Intersexual niche segregation in Cepero's Ground-hopper, *Tetrix ceperoi*

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Abstract   Sexual differences in habitat preferences have been reported from a variety of animal taxa. However, the ultimate causes for this intersexual niche segregation remain poorly understood. It has been suggested that sexual dimorphism is a consequence of dimorphic niches based upon different reproductive costs and activities of the sexes. Here we provide evidence from field data to examine this hypothesis by studying the behavioral background of niche segregation in *Tetrix ceperoi*. Our data revealed distinct sexual differences in the substrates on which the insects perched and in the solar radiation of these locations. Males were found at brighter locations and more often on bare ground than females. Incorporation of behavioral data in our analysis showed that patches of bare ground were mainly utilized during mating behavior, in which males invested more time than females. In contrast, females spent more time resting and feeding in the vegetation. Intersexual differences in the proportion of autotomized individuals indicate that males might suffer higher predation risks. These patterns support the dimorphic niches hypothesis, which suggests that differential habitat utilization is caused by differences in the life history strategies of males and females, since males should accept a higher predation risk due to the benefits of multiple matings. Females should invest more time in gaining nutrients and energy for egg production and survival, whereas males should spend more time with searching for mates. We suggest that behavioral covariates should more often be implemented in ecological analyses, since these might have a strong explanatory power.

Keywords   Sexual dimorphism · Microhabitat choice · Intersexual competition · Habitat preferences · Sexual selection

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Introduction

Individuals of a population or species often exhibit noticeable differences in habitat utilization (Bolnick et al. 2003), which are particularly pronounced in differential habitat use of the sexes in many taxa (Selander 1966; Schoener 1967; Lewin 1985; Jormalainen and Tuomi 1989; Andersson 1994; Ardia and Bildstein 1997; Temeles et al. 2000). The causes for such intersexual differentiation remain poorly understood and controversial (Lande 1980; Slatkin 1984; Shine 1989). During the last decades, a number of hypotheses have been proposed to explain this phenomenon (Slatkin 1984; Hedrick and Temeles 1989; Shine 1989; Ruckstuhl and Neuhaus 2000).

A major hypothesis explaining intersexual niche segregation (INS) is the dimorphic niches hypothesis, which proposes that INS is mainly caused by differential energetic requirements of the sexes due to different costs of reproduction (Slatkin 1984; Hedrick and Temeles 1989; Bowyer 2004). Female egg production is generally believed to be more expensive than male sperm production (Andersson 1994; Gherardi 2004) and the benefits of multiple matings are often higher for males than for females, which are constrained by their own egg production (Andersson 1994; Rowe 1994). Hence, females should maximize their egg production by feeding and resting and males should maximize their own fitness by increasing their mating frequency. The dimorphic niches hypothesis, therefore, implies a correlation between niche utilization and behavioral traits related to the life history strategies of the sexes, such as females utilizing special feeding habitats to gain more energy for egg production and males accumulating in microhabitats, which are used for courtship or mating. Another hypothesis explaining INS is the sexual selection hypothesis (Lande 1980), which predicts that sexual dimorphism might be caused by competition for mates. However, it should be noted that different life history strategies of males and females also imply different strategies to obtain matings. If males benefit from multiple matings more than females, this increases competition among males and causes sexual selection. Hence, it will be difficult to distinguish between both hypotheses and the latter hypothesis should be encompassed under the dimorphic niches hypothesis.

The dimorphic niches hypothesis is also referred to as "fecundity selection" (Reeve and Fairbairn 1999) or "predation risk hypothesis" (Main et al. 1996; Merilaita and Jormalainen 1997). The latter hypothesis predicts that sexual differences in the importance of avoiding predators can explain the sex difference in microhabitat choice (Merilaita and Jormalainen 1997). We consider avoidance of predation to be a special aspect of the dimorphic niches hypothesis, since males should also accept a higher predation risk due to the benefits from multiple matings. The same is true for the "activity budget hypothesis" (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000), which proposes that sexual differences in activity budgets and movement rates are key factors of intersexual social segregation, although this does not necessarily lead to habitat segregation (Ruckstuhl and Neuhaus 2000). Since grasshoppers are solitary insects, this hypothesis is not applicable to this group, but there is a strong overlap of the dimorphic niche hypothesis and the activity budget hypothesis, since both are based on intersexual differences in energetic requirements.

