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Research article

Differential habitat selection by pygmy grasshopper color morphs; interactive effects of temperature and predator avoidance

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Abstract. Habitat selection behavior is affected by complex interplays between competing requirements. Here we combine field observations with laboratory experiments to examine how thermal benefits and predator avoidance influences habitat selection by different color morphs of the pygmy grasshopper *Tetrix undulata*. The composition of substrate types and surface temperatures in areas selected by free-ranging individuals did not reflect relative availability, and varied among morphs and sexes. Surface temperatures of selected habitats deviated less from the range of preferred body temperatures than would result from a random utilization of surface temperatures, suggesting that grasshoppers selected habitats with thermal properties which were suitable for maintaining preferred body temperatures. The thermal property of habitats occupied by different color morphs suggests that darker morphs (which absorb more solar radiation) selected cooler habitats to avoid overheating. Dissimilarities in substrate use among color morphs in the field and laboratory emphasize a role also of predator avoidance by background matching for habitat choice. The degree of habitat selectivity was lowest in the striped morph, supporting the notion that a disruptive color pattern may constitute a solution to the trade-off between relative crypsis in different visual backgrounds. Finally, individuals modified their habitat use when subjected to elevated risk of predation, showing that habitat choice is governed by conflicting priorities. Collectively, our findings suggest that, as a result of direct and indirect effects of coloration on performance, alternative color morphs use different solutions to the trade-off between competing requirements. Our results also lend support to the notion that relative fitness of alternative color morphs and sexes may be dependent on microhabitat selection, as predicted by the theory of multiple niche polymorphisms.

Key words: behavior, color polymorphism, crypsis, disruptive coloration, habitat selection, Orthoptera, predation risk, thermoregulation, trade-off

Introduction

The importance of factors such as predator avoidance, food, social interaction and thermal benefits for habitat selection have been thoroughly examined in many different species. Although selecting habitats that reduce the risk of predation is likely to be of prime importance (Isley, 1938; Cott, 1940;

Sandoval, 1994), many animals must consider also thermal attributes of the environment (Kingsolver and Watt, 1983; Whitman, 1987; Peterson *et al.*, 1993; Coxwell and Bock, 1995; Brown, 1999; Kilpatrick, 2003). Selecting thermally suitable micro-habitats may be particularly important for ectotherms, such as insects and reptiles, as they depend on external heat sources for temperature regulation (Casey, 1981; Heinrich, 1993; Peterson *et al.*, 1993) and generally have narrow temperature intervals within which physiology, behavior and performance is optimal (Bennett, 1984; Huey and Hertz, 1984; Huey and Kingsolver, 1989; Forsman, 1999a). Studies considering the influence of more than one demand and one environmental factor at a time emphasize the complexity of habitat-selection behavior and the importance of trade-offs between competing requirements (e.g., Christian and Tracy, 1981; Downes and Shine, 1998; Lima, 1998). For instance, microhabitats that provide visually matching backgrounds and protection from predators may lack other important resources (e.g., food, mates, preferred temperatures, Brown, 1999; Merilaita *et al.*, 1999; Pitt, 1999; Shine *et al.*, 2002). If individuals have different preferences and tolerances they are expected to differ also in their choice between conflicting priorities, and hence in habitat selection behavior, a prediction that has been corroborated by comparisons between sexes and age-classes (Schultz, 1981; Schlosser, 1987; King, 1992; Merilaita and Jormalainen, 2000). However, habitat selection behavior may differ also among individuals of the same sex and age.

The theory of multiple niche polymorphism posits that different genotypes should evolve preferences for the microenvironment in which they enjoy the highest fitness (Levene, 1953; see also Halliburton, 2004 and references therein). Studies of color polymorphic populations, in which different phenotypes select different but visually matching substrates, have been interpreted as evidence in support of this notion (e.g., Kettlewell, 1973; Gillis, 1982; Majerus, 1998). In practice, however, this hypothesis is difficult to test because coloration may affect many aspects of individual performance and fitness.

In addition to influencing predation risk, body coloration affects the capability to thermoregulate, with dark individuals warming up faster and attaining higher equilibrium body temperatures than pale phenotypes (Watt, 1968; DeJong *et al.*, 1996; Forsman, 1997). Coloration may thus indirectly affect the performance of an organism, via body temperature (Kingsolver and Watt, 1983; Forsman and Appelqvist, 1998; Civantos *et al.*, 2004). Moreover, although darker individuals are more resistant to ultraviolet radiation (reviewed in Majerus, 1998) they may need to constrain their activity to relatively cool and shaded microhabitats to avoid overheating, whereas paler phenotypes may need to select sun-exposed, warm substrates to obtain sufficiently high body temperatures (Kingsolver and Watt, 1983; Karasov, 1986; Majerus, 1998; Forsman *et al.*, 2002; True, 2003). If we are to understand the complexity of habitat selection behavior we must not only recognize that individuals need to prioritize among conflicting requirements (Downes and Shine, 1998; Lima, 1998; Merilaita and Jormalainen, 1997), but also consider that a single trait may have both direct and indirect effects on an individual's performance. This makes it difficult to predict in which habitats alternative color morphs should obtain the highest fitness, and raises the possibility that differential habitat selection among color morphs may reflect constraints, rather than adaptive intra-population divergence. Sex- or genotype-specific habitat selection may affect the dynamics of polymorphism (Levene, 1953; Hedrick, 1986; Merilaita *et al.*, 1999) and ultimately result in evolution of reproductive barriers and speciation in sympatry (Sandoval, 1994; Dieckmann and Doebeli, 1999; Filchak *et al.*, 2000).

