Phenotype manipulation influences microhabitat choice in pygmy grasshoppers

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Abstract The matching habitat choice hypothesis posits that individuals actively choose those microhabitats that best match their specific phenotype to maximize fitness. Despite the profound implications, matching habitat choice has not been unequivocally demonstrated. We conducted two experiments to examine the impact of pigmentation pattern in the color polymorphic pygmy grasshopper Tetrix subulata on habitat choice in a laboratory thermal mosaic arena. We found no behavioral differences in the thermal mosaic among pygmy grasshoppers belonging to either pale, intermediate or dark natural color morphs. However, after manipulating the grasshoppers’ phenotype, the utilization through time of warmer and colder parts of the arena was different for black-painted and white-painted individuals. White-painted individuals used warmer parts of the arena, at least during the initial stage of the experiment. We conclude that microhabitat choice represents a form of behavioural plasticity. Thus, even if the choice itself is flexible and not genetically determined, it can still lead to spatial genetic structure in the population because the phenotypes themselves may be genetically mediated [Current Zoology 58 (3): 392–400, 2012].

Keywords Behavioral plasticity, Color polymorphism, Integrated phenotypes, Microhabitat use, Tetrix, Thermoregulation

The matching habitat choice hypothesis posits that individuals with different phenotypic attributes may prefer those patches with environmental characteristics that best suit their own particular phenotype as a result of self-assessment of individual well-being in specific environments (reviewed by Edelaar et al., 2008). It has been suggested that such matching microhabitat choice may contribute to genetic structuring within populations, result in directed gene flow, amplify differences between populations, promote the origin and maintenance of polymorphism, stabilize population dynamics, enhance local adaptation and adaptive peak shifts, and promote speciation (Edelaar et al., 2008; Holt and Barfield, 2008; Meylan et al., 2009; Ravigné et al., 2004; Räsänen and Hendry, 2008).

Although matching habitat choice may have consequences at the level of populations, it concerns mechanisms and processes at the level and spatial scale of the individual. In this context, population boundaries are not defined by the spatial arena delimiting the mating pool, but by the spatial arena as defined by microhabitat characteristics in the environment (Edelaar et al., 2008). Matching microhabitat preferences need not be genetically mediated; choices may be flexible and patterns of habitat utilization may change rapidly (Edelaar et al., 2008). It is driven by behavioral plasticity or flexibility whereby individuals change their environment according to phenotype, as opposed to developmental plasticity where the phenotype of individuals change according to the environment. To the extent that individuals have knowledge of environmental conditions in their available microhabitats, matching habitat choice may cause rapid spatial clustering of similar phenotypes and genotypes within populations (Edelaar et al., 2008).

Few attempts have been made to determine the presence, magnitude and impact of phenotype-dependency of microhabitat selection (Edelaar et al., 2008). Several studies have reported correlations between alternative phenotypic variants or morphs within a species and their environments, indicating that different phenotypes differ in their habitats use, or utilize different microhabitats within the same area (Hargeby et al., 2005; Holomuzki and Biggs, 2006; Jones, 1982; Nosil et al., 2008; Shine et al., 1998; Todd et al., 2006). However, such correlational data do not constitute firm evidence for matching habitat choice because selective mortality, exclusion by other individuals, homing behavior and developmental plasticity may generate similar patterns (Edelaar et al., 2008). Dissimilar behavior by phenotypically different individuals in experimentally manipulated environments (Bolnick et al., 2009, Ehlinger, 1990; Forsman, 2000; Harris and Jones, 1995; Jones, 1982; Powell and Taylor,
phenotype-dependent microhabitat choice and spatial
by differently coloured individuals may also give rise to
temperature of microhabitats with different thermal properties
thermic animals that use ambient energy sources to
avoid detection by predators. In insects and other ecto-
viduals may choose different backgrounds not only to
camouflage. Gillis (1982) demonstrated that phenotypic
manipulation changed choice of background color by
Circotettix rabula rabula grasshoppers. Unmanipulated,
naturally red and greenish grasshoppers chose matching
red and green backgrounds. However, red grasshoppers
which had been painted green in the circumocular mask
around their eyes that can be used for self color assess-
ment showed clear preferences for green backgrounds
(Gillis, 1982). In contrast, visually impaired grasshop-
per showed no preferences for background color (Gillis,
1982). In his study of color polymorphic tree frogs
Pseudacris regilla, Morey (1990) manipulated the
background color of cages by painting them in shades of
brown or green and demonstrated that naturally green
and brown frogs chose a matching green or brown
background respectively, and that this reduced their
susceptibility to visually oriented garter snake Tham-
nophis elegance predators. Differently coloured indi-
viduals may choose different backgrounds not only to
avoid detection by predators. In insects and other ecto-
thermic animals that use ambient energy sources to
generate body heat (Heinrich, 1993), differential utiliza-
tion of microhabitats with different thermal properties
by differently coloured individuals may also give rise to
phenotype-dependent microhabitat choice and spatial
structuring within populations.