Here we use evidence from field data to examine the dimorphic niche hypothesis by studying the behavioral background of niche segregation in Cepero's

Ground-hopper, *Tetrix ceperoi*. We first examine whether INS occurs in this species and in which factors the sexes differ in microhabitat utilization. We then analyze several expectations based upon the dimorphic niches hypothesis: (1) Due to the different life history strategies, males should invest more time in mating behavior and females should spend more time with feeding. (2) These differences in activity patterns should be related to microhabitat utilization and explain the pattern of INS, with females utilizing more often the type of microhabitat, which is most suitable for feeding and males the microhabitat, which increases the number of matings. (3) Since males may maximize their fitness by multiple matings, they should tolerate a higher predation risk than females. A higher predation pressure on males should lead to a higher number of autotomized individuals. (4) Adaptations to INS should incorporate adaptations to the microhabitat-specific background coloration in order to minimize predation risk. This should lead to intersexual differences in body coloration.

Methods

The study object

Cepero's Ground-hopper, *Tetrix ceperoi*, is a West-Mediterranean Orthopteran species, which reaches the north-eastern edge of its range in Central Europe (Kleukers et al. 1997). It is usually restricted to damp, warm habitats, such as dune valleys, sand pits, drainage ditches or heath ponds (Marshall and Haes 1988). On the isle of Langeoog (East Frisian Islands, Lower Saxony, Germany), this pioneer species is rather common and can be found in virtually all damp habitats, except for extremely salty sites (Gröning et al. 2005, in press). On the mainland it is rare and specialized on warm, open habitats, where it seems to compete with other *Tetrix* species. As most Tetrigidae, *T. ceperoi* is terricolous and color polymorphic with all the common morphs being cryptic (Paul 1988). Sexual size dimorphism (SSD) is distinct and, as in all Caelifera, the females are much larger than the males due to one additional instar (Ingrisch and Köhler 1998). Adults of this species reproduce in May and June (Kleukers et al. 1997). Tetrigidae do not possess a tympanum and do not stridulate, but males perform visual courtship displays when they encounter a female (Hochkirch et al. 2006). Ground-hoppers feed on a variety of algae, mosses, small plants and detritus (Hochkirch et al. 2000), which were abundant on all of our study sites.

Collection of field data

We studied microhabitat parameters in relation to behavior and sex of 487 randomly chosen individuals on the isle of Langeoog, where the species occurs in its only remaining natural habitats in Germany (Gröning et al. 2005). Field work was carried out during the main reproductive period of *T. ceperoi* from May 07, to June 26, 2004. Prior to the field work, the occurrence of *T. ceperoi* on the isle was mapped to locate study sites with sufficiently high abundances. Six sites were chosen for the field records, such as damp dune valleys and transition zones between dunes and salt marshes (see Gröning et al. in press for the exact geographic positions). Other Tetrigidae species (possible competitors) were virtually missing on Langeoog and

