A Field Study of the Escape Behaviour of *Tetrix subulata* (LINNAEUS, 1758) and *Tetrix tenuicornis* (SAHLBERG, 1893) (Orthoptera: Tetrigidae)

Axel Hochkirch, Marco Zimmermann, Christian Keithahn, Stefan Länder, Andrea Peiter, Michael Folger-Rüter, Carola Harmuth, Stefan Vogt, Marion Zimmermann, Frauke Hellwig, Anke Gulau & Helge Mühl

Zusammenfassung

Das Fluchtverhalten von Heuschrecken ist noch weitgehend unerforscht, obgleich es eine der auffälligsten Verhaltensweisen ist. Insbesondere fehlen Untersuchungen zur Fluchtstrategie, -richtung und der Auswirkung der Habitatstruktur auf das Fluchtverhalten. Gerade bei den unauffälligen Tetrigiden liegen nur sehr spärliche verhaltensbiologische Daten vor. Im Rahmen eines verhaltensökologischen Praktikums der Universität Bremen wurden im Frühjahr 1998 Freilanduntersuchungen zum Fluchtverhalten von *Tetrix subulata* und *Tetrix tenuicornis* gemacht. Hierbei sollten auch die Hypothesen kontrolliert werden, ob Tetrigiden bevorzugt in Richtung von Gewässern flüchten (HIRSCHFELDER 1994), oder ob es sich um zufällige Sprünge in Gewässer handelt (SCHMIDT 1996). Im Rahmen des Praktikums wurde das Fluchtverhalten der beiden Arten, der Geschlechter und von Tieren mit einem fehlenden Hinterbein verglichen. Der Einfluss ökologischer Faktoren (Temperatur, Wetter, Vegetationsdichte, Vegetationshöhe und Aufenthaltsort) auf das Fluchtverhalten wurde bestimmt. Des weiteren wurde die Ausrichtung des Fluchtsprunges untersucht. Auf der Untersuchungsfläche (einer Sandgrube im Bremer Niedervieland) war *Tetrix subulata* deutlich häufiger als *Tetrix tenuicornis* und bei beiden Arten waren die Weibchen in der Überzahl. Tiere mit einem fehlenden Hinterbein traten recht häufig auf (ca. 18-20%). Beide Arten führen meist nur kurze Fluchtsprünge (⌀ 30 bis 40 cm) aus, die direkt von der Quelle der Störung wegführen (üblicherweise in einem Winkel von 180° von der Störung. Diese Fluchtrichtung ist weder von der Vegetationsstruktur oder nahe liegenden Gewässern, noch von der Ausrichtung der Körperlinie beeinflusst. Die Ursache hierfür könnte ein „trade-off" zwischen den Vor- und Nachteilen der Verhaltensweisen „Springen" und „Verstecken" sein. In der Vegetation können Tetrigiden sich verkriechen, haben allerdings Schwierigkeiten bei erneuten Fluchtsprüngen. Auf offenem Sand ist ein erneuter Fluchtsprung einfacher durchzuführen, jedoch sind die Tiere hier für einen potentiellen Prädator einfacher zu entdecken. Die gute Tarnung von Tetrigiden könnte hierbei ebenfalls eine wichtige Rolle spielen. Manchmal bringen sich die Tiere zunächst in eine bessere Position, um von der Störquelle zu fliehen. Die Sprungweite wird vom Geschlecht, der Zahl der Hinterbeine, der Lichteinstrahlung und der Vegetationshöhe beeinflusst. Männchen von *Tetrix subulata* springen weiter als Weibchen, was wahrscheinlich auf das höhere Gewicht der Weibchen durch Eipakete, aber auch auf den (damit zusammenhängenden) unterschiedlichen Energie-Haushalt

zurückzuführen ist. Individuen, die in der Sonne sitzen, springen weiter als bei Bewölkung. Höhere Vegetation verhindert lediglich die besonders weiten Sprünge, die von sonnenexponierten Individuen durchgeführt werden. Tetrigiden nutzen meist nicht ihre volle Sprungfähigkeit (bis zu 110 cm) um zu entkommen. Dies kann verschiedene Ursachen haben. Zum einen gibt es vermutlich physiologische Hindernisse, wie etwa die Biegung der Hinterbeine zum Zeitpunkt der Störung, oder die Synchronisierung beider Beine (nur bei synchroner Auslösung des Sprungmechanismus ist die maximale Weite erreichbar). Es ist allerdings wahrscheinlicher, dass die energetischen Kosten eines weiten Sprunges höher sind als der Profit. Aufgrund der guten Tarnung und der kleinen Körpergröße potentieller Prädatoren, ist ein kurzer Fluchtsprung (30-40 cm) ausreichend. Die Fluchtrichtung (weg von der Störung) scheint bedeutender zu sein als eine hohe Sprungdistanz.

