Habitat dependent differences in the flight behaviour of Collembola

Article *in* Pedobiologia · July 1987

DOI: 10.1016/S0031-4056(23)00374-8

Erhard Christian
University of Natural Resources and Life Sciences Vienna

Pedobiologia **30**, 233—239 (1987)
VEB Gustav Fischer Verlag Jena

Tierökologie I, Universität Bayreuth, FRG and Institut für Allgemeine Biologie, Universität Wien, Austria

Habitat dependent differences in the flight behaviour of Collembola

THOMAS BAUER and ERHARD CHRISTIAN

With 3 figures

(Accepted: 86-11-15)

1. Introduction

Springtails (Collembola) have developed several possibilities and methods for avoiding predation. For example, many species are quick runners. The Onychiuridae seem to have a kind of chemical weaponry in the form of their sticky and toxic haemolymph (for lit. see DUNGER 1983). The main escape mechanism in most species, however, seems to be the jumping ability. When they are stimulated mechanically, the action of their furca shoots them into the air within 10—15 ms (BAUER & VÖLLENKLE 1976, CHRISTIAN 1979, BAUER 1982a).

In the narrow-spaced cavities of the soil jumping as an escape mechanism is useless, and it has been known for a long time that the furca of springtails is more or less reduced in species which inhabit deeper layers of the soil (for lit. see SCHALLER 1970).

On the soil surface, however, jumping seems to be quite effective. CHRISTIAN (1979), found that even in springtails with a well developed furca single species differ considerably with respect to the energy needed for a jump and with respect to their maximum acceleration. The latter ranged from 120 ms^{-2} [*Orchesella cincta* (LINNÉ, 1758)] to 970 ms^{-2} [*Sminthurus viridis* (LINNÉ, 1758)]. This complies with the observation that *Orchesella* species, if disturbed, jump for a distance of only few centimetres while most Symphypleona jump several decimetres and with an acceleration that usually causes them to leave the observer's field of vision. Concomittantly with the jumping behaviour of surface dwelling springtails their predators have developed sophisticated behavioural strategies and morphological structures to overcome this flight mechanism (ALTNER & BAUER 1982, BAUER 1981, 1982a, 1982b, 1985, HINTZPETER & BAUER 1986).

In analyzing the jumping behaviour of springtails the immediate impression would be that long distance jumps should always be advantageous and a better flight strategy than short distance jumps. On film recordings at high speed, however, we observed that long distance jumping is accompanied by a longer time of recovery. *Allacma fusca* (LINNÉ, 1758) (Symphyleona), for example, lands with its furca extended and always needs more than half a second after a jump to refold it. If the jump fails to carry the springtail out of the range of the attacker, for example by collision with habitat structures, the springtail may by easily grasped.

Species that execute short jumps, on the other hand, refold their furca while still in the air. They are ready to jump again when they reach the ground. The average time from extension of the furca until it is refolded, for example, is 19 ms in *Orchesella flavescens* (BOURLET, 1939) (body length: 4,8 mm; n = 18 jumps), 20 ms in *Tomocerus flavescens* (TULLBERG, 1871 (4,1 mm; n = 9) and 19 ms in *Isotoma viridis* (BOURLET, 1839) (3,4 mm; n = 17) (BAUER, unpublished). This is the reason why some short distance jumping species are able to perform an optically confusing series of jumps before they disappear into the ground.

From these observations we derived the following hypothesis: Atmobiotic species which live mainly on plants and on the soil surface should exhibit a flight strategy that enables them to leave the range (and the field of view) of an attacker with a single far jump at high speed. Epedaphic species, on the other hand, which alternate between the soil surface and the litter cavities depending upon humidity conditions, should be short distance jumpers, not only because long distance jumping is more or less useless in the litter, but also because jumping at high speed increases the danger of damage if the animal collides with habitat structures.

Symphypleona and Arthropleona are hardly comparable with respect to jumping, since they are quite different in their anatomy. Therefore we chose Entomobryidae to test our hypothesis. It was assumed that species from surface habitats should be able to perform long distance jumps but fewer jumps per unit time than species from the litter layer. Finally we tried to define the life form and habitat choice of the species in a more ecophysiological way by investigating their resistance to desiccation: surface species should be more resistant.