Pygmy grasshoppers (Orthoptera: Tetrigidae) display a discrete genetically based polymorphism for color pattern and thus provide a good model system in these respects. Within a single population individuals may vary from black through yellowish brown to light grey (Holst, 1986). Results from a study based on experimental manipulation of body color of free-ranging pygmy grasshoppers suggest that color *per se* affects vulnerability to predation, presumably due to variation in crypsis (Forsman and Appelquist, 1999). Darker morphs warm up more quickly and achieve higher equilibrium body temperatures when exposed to irradiation, compared to paler morphs (Forsman, 1997), and color morphs differ in behavioral thermoregulation, with pale individuals preferring lower body temperatures and basking more frequently but for shorter periods than darker individuals (Forsman, 2000; Forsman *et al.*, 2002). As in other ectotherms, body temperature influences anti-predator behaviors of pygmy grasshoppers (Forsman, 1999a, b) and individuals experimentally subjected to predation experience greater escape rates at high compared to low temperature (Forsman and Appelquist, 1998; Civantos *et al.*, 2004). Body temperature also affects reproductive performance such as interclutch interval and clutch size (Forsman, 2001) and time to maturity (Ahnesjö and Forsman, 2003). Collectively, these findings suggest that direct and indirect effects of coloration are of considerable ecological importance. However, the role of coloration for habitat selection has not been investigated previously in pygmy grasshoppers.

Here we combine behavioral observations of free-ranging, un-manipulated individuals and laboratory experiments to investigate direct and indirect effects of coloration on habitat utilization by the pygmy grasshopper *Tetrix undulata*. We first test the null-hypothesis that free-ranging individuals use alternative substrate types in proportion to their relative availability. Next, we examine if they prefer or avoid certain surface temperatures, substrate types or background colors. We then test for differences in habitat utilization between sexes and among color morphs. Finally, we test the hypothesis that individuals modify their habitat selection behavior when subjected to an elevated risk of predation.

Methods

Natural history of Tetrix undulata

The pygmy grasshopper *Tetrix undulata* (Sow.) (Orthoptera, Tetrigidae) is a small (<15 mm body length), diurnal, ground dwelling insect. It is widely distributed in Europe and is locally very common, particularly on clear-cuttings where it feeds on plant material such as algae, mosses, fungi, and detritus (Holst, 1986). Adult grasshoppers over-winter and emerge in early spring when the reproductive season begins. Females produce multiple clutches of eggs, which are buried in moist soil and may contain up to 40 eggs that hatch after 20–30 days, depending on temperature (Forsman, 2001; Ahnesjö and Forsman, 2003).

T. undulata displays genetically encoded color polymorphism (Holst, 1986; Forsman *et al.*, 2002 and references therein). Individuals vary from black, through yellowish-brown to light grey, with some individuals being monochrome (e.g., the black and the brown color morphs) and others having a distinct pattern, such as the striped morph which is black or dark brown in ground color but has a narrow light yellowish longitudinal stripe running along on the mid-line of the upper surface from the fore-head to the apex of the pronotum. The grey morph is black in ground color but with the upper surface colored in light grey. Several speckled variants in different shades of brown also occur. Although relative morph frequencies show variation among populations and temporal variation within populations the brown, black, striped and grey morphs are more frequent than the others (e.g., Forsman, 1999a, b; Forsman and Appelqvist, 1999). In this study we focus on these four predominant morphs.

Results from a mark-recapture study of the con-generic *T. subulata* suggest that pygmy grasshoppers are sedentary, on average males moved 4.6 m (range 0.35–11.8 m, $n=22$) and females 7.4 m (range 0.8–32.8 m, $n=51$) in 4 days (Forsman and Appelqvist, 1999, see also Hochkirch *et al.*, 2002). Results from a pilot study of *T. undulata* based on 4 male and 4 female adult individuals that were closely observed for 30–60 min in their natural habitat suggest that this species also is sedentary. Individuals moved on average 40 cm during the entire observation period, usually to shuttle between sun-exposed and shaded areas and between different substrate types. Although capable of jumping several meters when threatened (Forsman, 1999b), they usually walk slowly on the ground surface, occasionally performing only short jumps.

Habitat selection by free-ranging individuals in the field

We observed adult males and females of *T. undulata* on 7 days with favorable weather conditions in late spring and early summer (8 May, 10 May, 11 May, 15 May, 23 May, 5 June and 11 June) of 2001. The population inhabited a burnt clear-cutting (approximately 10 ha), located in south-central Sweden. The populated part of the area measured approximately 200 m by 200 m and consisted of a small wetland and a surrounding 10 m wide corridor characterized by burnt organic matter, bare rocks and boulders, fallen logs and branches (including burnt and dry spruce needles), and live vegetation dominated by mosses (e.g., *Ceratodon purpureus*, *Pholia nutans*, *Sphagnum* ssp., *Polytrichum* ssp.), grass and some tussock sedges (*Carex* ssp.) (see also below). Animals used for Experiments 1–3 (see below) were also collected from the same population on 26 April and 11 May, 2000.

During each observation day, two or four people searched for grasshoppers while walking slowly through the area. When a resting individual was found we recorded sex, color morph, time and date. Surface temperature at the location of the grasshopper was measured (henceforth $T_{\text{flag } 1}$) and the point was marked with a numbered flag. Surface temperature was measured using a digital thermometer (Quicktemp 860-T1, Testo Gmbh and Co., D-79853 Lentzkirch, Germany) with an infrared sensor and a laser sight allowing temperature measurements of an area as small as 19 mm in diameter from a distance of 1.15 m. To quantify the thermal quality of the environment in the area surrounding the focal grasshopper, surface temperature was measured in eight additional spots, at 15 and 30 cm from the grasshopper in all four cardinal directions (henceforth $T_{\text{flag } 2\text{–}9}$). The spatial distribution of these additional spots is within the observed range of grasshopper movements in the field during a period of 30–60 min (see above and Forsman and Appelquist, 1999, see also Hochkirch *et al.*, 2002). This procedure yielded in total nine temperature readings per individual. All measured spots were marked with a numbered flag. A ring (70 cm in diameter) was placed on the ground with the point of grasshopper location in the centre (henceforth referred to as 'inhabited' rings) and the area was photographed for subsequent analyses of microhabitat composition (see below).

To obtain comparable data on surface temperatures available at the same time and under the same weather conditions prevailing when a grasshopper was located one control area was measured simultaneously, by another observer, for each focal grasshopper. Control areas were selected by placing another 70 cm ring in the study area at the point of the other observer, thereby avoiding the risk of selecting control areas outside the distribution range of the grasshopper population. Control areas were measured for surface temperature and photographed in the same way as 'inhabited' rings.