Abstract

The escape behaviour of *Tetrix subulata* and *Tetrix tenuicornis* was studied in their natural environment in northern Germany. Both species perform usually a short jump ($\varnothing$ 30 to 40 cm) directed straight from the stimulus when disturbed (usually in an angle of 180°). The jump direction is neither influenced by vegetation structure or nearby waters, nor by the direction of the body axis. A trade-off between the possibilities of jumping and hiding seems not to favour dense vegetation or bare sand as a landing point. The jumping range is affected by sex, number of hind legs, radiation and vegetation height. Male *Tetrix subulata* jump significantly longer than females, probably due to the weight of egg-loads and different energy budgets of egg-producing females. Sun-exposed individuals jump longer distances than during clouded conditions. High vegetation inhibits only longer jumps, which are performed by sun-exposed insects. The species usually do not use their full jumping power to escape (up to 110 cm). This might be influenced by physiological constraints, such as flexion of hind legs and synchrony of the movement, but it is more likely that the energetic costs of a long jump are higher than the profit. The good camouflage and the small size of potential predators favour short escape distances.

Introduction

The ability to jump is the most striking feature of grasshoppers. It is a major means of predator escape and, therefore, an important behaviour for the evolutionary fitness of those insects. Neural mechanisms, energetics and ontogenetic fluctuations of jumping performance in grasshoppers are rather well studied (PEARSON & O'SHEI 1984, BENNET-CLARK 1990, QUEATHEM 1991). The basic knowledge on escape strategies, however, is still limited. In particular nothing is known on the direction of the escape jump and on effects of the habitat structure on jumping performance, although it can be readily assessed.

Even among the well-studied fauna of Central Europe, ground-hoppers (Tetrigidae) belong to the worst studied group of Orthoptera. This is due to their small body size, their inconspicuous appearance, the lack of any sound production and

their unusual life cycle. Many Tetrigidae species are found in marshy places, some are even semi-aquatic and good swimmers and divers (PARANJAPE et al. 1987). They are regarded as a primitive group of caeliferan Orthoptera, feeding mainly on lower plants, such as algae, mosses, fungi, lichens and on detritus material (PARANJAPE et al. 1987). Ground-hoppers show polychromatism and, therefore, are well camouflaged. Only sparse data is available on escape behaviour of Tetrigidae. *Tetrix undulata* (SOWERBY, 1806) is known to jump a distance of 0.7 m, which is an enormous range in relation to its mass of 0.05 g (GABRIEL 1984). *Tetrix subulata* is believed to have a directed escape behaviour, trying to reach a water, where it escapes by swimming and diving (HIRSCHFELDER 1994). This observation, however, was doubted by SCHMIDT (1996), who assumed that jumps into waters are accidental and that the species escape in all directions.
The research objectives of this study were:

- a comparison of the escape strategy and jumping performance of two closely related, similar-sized *Tetrix* species in the same habitat, of males and females and of individuals with both hind legs and those missing one hind leg
- the influence of ecological factors on jumping performance, such as temperature, weather, vegetation density, vegetation height and location
- the direction of the escape jump in relation to the direction of the stimulus and to vegetation structure.

Methods

Subjects and Study Site
The two studied species *Tetrix subulata* and *Tetrix tenuicornis* are dimorphic in appearance. In both species a short-winged (and brachypronotal) and a long-winged (and macropronotal) morph exists (KLEUKERS et al. 1997). At the study site only the short-winged morphs occur, which are not able to fly. The Holarctic distributed *Tetrix subulata* can be found at marshy locations, such as river shores, stream valleys and ditches. It is threatened by dehydration of wetlands. The Palaearctic *Tetrix tenuicornis* is restricted to dry locations. It is endangered in north-western Germany and in urgent need of conservation in Bremen (GREIN 1995, HOCHKIRCH & KLUGKIST 1998). At the study site both species occur syntopic.
The study site ("Niederbürener Sandfeld") is located in the state of Bremen in a river marshland. The site was secondarily heaped up with sand, gained from the extension of the closely situated river Weser. All data was recorded at a sand pit with two ponds and an ephemeral puddle. The two ponds are anthropogenic in origin. They were dug out in 1996 and 1997 (KLUGKIST pers. comm.).