absent from all of our study sites. For the analysis of microhabitat preferences, data were obtained at the exact location of randomly chosen individuals during their time of activity (between 11.00 and 17.00). Recorded data included date, time, weather conditions, sex, and color morph. Tetrigidae are known to exhibit pronounced color polymorphism, which is often sex-related (Forsman and Appelqvist 1999; Paul 1988). We distinguished twenty different color morphs, which were grouped in six simpler categories (see Fig. 1d). The substrate, on which the specimen perched was noted, including the categories bare ground, litter, mosses, algae, and higher plants (grasses, forbs). Radiation was measured using a luxmeter, Elvos LM 1010. Temperature measurements of the substrate on which the insect perched and of the insect's body (pronotum) were made with a digital infrared thermometer (Raytek MiniTemp™). The vegetation cover was estimated in a circle of 30 cm diameter surrounding the focal insect, including the relative frequency of the following categories: bare ground, grasses, forbs and dwarf shrubs, litter, and mosses. Furthermore, the
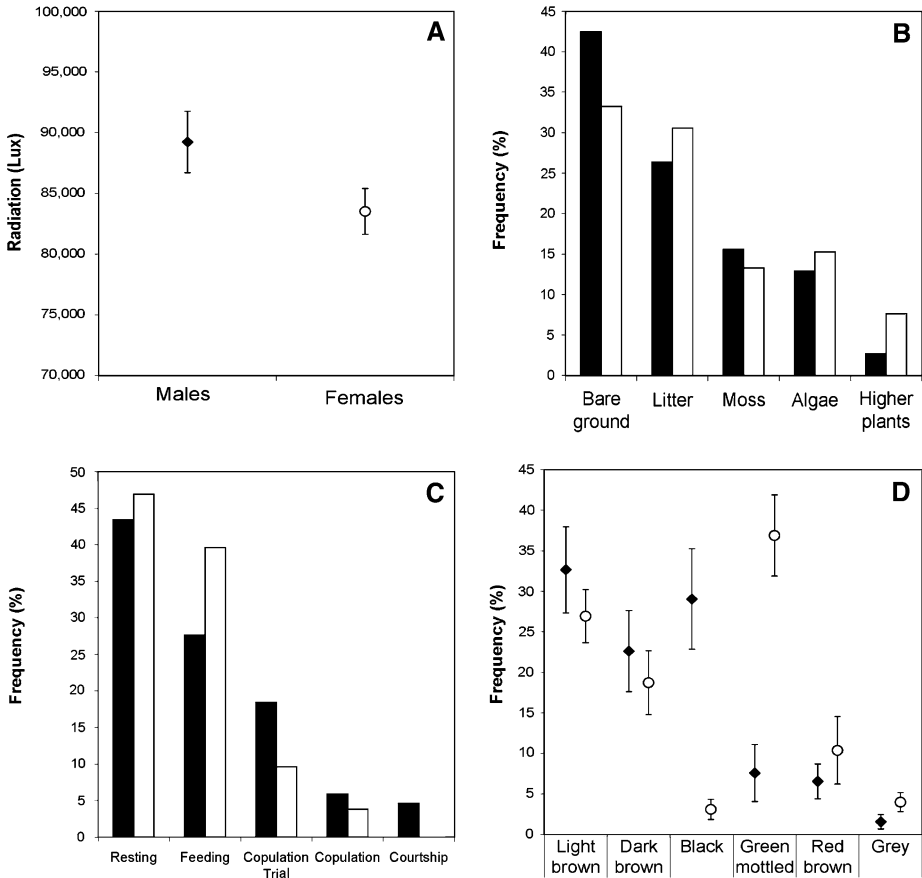

Fig. 1 Intersexual differences in regard to mean radiation (**A**), mean percentage of utilized substrates (**B**), behavior frequencies (**C**), and color morph frequencies across the six study sites (**D**). *Black columns* represent males, *white columns* females, and *error bars* are standard errors. Males were found more often on bare soil and at brighter locations than the females. They invested more time in mating behavior (copulation trials, copulation, and courtship) and less time in feeding. The *black color* morph was more common in males, while the *green-mottled* morph dominated in females

activities of each individual during the first minute of the observation were noted (e.g., resting, feeding, courtship, and mating). Since Orthoptera readily shed hind legs in response to predation (autotomy), we noted the number of autotomized hind legs as an indicator of predation pressure (Dixon 1989).

Statistical analyses

Microhabitat differences between the sexes (INS) were analyzed with the full data set of 487 records of adult individuals. Since we obtained individual data sets rather than abundance data, we used ''sex'' as explanatory factor and the measured parameters as response variables. Metric data were analyzed using ANOVA and if necessary boxcox-transformed using Venables and Ripley's MASS library for R (Venables and Ripley 2002). If even boxcox-transformation revealed no suitable distribution for ANOVAs, we conducted non-parametric Kruskal–Wallis rank sum tests (vegetation cover). We used chi-square cross table tests to analyze nominal data such as substrate, behavior patterns or autotomy rates. To test for sexual differences in color morph frequency, we performed generalized linear models (GLM, family: quasipoisson) with the proportion of each color morph for each study site and sex as response variable. This procedure should correct for effects of site-specific background coloration on the color morph frequency.