2. Materials and methods

The springtails used in the experiments were caught at the following places around Vienna, Austria: *Entomobrya dorsalis* (Uzel, 1891): orchard, Purkersdorf; *Entomobrya corticalis* (Nicolet, 1841): red beech forest, Wien-Gallitzienberg; *Entomobrya muscorum* (Nicolet, 1842) and *Orchesella flavescens* (Bourlet, 1839): red pine forest, Lackenbach, Burgenland; *Orchesella cincta* (Linné, 1758), *Orchesella villosa* (Geoffroy, 1784) and *Lepidocyrtus paradoxus* (Uzel, 1891): turnipfield, Zwölfaxing; *Heteromurus nitidus* (Tempelton, 1835): laboratory culture; *Lepidocyrtus curvicollis* (Bourlet, 1839): cellar, Wien-Simmering.

The animals were kept at 15 °C on moist plaster of Paris and fed with soya flakes for one day and then used for the experiments at the same temperature.

Jumping range: The jumping range was investigated in an arena with a bottom of moist plaster at 15 °C and 300 lx. Single springtails were touched at the hind end with a fine hair brush and the distance between the starting and landing places was measured with a compass. Ten animals per species were tested, and 10 unimpeded jumps in each individual were measured. The length of each individual was measured after the test.

Jumps per minute: In these experiments the animals were touched immediately after landing and this continuously for one minute. Ten animals per species were tested.

Resistance to desiccation: A population of 30 animals of each species was enclosed in vessels with a bottom of dry plaster and observed at 50% rH and 23 °C. The surviving rate was recorded in intervals of 15 min.

3. Results

Table 1 shows the list of species which were investigated with a specification of their habitat as compiled from several authors (cf. Stach 1960; Pallissa 1964) and personal observation. Fig. 1 shows their medium jumping range plotted against the body length. If the jumping range of these Entomobryidae depended only on the body size, all species should be arranged along one regression line. This is not the case (correlation coefficient: 0,0108). There are obviously 2 groups, one including more atmobiotic species (*E. dorsalis*, *L. curvi-*

Table 1. List of the investigated species

species	habitat
Entomobrya dorsalis (Uzel, 1891)	shrubs, trees
Entomobrya corticalis (Nicolet, 1841)	trees, under loose bark
Entomobrya muscorum (Nicolet, 1841)	shrubs, litter layer
Lepidocyrtus paradoxus (Uzel, 1891)	soil surface
Lepidocyrtus curvicollis (Bourlet, 1839)	soil surface, cellars, caves
Orchesella flavescens (Bourlet, 1839)	soil surface, litter layer
Orchesella villosa (Geoffroy, 1764)	soil surface, litter layer
Orchesella cincta (Linné, 1758)	soil surface, litter layer
Heteromurus nitidus (Templeton, 1835)	litter layer, caves

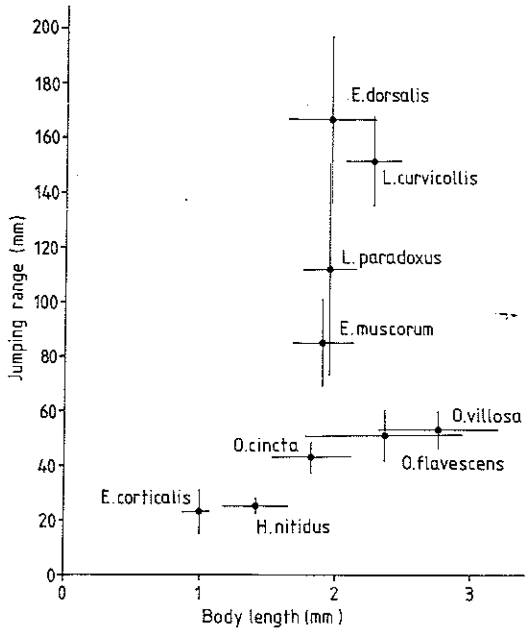

Fig. 1. Jumping range of the investigated Entomobryidae plotted against body size; measure of dispersion: standard deviation.