Here, we experimentally test for phenotype-depend-
ent microhabitat choice in pygmy grasshoppers Tetrix
subulata (Orthoptera: Tetrigidae). We manipulate their
phenotypes by painting the pronotum either black or
white and then compare their microhabitat use in a
laboratory thermal mosaic obtained by different light
intensity. We also compare microhabitat use among un-
painted individuals that belong to different natural color
morphs. In ectothermic organisms such as insects, color
is important for heat absorption and body temperature
regulation, and grasshoppers that have been painted
black warm up faster and attain higher body temperature
when subjected to augmented illumination, compared
with individuals painted in pale colors (Forsman et al.,
2002). Body temperature also influences several impor-
tant aspects of performance, such as reaction distance
(Forsman, 1999b), jumping performance and flight ca-
pacity (Forsman, 1999a), probability of escape when
attacked by predators (Forsman and Appelqvist, 1998),
development rate (Ahnesjö and Forsman, 2003), and
fecundity (Forsman, 2001). Like other insects, pygmy
grasshoppers behaviorally regulate their body tempera-
ture by shuttling between sun and shade and utilizing
microhabitats with different thermal properties (Ahnesjö
and Forsman, 2006; Forsman et al., 2002). The match-
ing habitat choice hypothesis therefore predicts that
individuals painted black or white will behave differ-
ently in the thermal spatial mosaic, to attain body tem-
peratures that optimize perceived well-being, and offer
the highest overall performance and expected fitness
prospects.

1 Material and Methods
1.1 Capture and housing of experimental animals
Pygmy grasshoppers are small (<15 mm total body
length, mean 0.07 g dry body mass), diurnal, ground
dwelling insects that inhabit biomes ranging from
tropical rainforests to arctic regions of Europe, Asia and
America. The species used in this study, Tetrix subulata,
surface at early spring around April-May in our study
area of south-east Sweden, after overwintering as late
instars or adults (Forsman and Appelqvist, 1999). We
collected adult grasshoppers by hand between May and
June 2009 from six populations. We used animals from
different populations to evaluate the hypothesis that
thermal physiology and thermoregulatory behavior have
undergone micro-evolutionary modifications due to
divergent selection in different habitats. Preliminary
analyses uncovered no behavioral differences among
populations, but we take into consideration that our
animals originated from different source populations
both in the experimental design and in the statistical
analysis. After capture, the grasshoppers were classified
by sex and color morph and housed outdoors in white
10-L plastic buckets with a 15–20 cm layer of a 1:3
mixture of moist peat and soil, and live mosses as food
(Karlsson et al., 2008) until the onset of the experiment.
The animals were moved indoors on the day before the
experiment and maintained in the laboratory at 21 °C
before they were placed in the experimental arena.

T. subulata exhibits a multitude of discrete color
morphs within populations. Ground colors are black, light grey to almost white, dark brown, pale brown, reddish-brown, yellowish-brown or olive green. Some morphs are monochrome, and others have patterning consisting of longitudinal stripes or spots of variable colors. Available evidence indicates that color patterns are genetically determined and not influenced by developmental plasticity in response to environmental cues (Karlsson et al., 2008; Karlsson and Forsman, 2010; Karlsson et al., 2009; Nabours, 1929) (but see Hochkirch et al., 2008).

1.2 Study animals and experimental manipulation of color patterns

We recorded the behaviors of three individuals at a time, in three separate experimental thermal mosaic arenas, one individual in each arena. All observations were made by LW and EK, who alternated between trials. Each trio consisted of females that originated from the same source population, and belonged to the same natural color morph. In each trio, grasshoppers were randomly assigned to a paint treatment: white, black or natural (unpainted). Color patterns were experimentally manipulated by painting the dorsal side of the pronotum black or white using water based acryl paint (Panduro Hobbylack, black 70, white 01; Pebeo, fabricant de couleurs). Grasshoppers did not appear to be harmed by the treatment, there was no sign of necrosis or abnormal behavior. Furthermore, Forsman and Appelqvist (1999) found that some individuals that were marked, painted and released in the wild were still alive six weeks later.