Behaviour Records
The data was recorded at 3 days in spring (27 May, 10 June and 17 June 1998) from 13:00 to 16:00 h. *Tetrix* specimens were evoked to jump in their natural environment. The stimulus was a fast movement with the hand towards the animal. In some cases more than one stimulus was necessary to evoke an escape

jump. Every specimen was listed in a table with data on jump distance, jump direction, vegetation of take-off and landing point and temperature. To avoid double measurements the specimens were marked individually with a water-resistant, lightfast paint marker (edding 780). The following data was recorded in particular:

- Date, weather, wind direction, time, species, number and colour of marking, sex, number of hind legs (0, 1, 2)
- Radiation (sunny or clouded) during jump
- Temperature of location: The temperature was measured by a digital thermometer at the exact location of take-off. It was rounded to 1°C for this report.
- Vegetation cover, prior to jump and hereafter: in a circle of 40 cm diameter surrounding the insect the density of vegetation was estimated (divided into bare sand, moss, grasses, herbs and water)
- Vegetation height: the highest plant in a circle of 40 cm diameter surrounding the insect was measured with a folding rule from the ground and noted in classes of 10 cm (0 cm, 1-10 cm, 11-20 cm, 21-30 cm, etc.); this data was recorded prior to jump and hereafter for an analysis of escape direction
- Location prior to jump and hereafter: divided into sand, moss, grasses and herbs; other items (leaf litter, bushes, twigs, water) were ignored for the analysis, because they hardly ever occurred
- Jump distance: take-off and landing point was marked with small flags and the distance measured with a folding rule
- Direction of the jump: the angle between stimulus, take-off and landing point of the jump was measured with a protractor; on the last day it was also noted, whether the animal jumped in line of vision or not
- Special features

At two locations temperature data loggers were situated. One was located at the shore of a pond, the other one in dense vegetation. These data loggers recorded temperature every 8 min 32 s at ground level.

Statistical Analyses

Data on jump distance and temperature rendered normal distributions (χ^2 test), so t-tests were performed to test for differences in jumping ability and temperature preferences (PRECHT 1979). Mann-Whitney U-tests adjusted for large sample size were used to test data on the habitat, such as vegetation cover (SACHS 1974).

Results

At the study site *Tetrix subulata* (n = 188) was more common than *Tetrix tenuicornis* (n = 45). In *Tetrix subulata* specimens missing one or two hind legs made up 19.6%, in *Tetrix tenuicornis* 17.8%. The percentage of females was 75.8% for *Tetrix subulata* and 82.2% for *Tetrix tenuicornis*. Subsequently all analyses concerning jump distance were done only for *Tetrix subulata* females with both hind legs.

Jump Distance

The jumping ability of *Tetrix subulata* males (n = 34) was significantly greater than in females (n = 109), when only specimens with both hind legs were

regarded (t-test, DF: 141, P < 0.1, Fig. 1). The jump distance for males was in mean 39.3 cm (maximum 98 cm), for females 33.4 cm (max. 110 cm).

Females of *Tetrix subulata* with both hind legs jumped significantly longer than those females, which were missing one leg (t-test, DF: 132, P < 0.1, Fig. 2). The mean jump distance for one-legged females was 28.08 cm (n = 25; max. 73 cm).