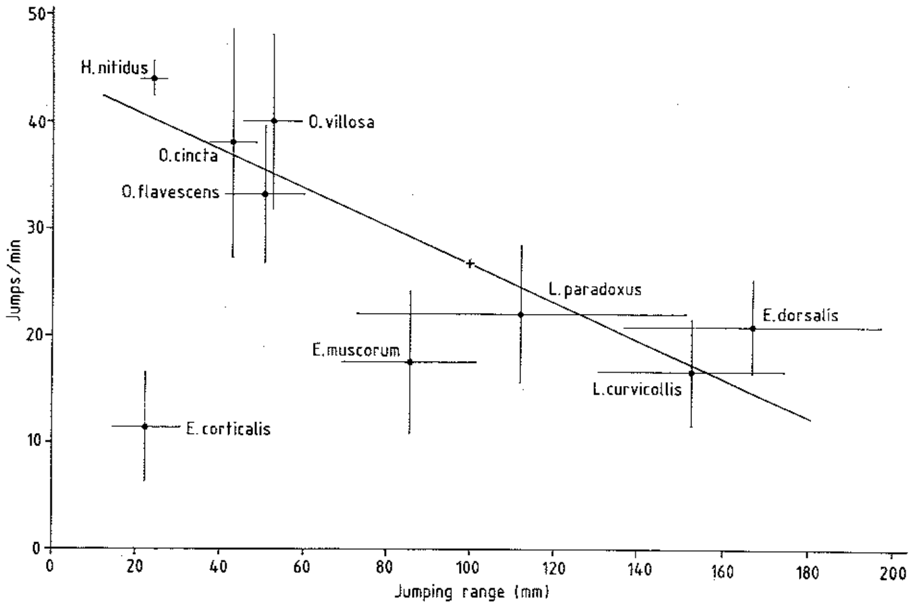

Fig. 2. Jumps per minute under continuous stimulation plotted against jumping range; measure of dispersion: standard deviation; correlation coefficient (without *E. corticalis*): —0,8616, $p < 0,01$.

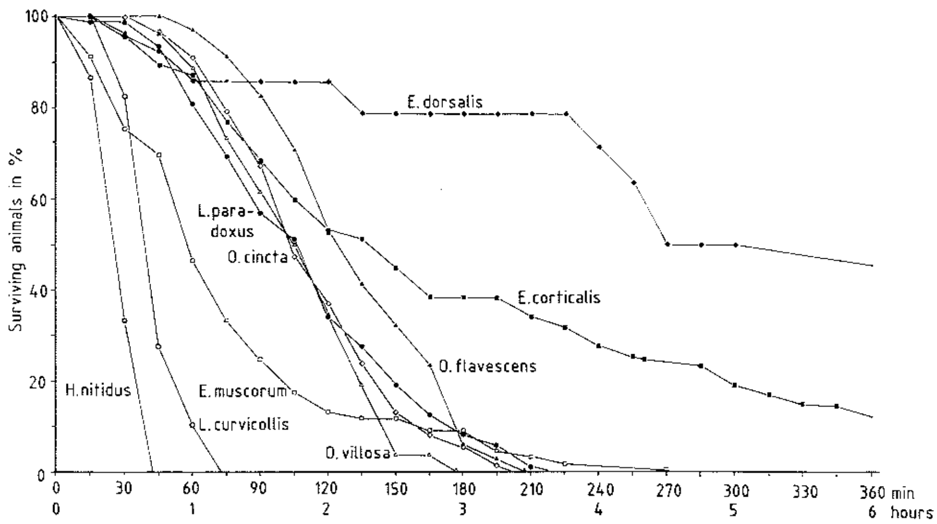

Fig. 3. Survival of the investigated species at 50% rH and 23 °C.

collis, *L. paradoxus*, *E. muscorum*) and another consisting of epedaphic species (*H. nitidus* and the *Orchesella* species). The exception is *E. corticalis*. These animals normally try to escape by running if they are touched and only make short jumps in cases of extreme duress, a behaviour pattern which differs significantly from that of the other species (*cf.* Discussion).

Figure 2 shows the number of leaps per minute under continuous stimulation plotted against the jumping range. There is a significant correlation (correlation coefficient (without *E. corticalis*): 0,8616, $p < 0{,}01$). The surface species perform only 16—22 jumps per minute, while the litter species are able to carry out 33—44 leaps per min. Even in this test *E. corticalis* differs from the other species because of its different flight reaction.