We used individuals belonging to different color morphs in this experiment to enable comparisons of behaviors among different unpainted natural color morphs. This does not confound our comparisons between paint treatments because the three individuals within each trio were matched with regard to color morph and source population. We did not use all color morphs that existed in the populations for the experiment. We instead selected morphs that differed in overall darkness, and hence presumably in thermal biology. Individuals belonging to different color morphs were pooled into one of three color morph categories (dark, brown [i.e., intermediate], and pale) to obtain sufficient sample sizes in our test for effects of natural color morph on behavior. The category dark included general dark brown and black individuals, the category brown included medium brown and reddish brown individuals, and the category pale included grey and very light yellowish brown individuals.

To confirm that our paint treatments and light conditions in the thermal mosaic arena (see below) affected heating rates and equilibrium body temperatures, we compared body temperature of three sacrificed individuals painted black and three individuals painted white when placed 16 cm under a lamp (Philips, daylight, 60 W, 230 V) with a micro-thermocouple connected to a quick-reading digital thermometer (Fluke model 52 K/J, John Fluke Mfg. Co., Everett, WA) inserted in the thorax (Forsman et al., 2002). Temperature was recorded (to the nearest 0.1 °C) every 20 seconds for 10 minutes. As expected and shown before (Forsman et al., 2002), grasshoppers painted black warmed up faster and attained higher body temperature than grasshoppers painted white (Fig. 1).

1.3 Experimental thermal mosaic arenas

The experiment was performed in a laboratory room with constant temperature of 21.2 °C (±0.2 °C) during two weeks in late June 2009. Experimental arenas consisted of circular thermal mosaic gradients (Fig. 2). We know from earlier experience (Forsman, 2000) that individuals attempt to escape by jumping vigorously when close to the warmest end of a linear thermal gradient; to avoid this problem we used a circular arena that did not restrict the movements or expose animals to harmful body temperatures. The floor of each arena was made from a circular (32 cm diameter) piece of Styrofoam. The outer wall consisted of a cylinder (32 cm diameter, 9 cm high) made from premium transparencies for Xerox that enabled observation of animals inside the arena. The inner wall consisted of a smaller cylinder (16 cm diameter, 11 cm high) made from card board, to prevent light from the different lamps to interact. This design created an 8 cm wide circular ‘runway’ between...
the outer and inner cylinders, the floor of which was covered with white paper divided into 23 equal sized zones (Fig. 2). To manipulate the level of illumination and create a thermal mosaic, four lamps (Philips, daylight, 60 W, 230 V) were placed at different distances from the floor of the arena: 16 cm above zone 1; on the opposite side 43 cm above zone 12; and 28 cm above zone 7 and zone 18, respectively. The arena was covered with fine meshed mosquito net to prevent the grasshoppers from escaping while allowing illumination to penetrate into the cage. Three identical arenas were used, allowing simultaneous observations of three individuals. The arenas and attached light sources were rotated between trials to avoid systematic biases that may arise due to movements towards or away from certain directions or stimuli in the room.

At the onset of a trial, the black-painted, white-painted and unpainted individuals within a trio were arbitrarily assigned and transferred to one of the three identical arenas (A, B or C). All individuals were initially placed in zone 18, which was thermally intermediate. The position (i.e., zone number) of each grasshopper was recorded for the first time after 3 min and then again every 3 min for 1 h, giving 20 observations per individual. A total of 50 trios or 150 females were used in the experiment.