An estimate of measurement repeatability of temperature measurements was obtained based on two repeated measurements of 81 randomly selected spots analyzed using a one-way ANOVA as $S_B^2/(S_B^2 + S_W^2)$, where $S_B^2 = (\mathrm{MS_B} - \mathrm{MS_W})/k$, $S_W^2 = \mathrm{MS_W}$, $k =$ number of measurements per point and $\mathrm{MS_W}$ and $\mathrm{MS_B}$ are the mean squares obtained within and between measurement spots, respectively (Sokal and Rohlf, 1981). This showed that measurement repeatability was very high (99.2%, $F_{1,79} = 235.49$, $p < 0.0001$) with only 0.8% of the variance in surface temperature among spots being due to measurement error. The infrared thermometer measures surface temperature of an area larger than the grasshopper. However, repeated measurements of 30 spots using the infrared thermometer and a thin thermocouple (Greisinger electronic GmbH GTF 300) attached to a digital thermometer (FLUKE model 52K/J) that measures temperature in an area much smaller than a grasshopper, revealed that the two methods yield highly repeatable estimates (measurement repeatability being 99.4%, $F_{29,30} = 126.89$, $p < 0.0001$), with only 0.6% of the variance being attributable to measurement method.

In the analyses of the photographs, substrate type was recorded for each of the nine marked spots in all 'rings'. Substrates were classified into six categories: bare soil; dead wood (branches and fallen logs); mosses; charcoal (mainly burnt wood, spruce needles and other burnt organic matter); green plants; and bare rocks and stones.

Analyses of habitat selection

Surface temperature

Studies of ectotherms commonly use physical models of the animals studied to estimate operative temperatures and the thermal quality of the habitat. The operative temperature is an estimate of the body temperature for an object that does not behaviorally or physiologically thermoregulate, and that has reached the thermal equilibrium (e.g., Hertz *et al.*, 1993). Due to their small body size, however, body temperatures of non-behaving (i. e. dead) pygmy grasshoppers correspond closely with surface temperature ($r = 0.999$, $p < 0.0001$, $n = 27$, data from Forsman, 2000, see also Coxwell and Bock, 1995). To quantify the quality of the thermal environment for pygmy grasshoppers we therefore computed the absolute value of the deviation of surface temperature from the preferred body temperature range of *Tetrix undulata*. The preferred body temperature range was estimated from data for 78 individuals in an artificial thermal gradient (for details see Forsman *et al.*, 2002), and the central 50% (i.e., within the 1st and 3rd quartiles) of the body temperature records (females 29.5–39.3 °C; males 27.5–37.5 °C) was used to represent the 'target' body temperature range of thermoregulation (Hertz *et al.*, 1993).

To test the hypotheses that alternative color morphs select different habitats in a manner that can be predicted by morph-specific differences in capability of thermoregulation (i.e., the rate at which solar radiation is converted to body heat, as obtained from Forsman, 1997) we performed an ordered heterogeneity test, a powerful composite test statistic for evaluating directional hypotheses (Rice and Gaines, 1994). This test combined the magnitude of the deviations of surface temperature from the range of preferred body temperatures among habitats selected by alternative morphs (obtained from an ANOVA of data for $T_{\mathrm{flag}\ 1\text{–}9}$ in inhabited rings) and the Spearman rank correlation between least-squares-means of selected surface temperature and heating rate.

Substrate composition

To test whether grasshoppers selected substrates in proportion to their availability we first estimated relative frequencies of different substrate types (based on information from all flags in all rings, i.e., $240 \times 9 = 2160$ observations). These data were then used to compute the distribution of grasshoppers on different substrates expected under the assumption that they were randomly distributed. The expected distribution was compared with the observed frequencies of substrate types at the points of grasshopper location (i.e., data from flag 1 in inhabited rings only) using the χ^2 goodness-of-fit test.

Differences in habitat selection between males and females and among color morphs were assessed by testing for independence of substrate composition and sex or color morph, respectively, using contingency table analyses (χ^2-tests) or Fishers' exact-test when expected cell frequencies were small.

Experiment 1: substrate use in a semi-natural micro-landscape

Our comparisons of habitat selection based on data for free-ranging individuals described above were based on observations of one individual at a time. Consequently, comparisons of substrate use between sexes or among color morphs may be confounded if habitat selection is influenced by weather conditions or time of day. To ameliorate this potential problem we collected data on substrate use under semi-natural conditions based on simultaneous observations of different color morphs. For this purpose a semi-natural micro-landscape comprising five different substrates was constructed in a plastic cage (20 cm in diameter, 11 cm high) filled with moist dark soil to a height of 3 cm. The surface was divided into four equal sized sections, covered either with: a dense layer of dry pale sticks; brownish humus and organic debris; green live moss, or an additional layer of moist dark soil. A burnt (charcoal) black branch (15 cm long, ca. 3 cm diameter) was placed in the two sections covered with sticks and humus. To prevent the grasshoppers from escaping while still allowing airflow, light penetration and observations of animal movements, the top of the cage was covered with a black mosquito net.

These experiments were performed out of doors, at daytime (9.00–16.00 h), in the sun, on days with clear or slightly overcast skies, May 15–17, 2000. At the onset of a trial three adult female *T. undulata* individuals, belonging to the black, grey and striped color morphs, were simultaneously placed on the section covered with moist soil. The animals were allowed 10 min to habituate. The position of each individual was then recorded every 5 min for 1 h, yielding 12 observations per individual. The experiment was replicated 10 times, yielding data for a total of 30 individuals. Each individual was used only once and animals used simultaneously appeared not to interact. Three similar arenas were used interchangeably for the different trials. The null-hypothesis of independence of substrate use and color morph was tested using logit-model analysis (Collett, 1991), implemented using procedure CATMOD and the Wald-statistic was used to assess the statistical significance of explanatory variables (SAS Inst., 1988). To allow visualization of the variation in substrate use among color morphs, the mean proportion of observations on each substrate was computed for each of the three color morphs.