Our hypothesis concerning resistance to desiccation was that the more atmobiotic species should generally be more resistant. Fig. 3 shows the result of this experiment. *E. dorsalis*, the extreme long distance jumper, does indeed survive the longest under dry conditions. The bark-inhabiting *E. corticalis* is also quite resistant, while the survival time for *H. nitidus* is the lowest. This agrees well with the hemiedaphic-troglophile life form of *H. nitidus*. *L. curvicollis*, the other species attached to cave-like habitats, is also very sensitive to desiccation, although it looks and jumps like a typical surface dweller. In the other species the differences are not so conspicuous.

4. Discussion

The experiments confirm our hypothesis: There are different flight strategies even in springtails with a well developed furca. Species which spend most of their life outside the litter layer are able to perform long distance jumps; species which alternate between the litter layer and the surface jump only short distances but more often per unit time.

We propose that these differences in flight behaviour reflect on the one hand the selective pressure of predators with different orientation mechanisms and on the other hand the different spatial conditions of the habitat. Predators in litter cavities hunt by chemical and tactile cues (*cf.* Bauer 1982a), and long distance jumping is useless for springtails in this habitat. Outside the litter springtails seem to be more threatened by visual hunters like birds, certain spiders and visually hunting insects (Bauer 1981), and the space available allows long distance jumping.

Most springtail species which regularly leave the soil cavities in their search for food seem to be protected by a cryptic colour (DUNGER 1983). In plant-inhabiting Entomobryidae (*Entomobrya sp.*) the camouflaging effect of the colour patterns is especially conspicuous and enhanced by their behaviour. They are mostly motionless or move very slowly durin food uptake. A single far jump at high speed should foil a visual hunter by removing the springtail from its range and field of view.

Short range jumping species are able to carry out a quick series of jumps. This behaviour probably has a similar effect: like a single long distance jump at high speed it confuses an optically oriented predator such as birds on the soil surface and allows the springtail to disappear into the litter. Many hemiedaphic springtails show this behaviour if they are stimulated by soil vibrations or if the litter is removed. It may have evolved against predators like birds which poke about in the litter in search of prey and compensates the insect's lack of ability to escape by a long distance jump.

Only *E. corticalis* behaved in an unpredictable manner. These animals avoid jumping until they are placed under extreme pressure. Jumping seems to be only their last resort. This too can be explained by the conditions under and on the bark of trees. Under the bark jumping would be useless, and if they jumped from the bark surface, they would fall to the ground. They probably avoid a flight behaviour which would remove them from their habitat. We have the impression that members of this species are generally protected by their small size and by their fast running ability, which allows them to escape into narrow-spaced cavities on and under the bark.

Although the species investigated are rather similar with respect to their morphology, they differ considerably in their jumping range. The question arises as to whether this is due to different forces of the muscle system or to the mechanical properties of the accessory structures.

PISTOR (1955), BRETFELD (1963) and EISENBEIS (1978) described the muscle system of Collembola and EISENBEIS & ULMER (1978) analyzed the jumping apparatus of *Tomocerus sp.* Their results indicate that there is a kind of energy storage system in Collembola such as it was found in several other fast jumping insects (cf. EVANS 1973; 1975; HEITLER 1974; BENNET-CLARK 1976). This system consists mainly of 3 pairs of plates with an elastic ledge system around the furca basis. During extension and flexion of the furca the plates are moved in a complicated way by several muscles and alter their position with respect to each other. Even the position of the turning point of the whole system is changed during the furca movement. Not only this system but also the shape of parts of the furca may influence the amount of energy storage (CHRISTIAN 1979).

Considering the differences in the recovery time for various springtail species, we suppose that long distance jumping in springtails is based mainly on a change of the accessory structures of the jumping apparatus which has led to strengthening of the energy storage system. It is still unknown, however, which structures have been changed and in which way.

The resistance experiments (*cf.* Fig. 3) have shown that it is impossible to characterize the habitat choice of springtails simply by their resistance to desiccation. While the inhabitants of bark, *E. dorsalis* and *E. corticalis* do indeed exhibit increased resistance to dryness, as expected, the more epedaphic *Lepidocyrtus* species which are "long distance jumpers", do not differ from the epedaphic *Orchesella* species. This may be due to the fact that they live on moist soils where liquid water is permanently available or in caves (*L. curvicollis*) with an atmosphere saturated with water vapor.