1.4 Thermal measurements

To confirm that the illumination conditions in the experimental arenas differently affected body temperatures, one white-painted and one black-painted grasshopper, both dead and attached side by side to a small piece of cardboard, were sequentially placed in the middle of each of the 23 zones in the experimental arena. Body temperature was recorded (when they had reached equilibrium, after approximately 5 min but with some variation among zones, to the nearest 0.1 °C) for the white and the black individual in each of the 23 zones, for each arena. To quantify the thermal mosaic, data from separate temperature recordings for the black and the white individual in each zone were used to compute a mean value for each zone and arena. This shows that the body temperatures available to grasshoppers inside the arena ranged from 29 to 40 °C depending on position, and that the same light gradient yields different temperatures for different color morphs at the same position (Fig. 2B & C). The magnitude of the difference in body temperature between black and white painted individuals within a given zone was small (ca 0.5 °C), and less than that among different zones. As a consequence, the resolution and statistical power is low, and our experiment constitutes as conservative test of the hypothesis. The range of temperatures in the arenas is narrower but within those experienced in the wild (Ahnesjö and Forsman, 2006).

To quantify repeatability of body temperatures obtained in different zones, we performed repeated measurements in three places (close to outer wall, in the middle and close to inner wall) in 8 zones (every third zone). A One-Way ANOVA ($r = 0.994$, $F_{7, 16} = 527.4$, $P < 0.0001$) indicated that differences in body temperature among zones are large and statistically significant relative to the minor differences in temperature among different spots within zones.

1.5 Statistical analyses

The spatial distances between different zones inside the arena did not correspond directly to thermal differences. For instance, zones 6 and 18 are separated by the maximum possible distance but similar in temperature, whereas zones 1 and 12 that differ most in temperature are separated by the same spatial distance as zones 6

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**Fig. 2** Experimental thermal mosaic arena

A. Circular experimental arena with four lamps (Philips, daylight, 60 W, 230 V) placed at different distances (16, 28 or 43 cm) above the arena to create a thermal mosaic gradient. B. Thermal environment, as quantified by average body temperatures obtained by *Tetrix subulata* individuals painted black or white, of the 23 different zones of the arena ranged from 29 to 40 °C. Dark and pale shading indicate warm and cold temperatures, respectively. Numbers 1, 2, 13 and 18 and 23 indicate position of different zones. C. Body temperatures obtained by individuals painted black or white inside different zones in the thermal arena. Values shown are means across the three different arenas.
and 18 (Fig. 2B). To account for this and evaluate the influence of thermal conditions per se on movement patterns inside the arena, while also taking into consideration that we performed repeated observations of each individual, we tested for differences in behavior between categories of individuals using repeated measures MANOVA on ‘mirror zones’. These were obtained by flipping all observations from the right-hand zones 2–12 onto the corresponding left-hand zones 13–23. Zone 1 was excluded from this flipping process and assigned a separate mirror zone, giving 12 different thermal mirror zones where mirror zone 1 was the coldest and mirror zone 12 was the warmest. Because our data violated the sphericity assumption, we used the MANOVA method for analyzing repeated measures designs, and the univariate tests of hypotheses for within subject effects (O’Brien and Kaiser, 1985, SAS, 1999). In this approach, the interaction between the within- and between-subjects factors answers the question whether individuals painted black or white differ in their temporal utilization of warm and cold zones in the arena.

In an additional analysis, we ignored the temporal patterns and instead tested for an effect on average mirror zone (i.e., temperature) of paint treatment and original colour morph using a mixed modelling approach, taking into account the repeated measures. This was implemented using procedure mixed in SAS (Littell et al., 2006). Mirror zone was the dependent variable, original color morph and paint treatment were fixed factors, and individual and population were random factors. The general Satterthwaite approximation was used for the denominator degrees of freedom.

Finally, we evaluated if our paint treatment influenced microhabitat utilization in a manner that recapitulated the natural tendencies in un-manipulated color morphs. For this purpose we tested for differences between naturally dark versus black painted individuals, and between naturally pale versus white painted individuals, using repeated measures MANOVAs on mirror zones, as described above.

All statistical analyses were performed with SAS 9.1.3 for Windows (SAS Inc., Cary, NC, USA) software package.

2 Results

Observations of the *T. subulata* grasshoppers’ behavior in the thermal mosaic showed that they moved around within the arena by walking or performing short jumps in what seemed to be an explorative manner and they frequently changed direction, as expected if they perceived that conditions became worse than where they came from. They seldom remained motionless for prolonged time periods or tried to escape.

Overall, our analyses of data on spatial distribution and movements of individuals revealed a relatively large overlap in the utilization of different zones between different categories of individuals. We also found significant behavioral differences between individuals that had been painted black or white, but not among unpainted individuals that belonged to natural pale, intermediate or dark color morphs.