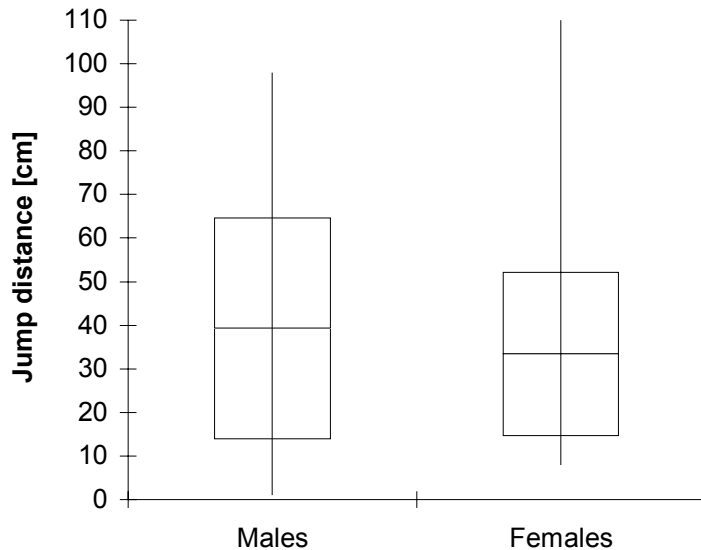Fig. 1: Jump distances of *Tetrix subulata* individuals, divided into males and females (only two-legged individuals considered; t-test, df: 141, P < 0.1).
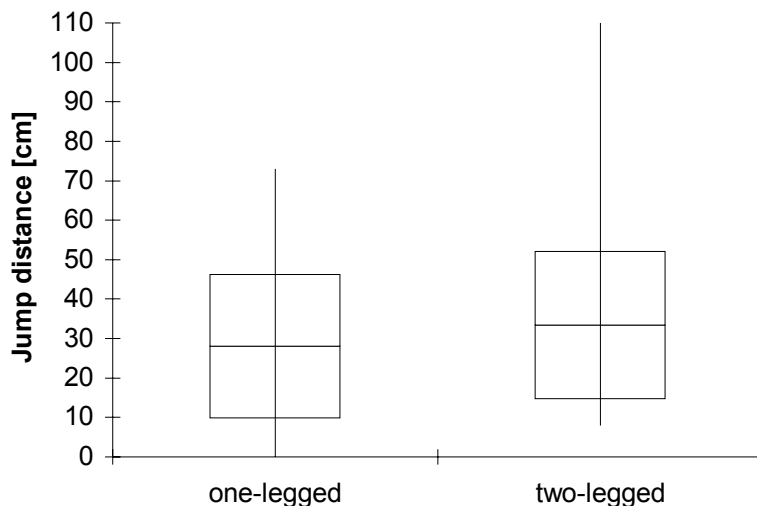

Fig. 2: Jump distances of *Tetrix subulata* females, divided into specimens missing one leg ("one-legged") and those with both hind legs ("two-legged"; t-test, DF: 132, P < 0.1).

Comparing females of *Tetrix subulata* and *Tetrix tenuicornis* (only those with both hind legs), no significant difference was found (t-test, DF: 136, ns). Females of *Tetrix tenuicornis* jumped in average 35.9 cm (n = 29; max. 70 cm).

No correlation was found between jump distance and temperature at the take-off. However, there was a significant difference (t-test, DF: 104, P < 0.05) in the jumping ability of specimens leaping in sunshine (n = 35, ∅ 37.3 cm, max.

110 cm) and those leaping when the sky was clouded (n = 71, ∅ 30.6 cm, max. 72 cm, Fig. 3).
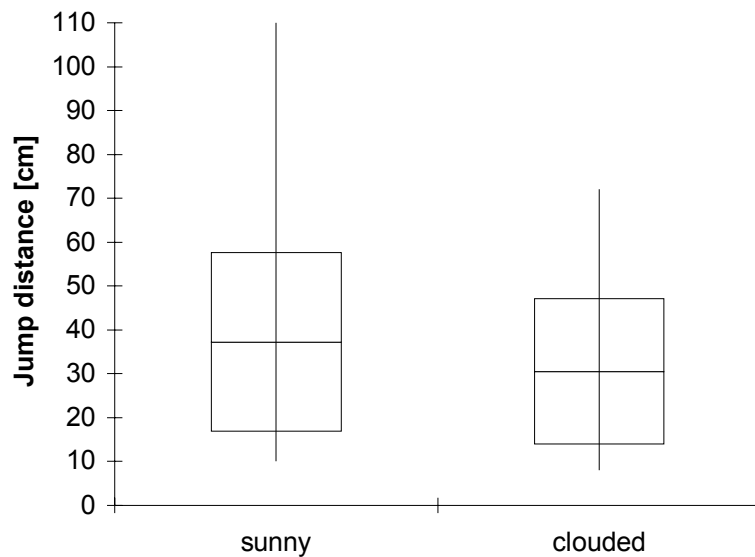

Fig. 3:   Jump distances of *Tetrix subulata* females, divided into individuals jumping during sunshine and during clouds
(only specimens with both hind legs; t-test, DF: 104, P < 0.05).