Experiment 2: investigating the role of color per se *on substrate use*

Because different kinds of substrates vary in many important respects, including color, structure, humidity and surface temperature it is difficult to disentangle why individuals prefer certain substrates to others and why different categories of individuals vary in substrate use. To test if habitat selection and substrate use in *T. undulata* is influenced by background color *per se*, three identical circular test arenas were used. Each arena consisted of a wooden board, with a diameter of 70 cm, painted in three different colors (Natural Color System code, green G10Y. 5030, brown Y30R. 7010, and grey N. 3000) chosen to resemble different substrates encountered by grasshoppers in their natural habitat (i.e., green simulated vegetation, brown simulated bare soil and dead wood and grey simulated bare rock). Fine sand was blended into the paint to provide a rough texture and prevent the grasshoppers from sliding. The board was painted so that there were twelve equal sized (30° angle) sectors, with each of the three colors being represented by four sectors arranged so that grey fields were neighbored by brown and green fields. The arena was surrounded by a 20 cm high border, painted in the same colors as the bottom. To prevent the grasshoppers from escaping during the experiment the arena was covered with transparent plastic foil. To avoid large variation in light conditions and temperature among trials these experiments were performed in the laboratory at room temperature (22–24 °C), in May, 2000. The light source consisted of fluorescent strip lights mounted in the ceiling 2.1 m above the arena, and a daylight light bulb (SOL, 60 W) placed 42 cm above the centre of each of the test arenas.

Because different sexes and color morphs vary in temperature preferences and thermoregulatory behavior (Forsman, 1999a, Forsman *et al.*, 2002) the comparison of position among color morphs within the arena may potentially be influenced by differences in substrate temperature among the three background colors. To evaluate this possibility we measured surface temperature at 48 points in each of the three arenas (four points in each of the twelve color fields, located 2, 12, 22 and 32 cm from the centre) after 1 h of exposure to the light source. A three-way ANOVA (with surface temperature as the dependent variable, arena and substrate color as independent class variables and distance from the centre as a covariate) revealed that surface temperature did not differ between the fields painted grey, brown and green ($F_{2,138} = 1.86$, $p = 0.16$; least squares means being 28.7, 28.8 and 28.8 °C), suggesting that morph-specific thermal properties are unlikely to confound our estimates of background color preferences.

Three individuals were tested simultaneously but in separate arenas. We strived for simultaneous testing of all color morphs, but this was not always possible due to differences in sample size among color morphs (Table 1). However, individuals were chosen so that at least two different color morphs were tested at the same time. At the onset of a trial one grasshopper was placed in the centre of each of the three arenas under a plastic cup (90 mm diameter, 60 mm height). The arenas were then covered with plastic foil and the animals were released by removal of the plastic cups and allowed to habituate for 3 min. The position of the grasshoppers was then recorded every 30 s for 10 min, yielding 20 observations per individual.

Experiment 3: investigating the influence of predation risk on substrate use

To examine whether individuals adjust microhabitat use when subjected to an elevated risk of predation two identical micro-landscapes, each comprising two different substrate types, were constructed in a plastic cage (20 cm in diameter, 11 cm high) filled with moist dark soil to a height of 3 cm. The surface of the soil was divided into four equal-sized sections. Two of the sections were covered with a thin layer of a mixture of burnt (i.e., black) and dry (yellowish brown) spruce (*Picea abies*) needles, a background that constitutes a considerable part of the area inhabited by the source population (see above). To a human observer this background provides good crypsis for the striped color morph. The other two sections were covered with a thin layer of burnt (black) spruce needles only, visually matching the black color morph. Each arena was covered with a mosquito net in order to prevent the grasshoppers from

Table 1. Distribution among color morphs and sexes of *Tetrix undulata* individuals included in the field-study and experiments used to investigate microhabitat selection

Category	Color morph			
	Black	Striped	Gray	Brown
Microhabitat selection in free-ranging individuals in the field				
Females	21	17	16	26
Males	14	9	11	6
Experiment 1. Controlling for confounding effects of weather conditions and time dependence of habitat selection behavior				
Females	10	10	10	
Experiment 2. Testing for effects of substrate color per se				
Females	22	20	15	
Males	11	5	9	
Experiment 3. Testing for effects of elevated predation risk				
Females	15	15		

escaping while still allowing observations during the experiment. To minimize confounding effects of variation in light conditions and temperature among trials these experiments were performed in the laboratory at room temperature (22–24 °C), 15–16 May, 2000. The light sources were the same as in Experiment 2.

For this experiment adult *T. undulata* females belonging to the black ($N = 15$) and the striped ($N = 15$) color morph were used. Two individuals (one black and one striped) were tested simultaneously but in separate arenas, and each individual was used only once. At the onset of a trial one grasshopper was placed in each of the two micro-landscapes and allowed to habituate for 2 min. The position of the grasshoppers was then recorded every 30 s for 10 min, yielding 20 observations per individual. After 10 min a predator attack was simulated by lightly tapping on the net covering the cage to induce an escape response and the position of the grasshoppers after the disturbance was recorded. In all cases the grasshopper jumped in response to the disturbance, suggesting that the method was successful.

Results

Habitat selection in free-ranging individuals in the field

Surface temperature

Surface temperature displayed a curvilinear (negative quadratic) relationship with time of day (Figure 1) as described by the equation.

$$\text{Temperature} = -178.2 + 35.46 \times \text{Time} - 1.46 \times \text{Time}^2, \ R^2 = 0.29, p < 0.0001$$

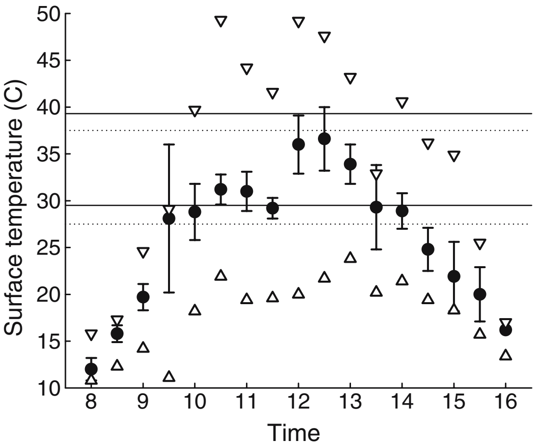

Figure 1. Ground surface temperature as a function of time of day in spots selected by 120 free-ranging adult *Tetrix undulata* (filled circles, mean ± 1 S.E.). Open triangles indicate the range of available surface temperatures, as estimated based on data for control areas (see text for details). Horizontal lines represent the upper and lower boundaries of the preferred body temperature range of female (29.5–39.3 °C) and male (dotted, 27.5–37.5 °C) *T. undulata* as estimated in a laboratory thermal gradient.