2.1 Comparing different natural, unpainted color morphs

Results from repeated measures MANOVA on ‘mirror zones’ revealed no significant differences in temporal utilization of warm and cold zones in the thermal gradient among unpainted individuals that belonged to pale (*n* = 8), intermediate (*n* = 25) and dark (*n* = 17) morphs (effect of interaction of natural morph by time, $F_{2,38} = 0.63, P = 0.96$). Visual inspection of the data confirms that behavioral shuttling between warmer and colder zones through time was independent of natural color morph (Fig. 3).

When we ignored the temporal patterns and instead tested for an average effect, while taking into account the repeated measures by modelling individual as a random factor, we found significant differences among individuals (GLMM: $Z = 4.14, P < 0.0001$), but no effect on the average utilization of warm and cold zones of natural color morph (pale, brown or dark; $F_{2,43} = 0.75, P = 0.48$) or population of origin ($Z = 0.66, P = 0.25$).

2.2 Comparing individuals painted black or white

Repeated measures MANOVA on ‘mirror zones’ revealed a highly significant overall effect of time ($F_{1,19} = 2.32, P = 0.0011$) and a significant interaction of paint treatment by time (observation number 1 to 20) ($F_{1,19} = 1.63, P = 0.043$) on the behavioral utilization of warm and cold zones in the thermal gradient. Visual inspection of the data shows that, during the initial stage of the experiment, white-painted individuals used warmer zones than black-painted individuals (Fig. 4B).

When we ignored the temporal patterns and instead tested for an average effect, while taking into account the repeated measures by modeling individual as a random factor, we found significant differences among individuals (GLMM: $Z = 6.21, P < 0.0001$), but no effect on the average utilization of warm and cold zones of either paint treatment (GLMM: $F_{1,87.4} = 0.15, P = 0.70$), original color morph (pale, brown or dark; $F_{2,40.6} =$
Fig. 3 Utilization by *Tetrix subulata* individuals belonging to naturally dark, brown (intermediate) or pale color morphs of warm and cold zones inside the thermal arena as a function of time
Mirror zones were obtained by flipping all observations from the right-hand zones onto the corresponding left-hand zones, giving 12 mirror zones. Figure is based on pooled data for three arenas.

Fig. 4 Differential utilization by *Tetrix subulata* individuals painted black (black symbols) or white (white symbols) of different zones of a laboratory thermal mosaic
A. Frequency of observations for black- and white-painted individuals for each of the 23 thermal zones. Data for one arena only. The average body temperature of white and black painted grasshoppers in the mosaic ranged from 29 °C in zone 13 to 40 °C in zone 1. B. Utilization by black and white individuals of warm and cold zones inside the thermal arena as a function of time. Mirror zones were obtained by flipping all observations from the right-hand zones onto the corresponding left-hand zones, giving 12 mirror zones. Figure is based on pooled data for three arenas.

When we ignored the temporal patterns and tested for an average effect, while taking into account the repeated measures by modelling individual as a random factor, we again found no significant differences in the average utilization of warm and cold zones between naturally dark and black-painted individuals (GLMM: $F_{1, 64} = 0.63, P = 0.43$) nor between naturally pale and white-painted individuals (GLMM: $F_{1, 54} = 3.21, P = 0.079$) (Fig. 5).

3 Discussion
The matching habitat choice hypothesis posits that individuals with different phenotypes should choose different microhabitats, and that they should favor those habitats that best match their specific requirements in a manner that leads to increased fitness (Armsworth and Roughgarden, 2008; Edelaar et al., 2008; Ravigné et al., 2004). Edelaar et al. (2008) state that the most convincing evidence for matching habitat choice would be to demonstrate (i) that habitat preference is influenced by manipulation of an individual’s phenotype; and (ii) that the habitat preference translates into enhanced fitness.
In our present study, we have taken the first step by showing that black-painted *Tetrix subulata* pygmy grasshopper individuals attained higher body temperatures (Fig. 1) and behaved differently in the experimental thermal mosaic compared with white-painted individuals, at least during the initial stage of the experiment (Fig. 4). The differential preferences were not genetically determined, but resulted from modification of behavioral decisions in response to body temperature, affected by our manipulation of body coloration. Our findings demonstrate that microhabitat choice is plastic and represents a form of phenotypic flexibility. However, to the extent that choices and preferences of individuals are affected by phenotypic characteristics which are under the influence of genes, matching habitat choice may lead to spatial genetic structure within populations even if choice itself is flexible (Edelaar et al., 2008).

