperature (Forsman and Appelqvist, 1998). However, ectothermic prey may not necessarily enjoy an enhanced escape performance under warmer conditions, because the foraging performance of the predator also may improve with higher temperatures (Avery *et al.*, 1982; Bozinovic and Vásquez, 1999; Kilpatrick, 2003). Because ectothermic animals (lizards) were used as predators in these experiments, we predicted no difference in overall escape rate of grasshoppers between trials performed in the sun (where both predator and prey will experience high body temperatures) versus shade (where both predator and prey will experience low body temperatures).

MATERIALS AND METHODS

Animals and housing conditions

We used *Tetrix subulata* as prey, a small (up to 14 mm body length, 0.07 g), short-limbed, diurnal pygmy grasshopper that is characterized by a long pronotum and is widely distributed in Europe (Holst, 1986). It lives on the surface of the soil where it feeds on moss, algae and humus. *Tetrix subulata* exhibits genetically based discontinuous variation in colour and pattern of the pronotum: within a single population, individuals may vary from black, through yellowish-brown to light grey (Holst, 1986; Forsman *et al.*, 2002).

We collected adult female *T. subulata* in April 2001 from a wet meadow outside ‘El Ventorrillo’ Field Station, located in a mountainous area (1500 m above sea level) in central Spain (50 km from Madrid). Individuals were brought to the laboratory at the field station where they were housed in plastic cages (measuring 30 × 20 × 20 cm) at room temperature and given a mossy piece of cotton and slice of fresh potato as food (Forsman, 2001).

We manipulated colour pattern of grasshoppers to identify the mechanism responsible for the differences in behaviour between grey and black individuals in the experiments and to influence the capacity to achieve body heating under sun/shade conditions used during the experiments. To avoid any confounding effects of genetic correlations between colour pattern and behaviour (Brodie, 1989; Forsman *et al.*, 2002), all individuals used in the experiments belonged to the brown natural colour pattern. Any difference in behaviours between individuals painted black or grey thus can be ascribed to a modification of behaviours in response to heating rates and body temperature (Forsman *et al.*, 2002). Each individual was randomly assigned to one of the two paint treatments (grey or black) and colour patterns were manipulated by painting the dorsal side of the pronotum either uniformly grey or black using water-based modelling paint (Humbrol Fantasy, Humbrol Ltd, Marfleet, Hull, UK). Grasshoppers did not appear to suffer from the paint treatment; there were no signs of necrosis or abnormal behaviours (see also Forsman and Appelqvist, 1998, 1999). Painting grasshoppers black or grey significantly affects their heating rates and asymptotic body temperature when exposed to radiation (Forsman *et al.*, 2002), and body temperature has been shown to influence jumping performance, reaction distance and the propensity to use wings during escape (Forsman, 1999a,b).

As predators we used *Psammodromus algirus*, a medium-sized (adult snout-to-vent length 65–90 mm), terrestrial, diurnal, oviparous lacertid lizard (Civantos and Forsman, 2000) that inhabits the Iberian Peninsula, southern France and northwestern Africa (Pérez-Mellado, 1998). *Psammodromus algirus* is an active foraging lizard that actively searches for a variety of arthropod prey. It is a shuttling heliotherm whose microhabitat selection is strongly related to thermoregulatory behaviour (Díaz, 1994).

Adult *P. algirus* lizards were captured in April 2001 by noose in a deciduous oak forest located near Navacerrada, at the same mountain area in central Spain where the grasshoppers were captured. All lizards were housed together in a single cage in the laboratory without food but with water *ad libitum*. Each lizard and grasshopper was only used once.

Predation trials

The experiments were conducted at ‘El Ventorrillo’ Field Station between 11.00 and 17.00 h during April 2001. Experimental enclosures consisted of two terrariums (one for each treatment) measuring 40 × 30 × 60 cm. The floor of the terrarium was covered with rough paper that provided friction for take-off and prevented the grasshoppers from sliding after landing. The paper was painted in black and grey squares (10 × 15 cm) at the same proportion to ensure that both black and grey grasshoppers had equal probability to achieve crypsis (i.e. matching backgrounds).