Surfacetemperature also varied significantly among the six kinds of substrates (ANOVA, $p < 0.0001$, $F_{5,2145} = 27.93$), being highest for soil (33.9 °C ± 0.45), followed by wood (31.5 °C ± 0.81), charcoal (31.3 °C ± 1.42), mosses (27.6 °C ± 0.42), plants (26.9 °C ± 0.70) and rock (22.6 °C ± 1.36). The six substrate types varied also in thermal quality, measured as the deviation of surface temperature from the range of preferred body temperatures, in control rings ($F_{5,1056} = 4.36$, $p = 0.0006$) but not in inhabited rings ($F_{5,1069} = 1.45$, $p = 0.20$, effect of habitat by ring category interaction: $F_{5,2127} = 2.82$, $p < 0.05$), suggesting that at the larger scale grasshoppers selected environments where all substrate types had surface temperatures close to or within their preferred body temperature range.

Data on microhabitat selection was collected for 80 female and 40 male free-ranging, adult *Tetrix undulata* in May and June 2001 (Table 1). Average surface temperature was significantly lower in inhabited rings (mean 28.3 °C, SD = 10.99, range 10.2–64.4 °C) treating inhabited versus control rings as fixed factor and ring number as a random factor, compared to control rings (mean 33.4 °C, SD = 13.68, range 6.1–70.5 °C; mixed-model ANOVA, $F_{1,119} = 46.12$, $p < 0.0001$). This difference, together with the slightly smaller variance and narrower range in inhabited as compared to control rings, suggests that grasshoppers actively avoided very high and very low surface temperatures. Within inhabited rings, the surface temperatures at each of the eight reference spots surrounding the focal grasshoppers deviated more from the range of preferred body temperatures than did surface temperature at the points of grasshoppers location (ANOVA with special contrasts and including time of day as covariate, $F_{1,1061} = 9.44$, $p = 0.0022$, mean contrast $= -1.5 \pm 0.48$ °C), a finding consistent with the hypothesis that, also at the smaller spatial scale, grasshoppers selected habitats where surface temperature was within or close to their preferred body temperature range (see also Figure 1). Notably, surface temperatures within the range of preferred body temperatures were not available in the morning (i.e., before 09.00 h) and afternoon (after 15.30 h).

Within inhabited rings, the average deviation of surface temperatures from the range of preferred body temperatures varied among habitats selected by different color morphs (lsmeans of deviations obtained from an ANOVA being highest for the black morph 6.9 °C, followed by the striped 6.3 °C, brown 5.8 °C and gray morph 5.1 °C), in a manner consistent with that predicted by morph-specific differences in the rate at which solar radiation is converted to body heat (ordered heterogeneity test, $r_s P_c = 0.80$, $k = 4$, $p < 0.01$). This indicates that alternative morphs selected habitats of different thermal quality and that avoidance of habitats characterized by high surface temperatures was stronger in dark as compared to pale color morphs.

When the analysis was restricted to data from the point of grasshopper location (i.e., flag 1 only), a significant difference in surface temperature was evident between sexes (lsmeans as obtained from ANOVA including time of day as a covariate, males = 25.7 °C; females = 29.1 °C, $F_{1,113} = 5.74$, $p < 0.05$), consistent with a preference for higher body temperatures in females than males.

Substrate composition

The rank order of relative frequencies of the six different substrate types in the area inhabited by the grasshopper population was (in descending order) soil, mosses, dead wood, plants, charcoal and rock (Figure 2).

The number of different substrate types did not differ between inhabited (mean = 2.98, range 1–5, $n = 120$) and control rings (2.96, range 1–5, $n = 120$, Wilcoxon two-sample test, $z = 0.22$, $p = 0.83$), suggesting that grasshoppers did not select habitats characterized by an unusually high degree of substrate diversity. The relative frequencies of substrate types differed between inhabited rings and control rings ($\chi^2 = 52.67$, df = 5, $p < 0.0001$), suggesting that grasshoppers were not randomly distributed in the area with respect to substrate composition. Females did not use substrate types in direct proportion to their availability in the area (χ^2 goodness of fit-test; $\chi^2 = 16.2$, df = 5, $p < 0.001$, $n = 80$), but were observed on mosses, wood and charcoal more often than expected by chance (Figure 2). In males, the use of substrate types did not differ significantly from the random expectation ($\chi^2 = 8.96$, df = 5, $p > 0.10$, $n = 40$, Figure 2).

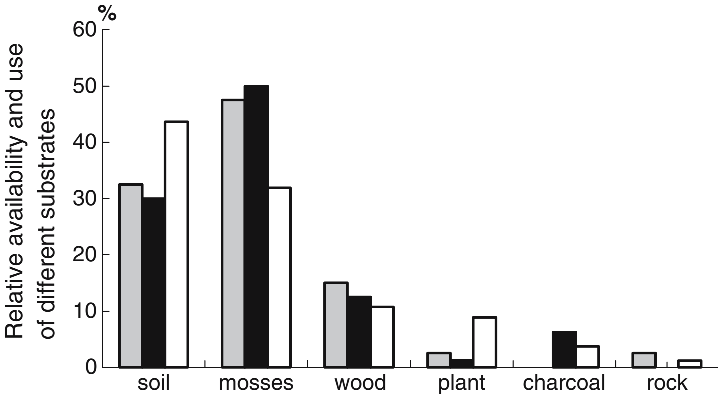

Figure 2. Relative availability (white bars) and utilization of six different substrate types by free-ranging adult female (black bars) and male (gray bars) *Tetrix undulata*.