Our study was not designed to test if phenotype dependent choice enhances fitness. However, earlier investigations in pygmy grasshoppers have shown that body temperature in this species is crucial for many important physiological, behavioral and life-history traits (Ahnesjö and Forsman, 2003, Forsman, 1999a, b, 2000, 2001, Forsman and Appelqvist, 1998). For instance, we have previously demonstrated that dark morphs not only warm up faster and attain higher body temperatures when illuminated, they also prefer higher body temperatures (as estimated in a laboratory thermal gradient where heat came below from the surface and influenced all color morphs similarly, as opposed to via differential illumination as in the present study) compared with paler morphs (Forsman, 2000). Observations of free-ranging individuals in natural environments and laboratory thermal gradients have shown that differences in thermal properties and physiology among alternative color morphs translate into morph-specific microhabitat utilization (Ahnesjö and Forsman, 2006; Forsman, 2000; Forsman et al., 2002). The large spatial and temporal variation in morph frequencies documented in natural populations of *T. subulata* further indicate that relative fitness of alternative color morphs vary across different environments (Forsman et al., 2011). A long-term study of manipulated phenotypes should therefore provide a powerful means to evaluate the prediction that phenotype-dependent habitat choice will increase fitness (Edelaar et al., 2008). One way to test this would be to paint individuals black or white, experimentally subject half of them to the preferred environment and the other half to the less preferred environment without ability to choose, and then compare their survival and reproductive output.

A comparison of the outcomes of the two separate experiments reported here indicates that our phenotype manipulation did not completely recapitulate the natural tendencies seen in unmanipulated color morphs. Individuals that had been painted white used warmer zones than black-painted individuals, at least during the initial stage of the experiment (Fig. 4B). No such difference was evident between unpainted pale and dark individuals, if anything naturally pale individuals used slightly (but not significantly) colder zones on average compared with darker morphs (Fig. 3). A possible explanation to this discrepancy is that our comparison between natural morphs was based on a smaller sample size (50 individuals distributed among three color morphs) than our comparison between paint treatments (100 individuals distributed between two paint treatments), resulting in lower statistical power. An additional explanation for the discrepancy between painted and natural morphs is that natural individuals represent highly integrated com-

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**Fig. 5** Utilization by unpainted and painted *Tetrix subulata* individuals of warm and cold zones inside the thermal mosaic arena as a function of time

A. Comparison between unpainted individuals belonging to dark color morphs and individuals that had been painted black. B. Comparison between unpainted individuals belonging to pale color morphs and individuals that had been painted white. Mirror zones were obtained by flipping all observations from the right-hand zones onto the corresponding left-hand zones, giving 12 mirror zones. Figure is based on pooled data for three arenas.
bimations of morphology, physiology and behavior (Olson and Miller, 1958; Pigliucci and Preston, 2004; Sinervo and Svensson, 2002). Color patterns have been shown to be genetically, developmentally and functionally associated with morphology, physiology, behavior and life-history traits in several different species of animals (True, 2003; McKinnon and Pierotti, 2010), including pygmy grasshoppers (Ahnesjö and Forsman, 2003; Forsman et al., 2002; but see Hochkirch et al., 2008). It is therefore possible that, since darker morphs warm up faster when illuminated but also prefer higher body temperatures compared to paler morphs (Forsman, 2000), naturally dark and pale morphs may have been able to fulfill their specific thermal requirements without behaving differently in the arenas. It is also possible that, by experimentally decoupling the individual’s pigmentation pattern and heating rates from their natural physiological and behavioral phenotypic properties, we may have prevented the painted animals from making appropriate microhabitat choices in the current experiment.

We did not evaluate fitness consequences of microhabitat choice in the current study, but the color polymorphism in *T. subulata* may represent a candidate example of one of the main ideas of the matching habitat choice hypothesis, namely that as a consequence of phenotype dependent choice, different individuals within the same population may simultaneously reach different fitness peaks in the adaptive landscape (Edelaar et al., 2008). Whether the alternative pygmy grasshopper morphs have evolved because different color variants originally chose different but matching habitats or whether different morph-specific microhabitat preferences have evolved because the alternative morphs represent complex phenotypes with different demands and requirements remains an open question.

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