For the analysis of behavior-related microhabitats a relevant subset of the data was considered (412 records), including only the major behavior categories ''Mating behavior'' (including copulations, copulation trials, and courtship), ''Resting'', and ''Feeding.'' For categorical data (substrate), we analyzed a multidimensional contingency table to test for interactions between the explanatory variables ''sex'' and ''behavior.'' We first fitted a saturated generalized linear model (GLM, family: poisson, equivalent to log-linear model), by including all possible interactions. Then we simplified the model by stepwise removing non-significant interactions (Crawley 2005). For suitable metric data (temperature, vegetation height), we performed two-way ANOVAs, using ''sex'' and ''behavior'' as explanatory variables to test for interactions among these factors. In case of significance, we conducted multiple t-tests with Bonferroni correction to find the most important behavior type influencing our data. All tests were carried out with ''R 2.3.0'' (R Development Core Team 2006).

Results

Intersexual niche segregation

Males and females differed in their microhabitat utilization with respect to radiation and substrate (Fig. 1). The radiation was higher at the location of males than at the location of females (Fig. 1a, ANOVA: $\lambda = 1.39$, $F_{1,485} = 4.56$, $P = 0.033$). In addition, the utilized substrates differed significantly between the sexes (Fig. 1b, chi-square cross table test: $\chi^2_5 = 33.52$, $P < 0.001$). While males were found more often on bare ground and mosses, females perched more frequently on grass litter and algae. Moreover, the frequencies of behavior types differed significantly between the sexes (Fig. 1c, chi-square cross table test: $\chi^2_5 = 42,57$, $P < 0.001$). Males invested more time in mating behavior (courtship, copulation trials, and copulations), while

females were found more often resting or feeding. The analysis also revealed intersexual differences in color morph frequencies (Fig. 1d). While the black morph was more common among males (GLM, t_{11} = 3.92, P = 0.003), the green-mottled morph was predominant in the female sex (GLM, t_{11} = -3.69, P = 0.004). The autotomy rate was significantly higher in males than in females. Whereas 14.4% of the males had lost a hind leg, only 9.6% of the females suffered a loss of legs (chi-square cross table test: χ^2_1 = 29.11, P < 0.001).

Behavior-related microhabitats

A strong relation between behavior types and microhabitats was detected, especially with respect to feeding and mating behavior. While the latter type of behavior was mainly performed in areas with a high percentage of bare ground, the feeding habitat had a higher vegetation cover, especially of grasses and mosses (Table 1). The habitat utilized during mating behavior was also characterized by a higher radiation compared to feeding and resting habitats (Fig. 2a). Concerning the substrate, *T. ceperoi* used to perch more often on bare ground during mating behavior than when resting or feeding (chi-square cross table test: χ^2_8 = 39.98, P < 0.001; Fig. 2b). To test for interactions between the explanatory variables "sex" and "behavior", we analyzed a multidimensional contingency table for the factor "substrate" and stepwise simplified the model. This analysis revealed no significant three-way interaction and no interaction between sex and substrate. Our final model explained 96.0% of the deviance and contained significant interactions between behavior and substrate (P < 0.001) as well as between sex and behavior (P < 0.001).

The data suitable for ANOVA (body temperature, temperature of the substrate, vegetation height) were tested with two-way ANOVAs for interactions between the explanatory variables behavior and sex. There was a significant relationship between body temperature and behavior (two-way ANOVA, λ = 0.85, $F_{2,406}$ = 4.38, P = 0.013), based on a difference between mating behavior (27.5°C ± 0.71) and feeding (25.1°C ± 0.48, pairwise *t*-test with Bonferroni correction, λ = 0.85, P = 0.014). Resting behavior (25.9°C ± 0.41) did not differ significantly from those

Table 1 Relation between the main behavior types and the microhabitat preferences of *T. ceperoi* (Kruskal–Wallis rank sum test, n = 412, df = 1)

| Factor	Behavior	χ^2	P
Radiation	Mating behavior[a]	3.869	0.049
	Foraging	1.265	0.261
	Resting	0.228	0.633
Vegetation cover			
Bare ground	Mating behavior[a]	10.011	<0.002
	Foraging	2.992	0.084
	Resting	0.713	0.398
Grasses	Mating behavior	0.037	0.848
	Foraging[a]	5.195	0.023
	Resting[a]	4.121	0.042
Mosses	Mating behavior	1.352	0.245
	Foraging[a]	4.385	0.036
	Resting	1.177	0.278
Forbs	Mating behavior[a]	5.097	0.024
	Foraging	3.663	0.056
	Resting	0.003	0.960