When the analyses were restricted to data for the point of grasshopper location (i.e., flag 1 only), the null-hypotheses of independence of substrate use and sex (Fishers' exact, $p = 0.42$) and substrate use and color morph (Fishers' exact, females: $p = 0.24$; males: $p = 0.99$) could not be rejected. However, the distribution of substrate types in the area surrounding the focal grasshopper was significantly dependent upon the sex of the individual ($\chi^2 = 11.08$, df = 5, $p < 0.05$). In males, substrate use differed significantly between individuals observed during midday and individuals observed during the morning or afternoon ($\chi^2 = 14.94$, df = 5, $p < 0.05$), with mosses and bare soil being used to a greater extent and dead wood to a lower extent during midday. No such temporal variation in substrate use was evident in females ($\chi^2 = 2.50$, df = 5, $p = 0.78$).

The composition of the six substrates was dependent upon color morph in both females ($\chi^2 = 31.13$, df = 15, $p < 0.01$, Figure 3) and males ($\chi^2 = 27.32$, df = 15, $p < 0.05$). Degree of habitat selectivity was measured as the sum of differences between the observed and the predicted proportion expected under the assumptions that individuals use substrate types in proportion to their relative availability. Habitat selectivity varied among morphs, being for females three times as high in black (31) and twice as high in gray (20), as compared to brown (13) and striped (9) individuals. Black and gray females avoided bare soil in favor of mosses, whereas brown and striped females used the six different substrate types in almost direct proportion to their relative availability (Figure 3). The differences in substrate use among the four color morphs were similar in males (not shown).

Experiment 1: substrate use in a semi-natural micro-landscape

The degree to which individuals used the different kinds of substrates in the micro-landscape was dependent upon color morph (logit-model analysis,

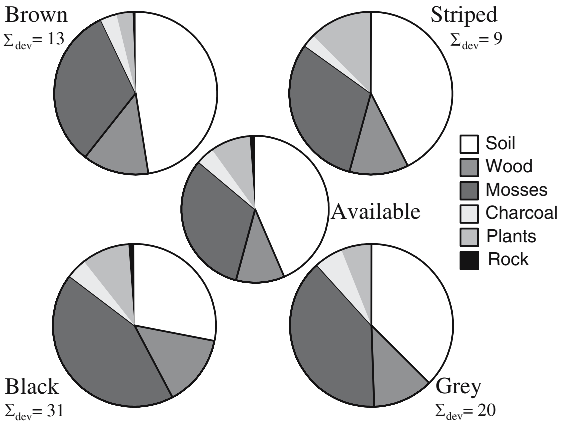

Figure 3. Variation in substrate composition in micro-environments selected by free-ranging female *Tetrix undulata* individuals belonging to four different color morphs, and relative availability of substrate types in the area. Σ_{dev} is an index of microhabitat selectivity, measured as the deviation of the observed utilization from that expected under the assumption that individuals use alternative substrate types in direct proportion to their relative availability.

$\chi^2 = 27.6$, df = 2, $p < 0.0001$, Figure 4). All three morphs used the moss to a high and similar extent. The black morph spent more time on humus and charcoal, and less time on the dry pale sticks, compared to the grey and striped morphs. The striped morph spent more time on bare soil, compared to the black and grey morphs.

Experiment 2: variation in substrate color preferences

The degree to which individuals used the grey, green and brown backgrounds depended upon color morph (logit-model analysis, $\chi^2 = 17.07$, df = 2, $p = 0.0002$) and the sex by color morph interaction ($\chi^2 = 11.07$, df = 2, $p = 0.0039$). The interaction reflected the fact that in males the black morph used the dark brown substrate more than expected by chance, whereas in females it was primarily the grey morph that used the brown background to a disproportionately high extent (Figure 5) Separate analyses of data for males and females revealed significant differences in color use among morphs in females ($\chi^2 = 38.55$, df = 2, $p < 0.0001$, $n = 57$), but not in males ($\chi^2 = 3.44$, df = 2, $p = 0.18$, $n = 25$). As in free-ranging individuals (see above), the degree of substrate selectivity was lowest in striped females, who used the three different substrate colors in almost direct proportion to their availability (Figure 5).

Experiment 3: color morphs respond differently to predation risk

Black and striped individuals did not differ in substrate use before the disturbance (Kruskall–Wallis, $\chi^2 = 1.08$, df = 1, $p = 0.30$), with both color morphs spending a somewhat higher proportion of the time on the “striped” back-

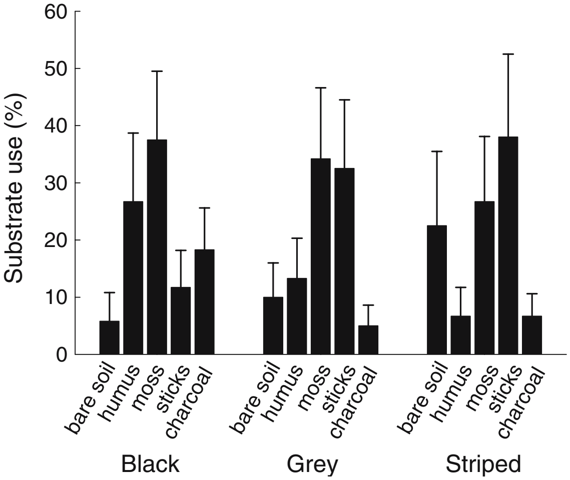

Figure 4. Variation in substrate use in the micro-landscape arena among female *Tetrix undulata* belonging to different color morphs. Substrate use was measured as the proportion of the total number of observations (12 for each individual) on each substrate. Data are based on simultaneous observations of a black, gray and a striped individual tested together in the same trial. Figure shows mean ± 1 S.E. across 10 different trials.

ground with yellowish spruce needles (Figure 6a). However, after the disturbance simulating an approaching predator, substrate use was dependent upon color morph ($\chi_{\text{adj.}}^2 = 10.85$, df = 1, $p < 0.001$), individuals belonging to the striped morph using primarily the striped background with yellowish needles,

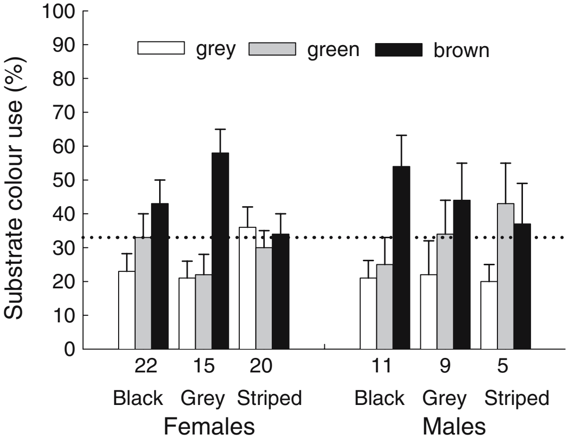

Figure 5. Variation in substrate color use in the experimental arena in female and male *Tetrix undulata* belonging to different color morphs. Substrate use was measured as the proportion of the total number of observations (20 for each individual) on each color. The dotted reference line indicates the random expectation (i.e., 33%). Numbers below bars denote sample size (number of individuals). Figure shows mean ± 1 S.E.

and individuals belonging to the black morph using primarily the background with only black spruce needles (Figure 6b), suggesting that individuals select visually matching backgrounds when disturbed.