Before the experiment, the cages with grasshoppers and lizards were moved outdoors. Then, one lizard and one black and one grey grasshopper were placed inside the terrarium 30 min before the onset of the trial to allow the experimental animals to habituate. The grasshoppers were initially placed underneath a holed petri dish to avoid them being eaten before the onset of the trial. During acclimation, grasshoppers under the petri dish had access to shade in the ‘sun’ treatment. After 30 min, the grasshoppers were released by removal of the petri dish. Each trial lasted for 15 min or until the first grasshopper was eaten (i.e. a mixed stopping rule).

We performed trials in the sun and shade treatments simultaneously to avoid confounding effects of cyclical daily changes in position of the sun, wind speed and temperature. To manipulate the thermal environment inside the experimental cage, we placed each terrarium either in a sunny or shaded location outside. To ensure that the thermal environment of the terrariums placed in the sun or shade was different, temperature inside the terrarium was measured at the beginning and end of each trial to obtain a range and average of the temperature during the trial. We measured the temperature with a probe resting on the terrarium floor – that is, surface temperature rather than air temperature. The surface temperature inside the terrarium was higher in the sunny area (mean ± standard error = 38.6 ± 0.5°C; range 32.8–46.7°C) than in the shaded area (16.6 ± 0.5°C; range 10.5–23.3°C). These values are within the range of surface temperatures measured in the area of location of free-ranging *P. algirus* lizards during the activity hours (unpublished data). Furthermore, operative temperatures measured during the activity hours of free-ranging *P. algirus* lizards ranged from 20.6 to 47.4°C (Díaz, 1997). Behavioural observations of pygmy grasshoppers in a laboratory thermal gradient have further revealed that body temperature selected by *T. subulata* ranged from 21 to 44°C among individuals, with significant differences between the sexes and among colour morphs (Forsman, 2000). Moreover, measurements of surface temperature at the point of location of free-ranging pygmy grasshopper individuals in the field averaged 28.0°C (standard deviation = 9.43°C) and ranged from 10.3 to 55.2°C (J. Ahnesjö and A. Forsman, unpublished). Experimental animals also did not show any sign of abnormal behaviours or stress during the trials. Collectively, this suggests that the temperatures inside the terrariums were non-stressful and ecologically relevant.

Four 'control' trials without predators were used for each treatment to measure the activity of grasshoppers (black and grey) in the absence of lizards. These control tests were performed in the same experimental enclosures used for the predation trials. Experiments were recorded on videotape (Hi-8 format, 25 frames per second) using a Sony CCD-V800E video-camera aligned perpendicularly over the terrarium, to enable subsequent more detailed analyses of predator–prey interactions.

To avoid possible confounding effects of predator body size, we selected individuals so that snout-to-vent length did not differ between lizards used in the sun (77.4 ± 1.05 mm) and shade (79.1 ± 1.12 mm) treatment (analysis of variance: $F_{1,44} = 1.12$, $P = 0.29$). Similarly, to avoid possible confounding effects of prey body size, we selected grasshoppers of similar size (pronotum length) for the grey (11.21 ± 0.07 mm) and black (11.19 ± 0.09 mm) paint treatment ($F_{1,90} = 0.03$, $P = 0.86$).

For each trial we recorded the sequence (time and order) of attacks on grey and black grasshoppers and if the attack was unsuccessful (i.e. if the grasshopper escaped) or successful (i.e. if the grasshopper was eaten). We also recorded the proportion of attacks on each colour that was unsuccessful, and the total number of attacks on each morph. No behaviours were recorded after the first grasshopper had been eaten.

To quantify and compare activity of prey in the two treatments, we calculated an activity index of grey and black grasshoppers based on information from the first 100 s of each trial. The 100 s recording session was divided into 10 s sample intervals. For each sample interval, we recorded if the grasshopper moved or remained motionless. Behavioural observations of lizards were conducted using the instantaneous sampling method. Each trial was divided into 30 s sample intervals, and every 30th second we recorded if the lizard was moving or not moving (one-zero sampled; Altmann, 1974). From these data we computed the percentage of time spent moving. The observations of lizards continued either until both grasshoppers had been eaten or for the entire duration of the trial (15 min). Both of these indices provide a frequency of activity or movements. We used different methods to measure activity in grasshoppers and lizards because the two species differ in behaviour, with lizards in general being more mobile than grasshoppers.