There was also no significant difference (t-test, DF: 105, ns), when the jump distance was compared for specimens surrounded by high (> 10 cm) plants (n = 71, ∅ 33.1 cm, max. 80 cm) and specimens surrounded by low (≤ 10 cm) vegetation (n = 36, ∅ 33.3 cm, max. 110 cm). When only those specimens jumping during sunny conditions were used for the analysis, there was a significant difference. During sunshine females in low vegetation leaped in mean 44.4 cm, those in high vegetation 29.5 cm (t-test, DF: 31, P < 0.025).

When the jumping ability of specimens leaping from patches with dense vegetation (70 to 100% vegetation cover) and specimens starting from patches with open soil (0 to 30% vegetation cover) was compared, no significant difference was found as well (t-test, DF: 95, ns). The average jump distance for specimens in dense vegetation was 31.5 cm (n = 52, max. 66 cm), in open vegetation 35.4 cm (n = 45, max. 110 cm).

No significant difference was found (t-test, DF: 104, ns), when the jumping ability was compared for specimens leaping from bare sand (n = 57, ∅ 34.5 cm; max. 110 cm) or from places covered with vegetation (n = 49, ∅ 32.9 cm, max. 66 cm).

Escape Direction
The vegetation structure and vegetation height at the point of take-off differed not significantly from the landing point (Mann-Whitney-test, ns). This can be also readily assessed, when calculating the difference of vegetation cover or vegetation height of point of landing and take-off (Fig. 4). Only two specimens were landing in water, and two more on grasses in the water.

The escape direction in relation to the stimulus was for most specimens 180° (*Tetrix subulata*: 40%). For *Tetrix subulata* only 7.2% of the specimens jumped in

angles lower than 90° (Fig. 5). Some individuals turned away from the stimulus before they jumped.

In *Tetrix subulata* 62.8% of the specimens (n = 86) jumped in line with the body direction, in *Tetrix tenuicornis* 75% (n = 24). When the escape direction of those specimens jumping in line with the body orientation was compared to the other specimens, no significant difference was found (Mann-Whitney-test, ns).
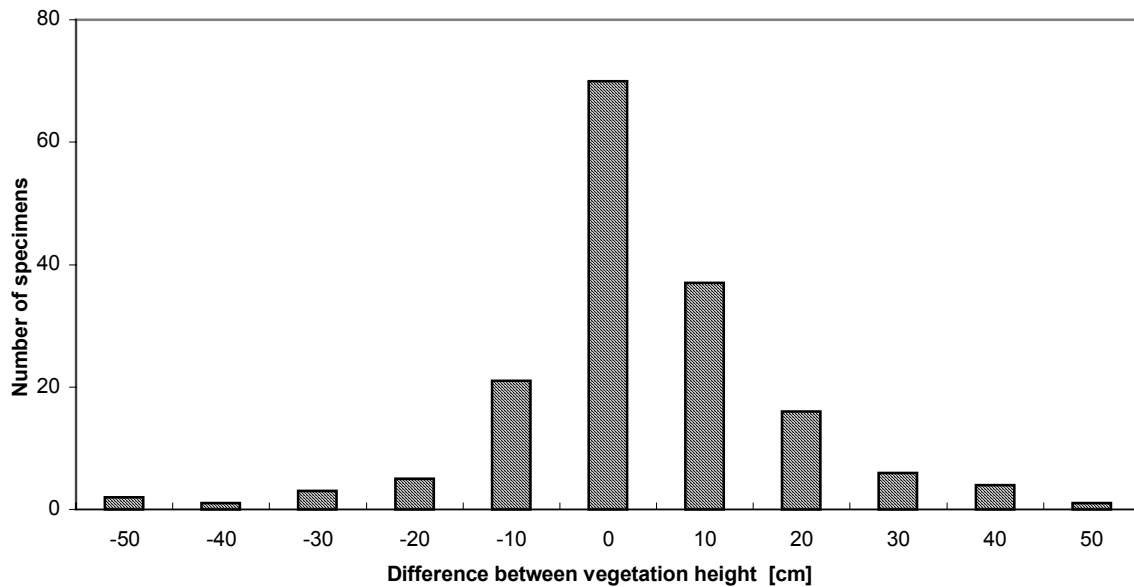