Discussion

Our results suggest that habitat selection is affected by the interplay between body temperature regulation and predator avoidance and further indicate that

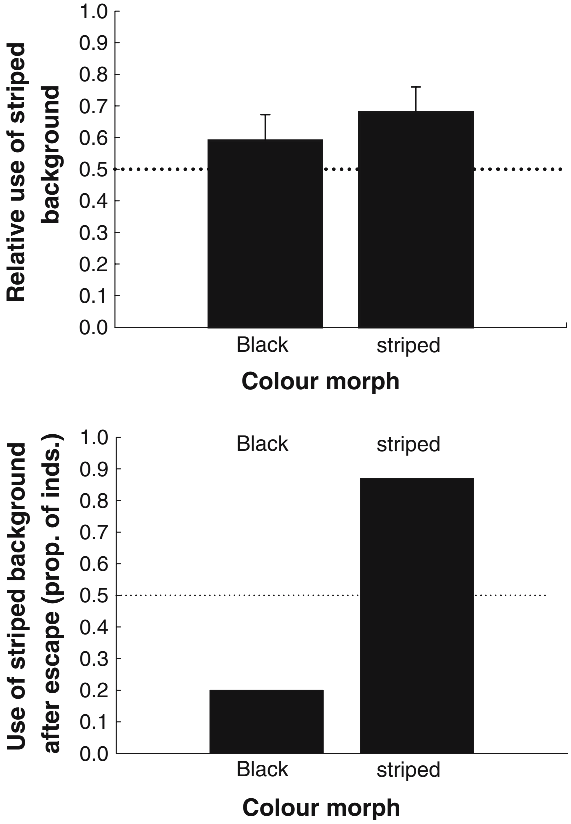

Figure 6. Comparison of substrate use in the test arena by female *Tetrix undulata* belonging to the black and striped color morph. Half of the arena was covered with a mixture of black and yellowish spruce needles, the other half contained only black needles. Top panel shows relative use of the sections covered with a mixture of black and yellowish needles before disturbance. Relative substrate use was measured as the observed proportion of the total number of observations (20 for each individual). The dotted line indicates the random expectation (i.e., 50%). Figure shows mean ± 1 S.E. Bottom panel shows substrate use immediately after an escape response to a disturbance simulating an approaching predator (see text for details). Figure shows the proportion of individuals that used substrates with yellowish needles after the escape, for each of the two color morphs.

sex and body coloration may translate into alternative ecological strategies regarding the solution to the trade-off between these priorities.

Our comparisons revealed that surface temperatures of habitats selected by free-ranging *Tetrix undulata* deviated significantly less from the range of preferred body temperatures (as estimated from a laboratory thermal gradient, see Forsman *et al.*, 2000) than would result from a random utilization of available habitats and surface temperatures, a pattern that was evident both at a large (inhabited vs. control rings) and small (point of grasshopper location vs. surrounding spots) spatial scale. This suggests that individuals utilized habitats with or when thermal properties were suitable for maintaining their preferred body temperature. The conclusion that individuals utilized habitats in part so as to maintain suitable temperatures is further supported by the finding that the substrates selected by males (but not females) during the warmest part of the day were different from those selected during morning and afternoon. Because temperature preferences and thermoregulatory behaviors vary between sexes and among color morphs (Forsman, 1999a, Forsman *et al.*, 2002) differences in substrate use between these categories of individuals may change with weather conditions and time of year.

Our analyses revealed a non-random distribution of grasshoppers across the different substrate types available in the study area. At first sight, the large variation in surface temperature among substrates (ranging from approximately 23 °C for bare rock to almost 34 °C for bare soil) might be expected to impose a constraint on habitat use. In keeping with this hypothesis, the disproportionate utilization of certain substrates (e.g., mosses) and avoidance of others (e.g., bare soil) may suggest that substrate use was influenced in part by temperature regulatory needs (e.g. Whitman, 1987). In cold temperate regions such as our study site (south central Sweden), overheating is not intuitively expected to be a problem. However, the preferred body temperature range for *T. undulata* is 27.5–39.3 °C (estimated from Forsman *et al.*, 2000), and although thermo-tolerance in *T. undulata* is not known the upper lethal body temperature for most insects is approximately 45 °C for short-term exposure (Clarke, 2003). This, in combination with the finding that surface temperatures above 40 °C were common (at least during midday) and occasionally reached 70.5 °C lends support to the interpretation that these insects frequently selected relatively cool habitats to avoid overheating. Interestingly, however, this does not seem to have constrained their use of different substrate types. Whereas thermal quality of the habitat (i.e., the degree to which surface temperature deviated from the range of body temperatures preferred by grasshoppers) varied significantly among substrate types in randomly selected control areas, no such variation was evident in habitats occupied by grasshoppers. This indicates that individuals selected habitats when and where they could maintain preferred body temperatures also when moving short distances between different kinds of substrates to fulfill different requirements, such as when in search of food, protection or oviposition sites, etc.