[a] Significant
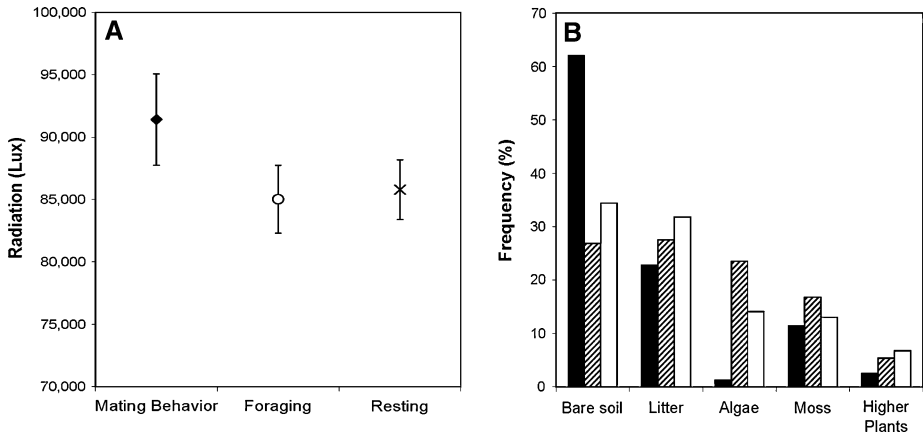
Fig. 2 Behavior-related microhabitats concerning radiation (**A**) and substrate (**B**). The three behavior types courtship, copulation trials, and copulations were summarized to mating behavior. Specimens engaged in mating behavior (*black columns*) were found at brighter conditions and more often on bare soil, while foraging specimens (*hatched columns*) were found more frequently on algae (*white columns*: resting)

behavior types. No effect of sex and no interaction between sex and behavior were found. Vegetation height and substrate temperature were not related to behavior or sex.

Discussion

Our data clearly support the dimorphic niches hypothesis, since we found (1) different activity patterns of males and females in the expected direction, (2) a strong relation of the most important behavior types (feeding, mating behavior) to special microhabitats, (3) a higher predation pressure on males than on females, and (4) even sex-specific color-polymorphism closely related to the preferred microhabitats. Males of *T. ceperoi* invest more time in mating activities than females and perform their courtship displays preferably on bare ground, which they generally prefer as substrate (Gröning et al. in press). The association of males with special habitats for courtship has been documented in a variety of other animal taxa (Andersson 1994). Females utilize these habitats less frequently, since they do not profit from multiple matings, being constrained by the number of eggs they can produce. Female grasshoppers oviposit every 3–4 days and are receptive only for a short time after oviposition (Ingrisch and Köhler 1998). In some grasshopper species, one copulation is sufficient to fertilize all subsequently produced eggs during a females life. Hence, females may maximize their offspring by increasing their life span, whereas males may maximize their reproductive success by copulating with a high number of females. The courtship displays of Tetrigidae mainly consists of visual signals. *T. ceperoi* males perform a fast synchronous movement of hind legs and pronotum with high amplitude ("pronotal bobbing") when they encounter a female (Hochkirch et al. 2006). It is reasonable to suggest that such visual signals are better visible in open habitats (Endler 1992). Males, therefore, might enhance their mating success by performing courtship displays on bare ground. Females also prefer bare

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ground as substrate (Fig. 1b), but the relative number of specimens on this substrate was lower than in males.

The higher autotomy rate in the male sex indicates a trade-off between improving courtship success and avoiding predators (Rowe 1994). Male mate finding behavior includes conspicuous movements, such as locomotion and courtship displays. This might increase their susceptibility to potential predators despite of their cryptic coloration. The coloration of both sexes closely resembles the preferred microhabitat: males are often black or brownish colored, which corresponds to the color of bare ground, whereas the green-mottled color morph predominates in the females, which are therefore well camouflaged in the vegetation (Fig. 1d). Nevertheless, the vegetation might provide additional shelter and females might thus suffer lower predation risks.