Statistical analyses

All variables used in the analyses of variance (ANOVA) were transformed (square root or natural logarithms) to make the data normally distributed and achieve homogeneity of variances. Data were analysed using two-way ANOVA with interaction, with paint treatment and thermal environment as independent variables. When the interaction was significant, separate analysis was performed on data for the sun and shade treatments to test for differences between black and grey individuals. In those cases where the assumptions of the parametric ANOVA were violated, the data were analysed using non-parametric tests.

RESULTS

Lizards were significantly more active in the sun (42 ± 4%) than in the shade (31 ± 3%) ($F_{1,44} = 5.1$, $P = 0.029$). This shows that our attempt to experimentally influence predator activity by performing trials under different thermal conditions was successful.

Grasshoppers maintained in cages together with a lizard were significantly less active than those maintained in cages without a lizard, both in the sun (pooled colours: $F_{1,46} = 29.2$, $P < 0.0001$; grey individuals: $F_{1,26} = 56.6$, $P < 0.0001$; black individuals: $F_{1,26} = 15.9$, $P < 0.0001$) and in the shade (pooled colours: $F_{1,50} = 33.7$, $P < 0.0001$; grey individuals: $F_{1,28} = 27.1$, $P < 0.0001$; black individuals: $F_{1,28} = 26.2$, $P < 0.0001$) (Fig. 1). Thus, all grasshoppers independently of colour treatment and temperature decreased their activity in the presence of a lizard, presumably to reduce the risk of being detected and attacked by nearby predators.

Moreover, the activity of grasshoppers did not differ significantly between the sun and shade treatments (two-way ANOVA with interaction, main effect of thermal environment:

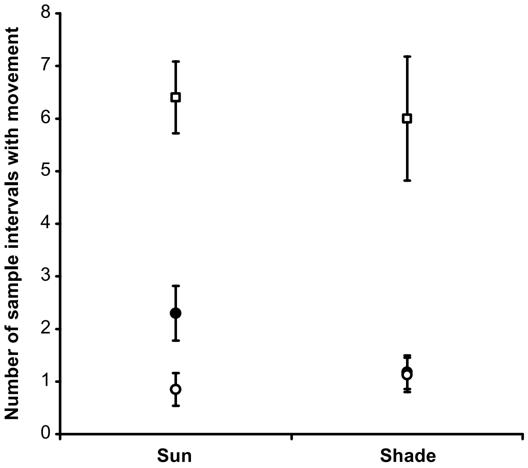

Fig. 1. Activity of grasshoppers painted black (filled circles) or grey (open circles) in the presence of a lizard under sunny and shaded conditions. The figure also shows activity of grasshoppers in the absence of lizards (pooled data for black and grey: squares). Activity was measured as the mean (± standard error) number of 10 s sample intervals in which the grasshopper moved (see text for details).

$F_{1,80} = 0.90$, $P = 0.34$) (Fig. 1). However, the effect of paint treatment on activity of grasshoppers seemed to be dependent upon thermal environment (effect of interaction between thermal environment and paint treatment: $F_{1,80} = 3.28$, $P = 0.07$), with black individuals being more active than grey ones in the sun ($F_{1,38} = 5.6$, $P = 0.023$) but not in the shade ($F_{1,42} = 5.6$, $P = 0.9$) (Fig. 1). This confirms that our experimental manipulation of grasshopper coloration influenced their behaviour only when they were exposed to solar radiation.