Fig. 4:   Difference of vegetation height at landing point and take-off for *Tetrix subulata*.
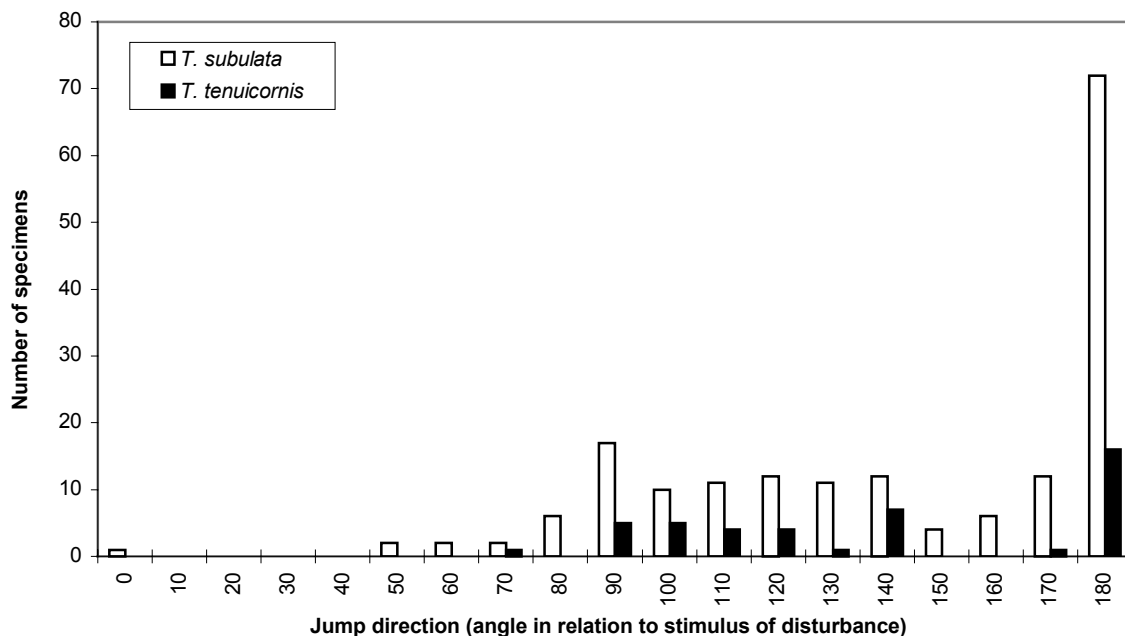

Fig. 5:   Jump direction of *Tetrix subulata* and *Tetrix tenuicornis* in relation to the stimulus of disturbance
(180° means straight from the stimulus, 0° towards the stimulus).

Discussion

Jump Distance

Tetrigids are enormous jumpers. Although female *Tetrix subulata* only measure around 10 mm (HARZ 1957), they are able to leap 110 cm, which is 110 times their body length, a width which among Orthoptera is only exceeded by *Lithidium punctifrons* (200 times body length, BROWN 1962, UVAROV 1977). Tiny insects must produce proportionally far more power than large animals to jump the same distance (BENNET-CLARK 1977). The energy, therefore, is stored before jumping in parts of the hind-legs, such as the semilunar process, the extensor tibiae apodeme and the walls of the hind femora (BENNET-CLARK 1990). The long jumping ranges of *Tetrix* species are probably due to their broad and thick hind femora (UVAROV 1977) and their well-developed semi-lunar process (GABRIEL 1984). The mass-specific jump distance is 22 m/g, which is much more than in any instar of the locust (QUEATHEM 1991). The amount of energy necessary for the jump to have occurred is approximated by $E = 5md$, where m is the mass in grams, d is the distance jumped in metres, and E is the amount of energy in millijoules (BENNET-CLARK 1975). For the longest jump distance of *Tetrix subulata* E is 0.275 mJ, which is similar to 3rd instar nymphs of *Schistocerca americana* (QUEATHEM 1991).