Females of *T. ceperoi* prefer algae and grass litter as substrates and spend more time with feeding, as has been shown in many other grasshopper species (Hochkirch 1999). This pattern matches their higher nutritional requirements, since egg production is more costly than sperm production (Shine 1989; Andersson 1994; Gherardi 2004). Moreover, the larger body size of females compared to males increases their energetic requirements further (Chapman 1990). Based upon the dimorphic niches hypothesis, females would be expected to achieve more energy by feeding and resting and males should be more active and invest more time in courtship and mating behavior (Jormalainen and Tuomi 1989; Ruckstuhl and Neuhaus 2000). These differential life history strategies and physiological demands will ultimately lead to differing natural and sexual selection pressures between the sexes (Lande 1980). The ecological effects of differential reproductive costs seem to be mainly mediated through intersexual differences in behavior frequencies. In fact, our multidimensional contingency table and the two-way ANOVAs revealed that behavioral effects accounted for all intersexual habitat differences and no statistic interactions occurred. Both, intersexual behavioral differences and INS are closely related considering the fact that all types of behavior have an ecological as well as an ethological dimension. Thus, animals should utilize special habitats for special behavior types due to the differential requirements for these activities. Many studies might have missed this relation, by studying INS and omitting behavior as a possible explanatory variable.

Intersexual differences in activity pattern have been found in many taxa and are particularly well studied in mammals (Ruckstuhl and Neuhaus 2002). It has been proposed that the costs of synchronizing male and female activity patterns might be higher than the costs of intersexual social segregation (activity budget hypothesis, Ruckstuhl 1998). In the case of *T. ceperoi* differences in the activity patterns occur, but they do not lead to social segregation since grasshoppers are non-social animals. The activity budget hypothesis is only applicable to social animals. Nevertheless, the background behind this hypothesis is rather similar to the dimorphic niches hypothesis (i.e., differential energetic requirements of the sexes).

The predation risk hypothesis suggests that the sexes should differ in the risks they are prepared to take in order to acquire resources (Main et al. 1996). Similar to the dimorphic niches hypothesis, the key assumption of this hypothesis is that the sexes differ in their reproductive strategies (Merilaita and Jormalainen 2000; Ruckstuhl and Neuhaus 2002). Indeed, we found a higher proportion of autotomized individuals in males than in females, supporting these hypotheses. In many species predation is greater in the male than in the female sex (e.g., Jormalainen and Tuomi

1989). Nevertheless, in the case of predation it is even more difficult to disentangle cause and effect. A differential predation risk might either be an effect of higher predation pressure on males due to their higher activity levels (Rowe 1994) or their displays in open habitats (Butler and Losos 2002), or it might be an effect of lower predation on females, which might select safer habitats in order to reduce the risk of predation (Bon et al. 2001). Based upon our data, it is not possible to distinguish whether microhabitat choice is influenced by the predation risk or vice versa. There are more drawbacks to these conclusions. Although autotomy rates have been used to estimate predation risks before (Dixon 1989) and are probably the easiest way to estimate predation pressure in the field, these results should be treated with caution. Firstly, leg-loss could be an indicator of successful escape rather than an indicator of predation risk. It remains unknown how it correlates with the numbers of killed individuals. Secondly, Orthoptera loose hind legs also during molt, which might be more difficult on bare ground than on plants (Hochkirch et al. 1999). In this case, one would expect a higher autotomy rate in females, which face a higher risk of leg loss due to an additional instar. This pattern was confirmed in breeding experiments in the absence of predation (unpublished data). Hence, the higher proportion of autotomized males in the field could in fact be caused by predators rather than by molt.

It is commonly assumed that color morphs in Tetrigidae are genetically determined (Nabours 1937; Forsman and Appelqvist 1999) and naturally rather than sexually selected. Evidence from laboratory breeding experiments (unpublished data) suggest that the body coloration of *T. ceperoi* is also environmentally influenced (homochromy). Specimens reared on dark substrates are more likely to become black than individuals reared on light substrates. Hence, the observed sex-specific color polymorphism could also be a consequence of INS rather than its cause. A strong correlation between color morph dimorphism and INS has also been found in other color polymorphic organisms (Jormalainen and Tuomi 1989; Calver and Bradley 1991; Forsman and Appelqvist 1999). Mate choice experiments did not support the hypothesis that sexual selection plays a role in color polymorphism of *T. ceperoi*, since female choice was not influenced by male coloration (unpublished data).