The number of trials in which at least one of the grasshoppers was attacked was higher in the sun (21 of 23 trials) than in the shade (9 of 23) ($\chi^2_1 = 13.8$, $P = 0.0002$). The distribution of the number of first attacks directed towards black and grey individuals did not differ significantly between trials performed in the sun and shade (Fisher's exact, $P = 0.30$). In the sun treatment, the black grasshopper was attacked first in 13 trials and the grey grasshopper in 8 trials (two-tailed binomial test, $P = 0.38$). In the shade treatment, the black individual was attacked first in 5 trials and the grey individual in 4 trials. These results suggest that the risk of being attacked was dependent on thermal environment but independent of paint treatment.

The mean number of attacks was higher in the sun than in the shade (two-way ANOVA with interaction, main effect of thermal environment: $F_{1,88} = 22.7$, $P < 0.0001$) (Fig. 2a). However, there was also a significant effect of the interaction between thermal environment and prey colour on number of attacks (effect of interaction: $F_{1,88} = 4.40$, $P = 0.039$). This interaction reflected the fact that black individuals tended to suffer a higher number of attacks than grey ones in the sun treatment ($F_{1,44} = 3.9$, $P = 0.054$), but not in the shade treatment ($F_{1,44} = 0.69$, $P = 0.41$) (Fig. 2a).

Not all attacks resulted in the grasshopper being captured and eaten by the lizard. The proportion of attacks in which the grasshopper was able to escape did not differ significantly between the two thermal environments (Wilcoxon two-sample test, $z = 1.21$, $P = 0.22$) (Fig. 2b). The proportion of attacks that were unsuccessful also did not differ between black and grey individuals, either in the sun (Wilcoxon two-sample test, $z = -0.38$, $P = 0.7$) or in the shade treatment ($z = 1.74$, $P = 0.08$) (Fig. 2b). This lack of difference in unsuccessful attacks between black and grey individuals in the sun treatment is surprising, given that black individuals did not suffer a higher mortality than grey individuals (see below) despite being attacked more often (see above). However, restricting the comparison to only those individuals in the sun treatment that were eventually eaten ($n = 13$) suggests that lizards had to make more attacks, on average, to capture black (3.1 ± 0.55) compared with grey (2.5 ± 0.56) individuals.

The distribution of alternative outcomes (i.e. no grasshopper eaten, black individual eaten, grey individual eaten) differed significantly between trials performed in the sun and shade (Fisher's exact, $P = 0.0028$). Overall, fewer grasshoppers were eaten in the shade (in 3 of 23 trials) than in the sun (13 of 23 trials) (Fisher's exact, $P = 0.0045$). In the sun treatment, an almost equal number of black ($n = 7$) and grey ($n = 6$) individuals were first eaten, whereas in the shade only 3 grey individuals and no black individuals were eaten (Fisher's exact, $P = 0.21$).

In the shade treatment, temperature inside the cage was negatively correlated with time to first attack ($n = 13$, $r_s = -0.76$, $P = 0.002$) but not with proportion unsuccessful attacks ($n = 13$, $r_s = -0.19$, $P = 0.53$). In the sun treatment, none of the correlations was statistically significant (proportion unsuccessful attacks: $n = 32$, $r_s = -0.03$, $P = 0.87$; time to first attack: $n = 32$, $r_s = -0.01$, $P = 0.95$; time to being eaten: $n = 13$, $r_s = -0.07$, $P = 0.82$).