Amazingly individuals missing one hind leg are able to leap enormous distances as well (70 cm). According to BENNET-CLARK (1975) both legs contribute equal amounts of energy to the jump and "one-legged" insects jump about half as far as those with both hind legs. Hence, *Tetrix subulata* might be able to jump distances around 140 cm. However, such a range never was observed, and so the two legs may not contribute the same amounts of energy. This also can be derived from the fact that the insects leap not always in line with the body orientation, but nearly always approximately straight from the stimulus, which means that the hind legs cannot move in precise synchrony. It even has been observed that individuals with two hind legs used only one leg (BENNET-CLARK 1975).

Females are often less efficient jumpers than males (UVAROV 1977). This might be due to the weight of eggs in females (HEMPEL 1952). Fluctuations in jumping ability of adult females occur as they produce and oviposit clutches, while male jumping ability remains stabile (QUEATHEM 1991). However, this difference cannot only be explained with the egg load alone (QUEATHEM 1991). Maybe the energy necessary for egg-production does also play an important role. This would also be an important factor for the greater mobility and dispersal of males in many Orthoptera species (INGRISCH & KÖHLER 1998). Escape strategies often differ between the sexes or change during development (SCHULTZ 1981). This is probably due to the different energy budgets of growing (nymphs), egg producing (females) and sperm producing (males) insects. The similar jumping ability of *Tetrix subulata* and *Tetrix tenuicornis* reflects their similar size.

Altogether, the mean jump distance (30 to 40 cm) is much shorter than the maximum (110 cm) and the variation is high. The variation in jumping performance in an individual grasshopper is much higher than among species (SCOTT & HEPBURN 1976). The jump of grasshoppers is not a rapid escape response, because the extensor muscle needs 500 ms for maximal tension. If the hind legs

are not fully flexed prior to the jump, the insect is only able to perform a small hop (HEITLER 1974). If the ground-hopper is not in the right position, it might just trigger without being fully cocked. Sometimes it also might bring itself in a better position for a jump, turning away from the stimulus.

Secondly, a fast approaching hand might be not a strong stimulus to jump. According to PEARSON & O'SHEI (1984) the visual responsiveness of LGMD and DCMD neurons of locusts is higher for rapid movements of small (5-10° of the 180° visual field) contrasted objects, while the responsiveness to larger objects is low. This might well reflect the size of potential predators. Only two predators (the Redstart – *Phoenicurus phoenicurus* and the Meadow-Pipit – *Anthus pratensis*) have been listed for *Tetrix* species so far (INGRISCH & KÖHLER 1998). Due to the small body size of Tetrigidae they will probably have small predators, such as spiders, bugs, tiger beetles (*Cicindela hybrida* was common at the study site), amphibians, reptiles and small birds. If the insects did not regard the hand as a predator, they might just try to avoid to be stepped on, as they do to escape grazing cattle (RICHARDS & WALOFF 1954). A short jump also might be sufficient for escaping a small predator. The energetic costs of a long jump might be higher than the profit, since Tetrigidae are well camouflaged. Thus, leg-loss in grasshoppers is less disastrous for predator escape than one would expect. Of course more studies are needed using a real predator as escape stimulus.

Another cause for the short jumps might be found in reflex modification. Animals are known to have a more intense startle reaction, when they startle without any signal prior to the stimulus (HOFFMAN 1984). This was confirmed for locusts as well (RIEDE 1993). Such signals cannot be avoided in the field. However, they probably often cannot be avoided by predators as well. Thus escape behaviour differs substantially from startle.

There are probably more causes influencing the range of an escape jump. Body temperature affects jumping ability as well (WHITMAN 1988), but the heat gain for grasshoppers is more influenced by the absorption of solar radiation than air or surface temperature (CHAPPELL & WHITMAN 1990). If sunlight is present, body temperature of grasshoppers can rise up to 26.7°C above air temperature (KRÜGER & DUSPIVA 1933). This will also be true for the dark coloured Tetrigids, which have their main adult appearance during spring and autumn. Thus it becomes clear that ground-hoppers jump longer distances during sunny conditions than when the sky is clouded. *Tetrix subulata* becomes active at temperatures higher than 15°C (SCHMIDT 1996). Most of the jumps were performed at temperatures around 19°C to 24°C, which is probably below the optimal temperature for jumping performance. This also can be concluded from the fact that both species were located at warmer patches than the two data loggers (HOCHKIRCH et al. 1999). They probably searched for those warmer patches actively, as is known for other grasshoppers (WHITMAN 1987). During very cold conditions (< 10°C) *Tetrix subulata* becomes inactive and hides in dense vegetation (SCHMIDT 1996).