Sexual dimorphism in resource use has been reported from a wide range of animal species. A number of studies have supported the dimorphic niches hypothesis (e.g., Shine 1991; Merilaita and Jormalainen 1997; Butler and Losos 2002; Ruckstuhl and Neuhaus 2002), but there is also evidence for intersexual competition in some taxa (Ardia and Bildstein 1997; Temeles et al. 2000). However, in systems with high food availability intersexual competition for food is unlikely (Merilaita and Jormalainen 1997). *T. ceperoi* feeds on a variety of algae, mosses, litter and grass sprouts, which were abundant at all study sites. Females of *Tetrix* species might be able to utilize a broader range of plants due to their larger body dimensions (Hochkirch et al. 2000), but there is no evidence for intersexual competition for food. Moreover, the intersexual differences in habitat utilization mainly concerned substrate and radiation (Fig. 1), which means that the sexes of *T. ceperoi* segregate in terms of space rather than in terms of food. Since competition for space is more likely to cause interference than exploitation, one would expect to observe aggression between individuals in order to attain the most suitable localities. However, aggressive interactions have never been reported in Tetrigidae, except for sexual harassment. Another argument against intersexual competition is the observation that the direction of niche

segregation in *T. ceperoi* is very similar to other Orthoptera species (Calver and Bradley 1991; Forsman and Appelqvist 1999; Hochkirch 1999; Hochkirch et al. 2000), while intersexual competition would predict that both sexes are equally likely to exploit a particular part of the environment. The stronger preference of bare ground in males is even identical to a related species, *Tetrix subulata* (Forsman and Appelqvist 1999; Hochkirch et al. 2000). It might be argued that under the special island conditions of Langeoog, the absence of congeneric competitors might allow the sexes to segregate further than on the mainland due to a broader range of available resources (Butler et al. 2000; Selander 1966). In our system it was indeed striking that *T. ceperoi* utilized a rather broad spectrum of habitats (salt marsh, damp pastures, ditches, ponds, and dune valleys), while on the mainland it occurs exclusively in warm habitats, such as sand pits (Gröning et al. 2005, in press). However, even if competitive release might reinforce INS, this does not imply that intersexual competition is the driving force for sex-specific habitat utilization.

Most studies on sexual dimorphisms deal with SSD rather than with INS. Intersexual differences in body size are common and often closely related to differential ecology of the sexes (Selander 1966; Ruckstuhl and Neuhaus 2002). Therefore, it has been questioned whether INS might be a selective force driving SSD, a passive consequence of SSD or a mechanism to allow a reduction or prevent an increase of SSD (Shine 1989). In contrast to vertebrates, where size dimorphism is rather variable (Carothers 1984; Lewin 1985; Ruckstuhl and Neuhaus 2002), the females of all grasshopper species are larger than the males (Ingrisch and Köhler 1998). SSD, therefore, seems to be an ancestral trait in Tetrigidae, particularly since it is constrained by an additional instar in the female sex. In such an advanced stage of SSD the primary selective forces are difficult to disentangle (Lande 1980). SSD might act as additional selective force supporting INS by reinforcing the sex-specific energy budgets. Since in many insects large body size and egg production are linked in the female sex, SSD and INS are possibly driven by the same selective force: the need of females to produce eggs (larger body size) and the benefits of multiple matings for males (higher mobility).

In conclusion, we suggest that the dimorphic niches hypothesis has the potential to explain all of the observed sexual differences in body size, behavior patterns, microhabitat use, predation risk and color polymorphism. The differential energetic requirements of the sexes force females to invest more time in feeding and males to maximize their number of matings. For these behavior types special microhabitats are utilized, which differ in predation pressure leading to sex-specific autotomy rates and color patterns. Since a suitable habitat of any species has to provide all necessary resources for both sexes and all life stages (Uvarov 1977), INS needs to be considered in conservation management (Bowyer 2004). INS is likely to have significant effects on the evolutionary future of an animal species, since it reduces intraspecific competition (Selander 1966), enhances the maintenance of genetic polymorphism (Hedrick 1993) and inhibits disruptive selection (Bolnick and Doebeli 2003). More experimental studies are needed to distinguish between the alternative hypotheses.

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