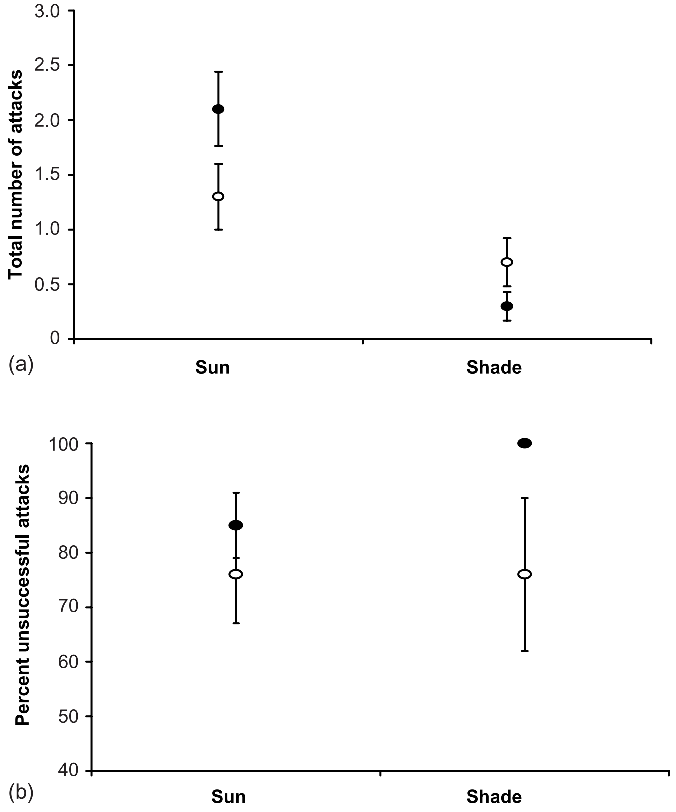

Fig. 2. Outcome of staged predator–prey interactions between lizards and grasshoppers painted either black (filled circles) or grey (open circles). In each trial, one black and one grey grasshopper was simultaneously exposed to predation from a lizard. Trials were performed both under sunny and shaded conditions (see text for details). (a) Total number of attacks (mean ± 1 standard error) towards black versus grey individuals. (b) Percentage of attacks (mean ± 1 standard error) in which the grasshopper was able to escape.

DISCUSSION

Most studies on predator–prey interactions assume a constant or fixed predator behaviour, which may result in erroneous conclusions (see review in Lima, 2002). In the present study, we influenced predator behaviour by conducting predation trials under different thermal conditions. In the sun treatment, the lizards were warmer and more active and, therefore, potentially more dangerous as predators, in comparison with the shade treatment. Thus, lizards attacked the grasshoppers more frequently in the sun than in the shade (Fig. 2b). Furthermore, the time interval to first attack decreased with increasing temperature inside the cage in the sun treatment. The manipulation of grasshopper colour patterns also translated into differential behaviour, as evidenced by the higher activity of black compared with grey individuals in the sun treatment. The outcome of these predator–prey interactions, therefore, is likely to provide an accurate reflection of the indirect effects of prey coloration on susceptibility to predation.

In line with the findings of many previous studies (e.g. Skelly and Werner, 1990; Skelly, 1994; Anholt and Werner, 1995; Richardson, 2001), grasshoppers adjusted their behaviour and became less active in the presence of a predator. This reduced activity appears to be an adaptive response, because activity increased the risk of being detected and attacked. Thus, in the sun treatment, where black individuals were more active than grey individuals, lizards tended to direct their first attack more often towards the black than the grey individual. In the shade treatment, where black and grey individuals were equally active, no such tendency was evident. Collectively, this suggests that the higher attack rate on black than on grey individuals reflected a difference in body temperature and behaviour, rather than a direct effect of relative crypsis. The fact that only the dorsal side of the grasshoppers was painted, and that lizards were almost at eye-level with the grasshoppers, also suggests that differences in crypsis were of little importance.

There is some evidence that prey individuals are able to balance the costs and benefits of alternative avoidance behaviours and respond differently to abundant, active or otherwise efficient predators than to less dangerous ones (e.g. Peckarsky, 1980; Soluk and Collins, 1988; Dickman, 1992). The lack of difference in activity of grasshoppers between the sun and shade treatments may reflect such a flexible anti-predator response. In the sun treatment, the grasshoppers presumably experienced higher body temperatures than in the shade (Forsman *et al.*, 2002) and, consequently, should have been more active (Forsman, 1999a,b). One possible explanation is that the presence of ectothermic lizard predators also makes the sun treatment a high-risk environment. The increased effectiveness of muscular contraction and neuromuscular coordination at higher temperatures (Putnam and Bennet, 1982) is known to result in higher sprint speeds (Bennett, 1980) and an improved ability of lizards to capture prey (Avery *et al.*, 1982; Van Damme *et al.*, 1991; Díaz, 1994). That the grasshoppers were not more likely to survive after being attacked under high than low temperatures, despite a better jumping performance (Forsman, 1999a,b), may thus reflect the fact that the foraging performance of the predator also increased with higher temperature. This result differs from that of a previous investigation (Forsman and Appelqvist, 1998), in which pygmy grasshoppers exposed to predation from domestic chicks (i.e. endothermic predators) were found to experience a significantly greater escape rate at high than at low temperatures. This illustrates the need to consider how predators behave under different conditions given their own limitations (see Lima, 2002). Temperature-dependent predation risk may also affect lizards. In fact, previous studies of the foraging behaviour of *P. algirus* suggest that this species may maximize energy intake by capturing large prey, thus decreasing the number of pursuits (Díaz and Carrascal, 1993) and possibly the probability of being detected by predators (Lima and Dill, 1990; Martín and Avery, 1997).