Thermal requirements may in part explain that the composition of substrate types in the area surrounding the focal individual was different for males and females. When the relationship between temperature and time of day was statistically controlled, females selected spots more than 3 °C warmer on average. This is consistent with a previous study showing that female pygmy grasshoppers selected higher body temperatures than males in a laboratory thermal gradient (Forsman, 2000). Because male pygmy grasshoppers are smaller than females (Ahnesjö and Forsman, 2003), their body temperature is influenced more by environmental temperature and subject to larger and more rapid fluctuations (Digby, 1955; Stevenson, 1985). Selecting habitats that help avoid overheating may therefore be more important to males than females, an interpretation consistent with the finding that, in males (but not in females), the substrate composition selected during the warmest part of the day differed from that selected during morning and afternoon. The preference for higher temperatures in females than males may also reflect the positive effect of high body temperature on female reproductive performance (Forsman, 2001).

A difference in selected substrate composition between males and females has been demonstrated also in the con-generic *T. subulata* (Forsman and Appelquist, 1999). This may reflect sexspecific requirements regarding factors other than thermoregulation, such as humidity, oviposition sites, food requirements, size-dependent crypsis and social interactions (e.g., Calver and Bradley, 1991; King, 1992; Merilaita and Jormalainen, 2000). Whatever the underlying mechanism, such sexual differences in habitat selection may contribute to the evolution of sex-related color morph frequencies, as has been suggested for other species (e.g., Slatkin, 1984; Jormalainen and Tuomi, 1989; Calver and Bradley, 1991; Merilaita and Jormalainen, 1997), and may influence the dynamics and maintenance of the polymorphism (Li, 1963; Kidwell *et al.*, 1977).

The differences in habitat use among free-ranging individuals belonging to different color morphs also reflected, at least in part, dissimilarities in thermal requirements. Although ground surface temperatures correlate with body temperature (See above and Coxwell and Bock, 1995), heat gain of grasshoppers is influenced also by the absorption of solar radiation (Chappell and Whitman, 1990). Dark color morphs warm up faster and attain higher asymptotic body temperatures compared to paler morphs (Forsman, 1997, 2000), and although darker morphs prefer higher body temperatures in a laboratory thermal gradient (Forsman, 2000), comparisons of thermoregulatory behavior have shown that they more frequently shuttle and seek out shade to avoid overheating when experimentally subjected to a trade-off between feeding and body temperature regulation (Forsman *et al.*, 2002). The variation in thermal property among habitats occupied by individuals belonging to different color morphs documented in the present study provides further evidence that behaving so as to avoid overheating is of greater importance to darker compared to paler color morphs. This interpretation is consistent also with the finding that black females had the highest degree of microhabitat selectivity and spent more time on relatively cold moist moss and less time on warm bare soil and dead wood (in the field as well as in the semi-natural landscape (Experiment 1)), compared to females belonging to paler morphs.

Because of differences in visual appearance, the dissimilarities among color morphs regarding utilization of substrate types (evident both in free-ranging individuals in the field and in the seminatural landscape (Experiment 1) probably reflect also a role of predator avoidance in habitat selection. This interpretation receives support also in Experiment 2 where color morphs differed in substrate use despite the fact that substrates were similar in all respects (texture, temperature) other than color *per se*. Crypsis is determined by complex interactive effects of animal pigmentation pattern, background coloration, ambient light conditions and the visual perceptive abilities of the beholder (e.g., Endler, 1978, 1990). Birds, which may constitute a selective force on these grasshoppers (Belowsky and Slade, 1993; Forsman and Appelquist, 1999), have a visual spectrum beyond that of humans, including wavelengths within the UV-spectrum (Vorobjev *et al.*, 2001). Although human vision thus may confound our assessment of crypsis, the fact that the gray morph spent most time on the dark brown and least time on the gray background is difficult to reconcile with a pure background matching strategy. Experimental evidence from another species of grasshopper has revealed that individuals select color matching substrates by means of visual comparisons with their body pigmentation (Gillis, 1982), but it is not known if also *Tetrix undulata* has this ability. It is possible that substrate color is used merely as an indicator of other aspects of environmental quality, e.g., temperature, humidity or food availability (see Calver and Bradley, 1991). However, the role of predator avoidance for habitat selection is emphasized by the results from Experiment 3, where the black and striped color morphs selected different but, to the human eye, visually matching backgrounds following a disturbance simulating an approaching predator (see also Eterovick *et al.*, 1997). This differential response to disturbance, combined with the lack of difference in substrate use between color morphs prior to the disturbance, may illustrate the influence of trade-offs between different requirements.

Because crypsis is background-specific, there is a trade-off between crypsis in visually different microhabitats (Merilaita *et al.*, 1999). The optimal solution to this trade-off may be either a compromise of the degree of crypsis between microhabitats, or an improved crypsis in a single habitat at the expense of decreased crypsis in alternative habitats. However, camouflage can be achieved also through disruptive coloration, that is, a pigmentation pattern that obscures the contour and true form of the animal, and thereby impairs detection and visual recognition (Cott, 1940; Merilaita, 1998). Because crypsis achieved through disruptive coloration is less background-specific, it may constitute a better option for a compromising coloration than crypsis achieved by background matching (Merilaita, 1998; Merilaita *et al.*, 1999). In keeping with this line of argument, the longitudinal yellowish line of the striped color morph may enhance camouflage via a disruptive effect. The low degree of substrate selectivity in striped females (as compared to gray, brown and black females), as observed in the field and in Experiment 2, may thus reflect a less important role of background matching for microhabitat selection behavior in the striped morph.

Whether the variation in habitat utilization among color morphs in these pygmy grasshoppers is the result of different morphs selecting the microhabitats in which they enjoy the highest fitness, as predicted by the theory of multiple niche polymorphism (Levene, 1953), remains an open question. To some extent, however, the differential habitat selection appears to reflect morph-specific constraints imposed by indirect effects of coloration on body temperature and performance. This variability in habitat selection may translate into temporal and spatial variation in fitness among color morphs, possibly increasing the likelihood of maintenance of stable polymorphisms (Levene, 1953; see also Halliburton, 2004). Taken together, our results support the notion that habitat selection behavior is influenced by compromises between competing requirements including (but not limited to) temperature regulation and predator avoidance, and illustrate that phenotypes differ in their choice between conflicting priorities. Although the dynamics of a polymorphism is likely to be influenced by several factors, variation in habitat use among sexes and color morphs may nevertheless contribute to the maintenance of chromatic polymorphisms (Levene, 1953; Li, 1963; Kidwell *et al.*, 1977; Hedrick, 1986).

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