No significant effect on jump performance was found for vegetation cover and locations, but the maximal and mean values were always higher for open vegetation than for dense vegetation. It is certainly no coincidence that the female which jumped 110 cm was taking off from bare sand, surrounded by only 30%

grassy vegetation and the highest plant being smaller than 10 cm. The only significant effect was found for vegetation height, when only specimens jumping during sunny conditions were regarded. High vegetation probably hinders the jumping performance, because the ground-hoppers sometimes jump against a stem of a plant. However, more studies are needed on the effect of vegetation on the jumping ability.

Escape Direction

The two studied species had no directed escape strategy towards water, as was posed by HIRSCHFELDER (1994), but also not towards vegetation or open patches. However, the escape direction is not a matter of coincidences and direction of the body line, as was assumed by JACOBS (1953), HARZ (1957) and SCHMIDT (1996). Only 63% of the *Tetrix subulata* specimens jumped in line with the body orientation which should be the usual direction of a jump according to HOYLE (1958). The overwhelming majority of specimens jumped in a direction more or less straight from the stimulus, or at least away from it (> 90°).

Why are the species not escaping into dense vegetation, where they are difficult to find? There is probably a trade-off between the better possibilities to hide in vegetation and the better possibilities to jump from open locations. For human beings it is difficult to find *Tetrix* in vegetation, but they are easier to catch here. Other advantages of open locations may be the better view on the predator or the warmer temperatures of open sand. *Tetrix* species are rather well camouflaged even on open ground. So in the end a direction straight from the predator is probably the best strategy, since both open patches and dense vegetation have advantages and risks. The good swimming and diving abilities of Tetrigidae offer them the advantage to survive even a jump into water, which is of importance for a species occurring mainly close to waters. A jump into water, however, does not save the insect, since it might be attacked here by water bugs, Odonata larvae, water beetles or fishes. Thus a directed jump into water is not of advantage and the insects are trying to reach land or a stem rapidly (HARZ 1958). Jumping seems to appear mainly during the escape reaction. LOCK (1996), who followed a *Tetrix subulata* female during one day did not record any jumps of the specimen. Small hops of males occur, however, when they approach a female.

Conclusions

Tetrix species react on disturbances with a short jump away from the potential predator. The jump direction is not influenced by vegetation structure or nearby waters, nor by the line of the body orientation. A trade-off between the possibilities of jumping or hiding does not favour dense vegetation or bare sand as a landing point. The jumping range is affected by radiation and vegetation height. The latter one inhibits only longer jumps, which are performed by sun-exposed insects. Although Tetrigidae are able to jump enormous distances (up to 110 cm), they usually do not use their full jumping power. They may not be able to bring their hind legs into full flexion prior to the jump or they do not move their legs in precise synchrony. However, a short jump might be a sufficient escape response to small predators. The energetic costs of a long jump might be higher than the profit. The direction of the escape jump seems to be of priority. The

insects do not always jump in line of the body orientation and sometimes crawl in a better position prior to the jump. More studies on the escape strategies of grasshoppers are needed using a real predator as escape stimulus.

Authors:

Dr. Axel Hochkirch
Universität Osnabrück
FB 5, Fachgebiet Ökologie
Barbarastr. 11
49076 Osnabrück
E-mail:
hochkirch@biologie.uni-osnabrueck.de

Michael Folger-Rüter
Akazienweg 1
27299 Daverden

Anke Gulau
Am Geesthang 13
27299 Langwedel

Carola Harmuth
Jaburgstr. 7
28757 Bremen

Frauke Hellwig
Feldstraße 19
27404 Zeven

Christian Keithahn
Argonnenstraße 24-26
28211 Bremen

Stefan Länder
Münchener Straße 124
28215 Bremen

Helge Mühl
Am Kastanienhof 13
28355 Bremen

Andrea Peiter
Stefan Vogt
Marco Zimmermann
Universität Bremen
FB 2, IFOE, AG Evolutionsbiologie
Postfach 330440
28334 Bremen

Marion Zimmermann
Tauroggener Straße 40
28201 Bremen

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