The physical condition, agility and vulnerability of the prey individual itself also may determine what defence tactics should be adopted (Endler, 1991). For instance, whether to freeze or flee is likely to be the most appropriate strategy for the prey probably depends on its speed of locomotion (Bauwens and Thoen, 1981; Martín and López, 1995). Although immobility appears to be a useful defensive behaviour, provided that predators rely on sensory modes that detect motion (Edmunds, 1974; Endler, 1986), the difference in activity between grey and black painted grasshoppers within the sun treatment was not accompanied by a difference in mortality rate. Previous investigations have uncovered that individuals painted black warm up faster and attain higher equilibrium body temperatures when subjected to augmented illumination, compared with paler individuals (Forsman *et al.*, 2002). The greater activity of black compared with grey individuals may thus partially reflect the fact that they need to actively thermoregulate to avoid overheating (Forsman *et al.*, 2002), and thereby induce a higher rate of predatory attacks. However, performance trials conducted in different thermal conditions have shown that both reaction distance and jumping performance of grasshoppers improve with increasing body temperature (Forsman, 1999a,b). Thus, as a result of the superior ability to avoid being captured, the higher activity of black individuals in the sun treatment did not translate into a higher predation rate. On the other hand, the relatively poor performance associated with the lower body temperature of grey individuals also was not manifested as a higher predation rate, because as a result of their inactive behaviour grey individuals avoided detection and tended to suffer fewer attacks than black individuals. Collectively, our results suggest that increased activity is not necessarily associated with an elevated predation risk, if the increased probability of detection is accompanied by an enhanced ability to escape. Conversely, a prey individual may compensate for the potential costs associated with a low body temperature and escape performance by reducing activity and thereby decreasing the risk of detection. Interestingly, the lack of a difference in mortality between individuals painted black or grey suggests that these two alternative strategies were equally effective. Thus, one might expect intermediate behaviours to be selected against, and that there exists a threshold temperature where activity increases from low to high, and that this threshold varies among colour morphs due to their different thermal sensitivities.

In conclusion, our results support the notion that selection imposed by predators may favour certain combinations of prey coloration and behaviour (e.g. Brodie, 1992; Forsman and Appelqvist, 1998, 1999; Martín and López, 1999). Theory posits that such correlational selection will promote functional integration and the evolution of genetic correlations between loci influencing different kinds of traits (e.g. Cheverud, 1982; Lande and Arnold, 1983; Lande, 1984). In line with this, previous researchers have reported both phenotypic and genetic correlations between colour pattern, physiology and behaviour in pygmy grasshoppers (e.g. Forsman, 1999b, 2000, 2001; Forsman *et al.*, 2002). For instance, individuals belonging to grey morphs not only attain lower body temperatures when exposed to illumination, they also select lower temperatures in a laboratory thermal gradient and seem to have lower optimal performance temperatures than darker morphs. Finally, our findings reinforce the notion that the colour polymorphism in pygmy grasshoppers, and possibly other ectotherms, is influenced by selection imposed by predators (e.g. Forsman and Appelqvist, 1998, 1999), albeit sometimes through indirect effects of coloration on performance mediated by differential body temperature. Counter to intuition, the existence of such indirect effects of coloration implies that the evolution of prey colour patterns may be influenced also by selection imposed by colour-blind predators or even predators relying primarily on non-visual cues.

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