The examples of Entomobryidae investigated clearly show that the jumping range is great in atmobiotic species and small in epedaphic species. However, it seems to be of no particular value to discriminate strictly between these two groups. An extension of this investigation to include more Entomobryidae would probably show that there are a lot of intermediate types between these extremes. In summary we conclude that the flight strategy of long distance jumping at high speed is much more developed in the atmobiotic Symphypleona.

5. Zusammenfassung

[Habitatbedingte Unterschiede im Fluchtverhalten von Collembolen]

Nach Beobachtungen des Fluchtverhaltens von Collembolen verschiedener Habitate wurde folgende Hypothese aufgestellt:

Atmobionte Arten sollten sich in Anpassung an die Orientierungsweise ihrer Feinde mit einem sehr schnellen und weiten Sprung aus deren Reichweite und Gesichtsfeld entfernen können, Bewohner der Streu dagegen kurze Sprünge ausführen, dafür öfter pro Zeiteinheit springen (Seriensprünge). 8 von 9 daraufhin untersuchte Arten der Fam. Entomobryidae verhielten sich im Experiment der Hypothese entsprechend: Die extrem atmobionte Art *Entomobrya dorsalis* springt z. B. ca. 4 × so weit wie epedaphische Arten ähnlicher Größe, kann aber nur ca. die Hälfte der Sprünge pro Zeiteinheit ausführen (Fig. 1 und 2). Abweichend verhielt sich nur der Rindenbewohner *E. corticalis*, der auch bei Berührung eher durch schnelles Laufen und nur selten durch kurze Sprünge flieht.

Versuche zur Trockenheitsresistenz zeigten, daß Baumbewohner einerseits und Bewohner tieferer Streuschichten andererseits durch große bzw. geringe Trockenheitsresistenz gekennzeichnet sind. Im Bereich der obersten Bodenstreu verwischen sich die diesbezüglichen Unterschiede zwischen Weit- und Kurzspringern.

Der adaptive Wert der verschiedenen Fluchtweisen in den unterschiedlichen Lebensräumen und die zugrunde liegenden physiologischen Mechanismen werden diskutiert.

6. Acknowledgements

We want to thank PATRICIA NEVERS, who corrected the English of this manuscript.

7. References

ALTNER, H., & TH. BAUER, 1982. Ultrastructure of a specialized, thrust-sensitive Insect mechanoreceptor: Stimulus-transmitting structure and sensory apparatus in the rostral horns of *Notiophilus biguttatus*. Cell Tissue Res. **226**, 337—354.

BAUER, TH., 1981. Prey capture and structure of the visual space of an insect that hunts by sight on the litter layer (*Notiophilus biguttatus* F., Carabidae, Coleoptera). Behav. Ecol. Sociobiol. **8**, 91—97.

— 1982a. Prey-capture in a ground-beetle larva. Anim. Behav. **30**, 203—208.

— 1982b. Predation by a carabid beetle specialized for catching Collembola. Pedobiologia **24**, 169 to 179.

— 1985. Beetles which use a setal trap to hunt springtails: The hunting strategy and apparatus of *Leistus* (Coleoptera, Carabidae). Pedobiologia **28**, 275—287.

— & VÖLLENKLE, 1976. Hochfrequente Filmaufnahmen als Hilfsmittel bei der Analyse von Angriffs- und Fluchtverhalten in einer Räuber-Beute-Beziehung unter Bodentieren (Collembolenfang visuell jagender Carabiden). Wiss. Film (Wien) **17**, 4—11.

BENNET-CLARK, H. C., 1976. Energy Storage in Jumping Insects. In: HEPBURN, H. R. (ed.), The Insect Integument. Elsevier Scientific Publishing Company, Amsterdam-Oxford-New York.

BRETFELD, G., 1963. Zur Anatomie und Embryologie der Rumpfmuskulatur und der abdominalen Anhänge der Collembolen. Zool. Jb. Anat. **80**, 309—384.

CHRISTIAN, E., 1979. Der Sprung der Collembola. Zool. Jb. Physiol. **83**, 457—490.

DUNGER, W., 1983. Tiere im Boden. Ziemsen-Verlag, Wittenberg-Lutherstadt.

EISENBEIS, G., 1978. Die Thorakal- und Abdominal-Muskulatur von Arten der Springschwanz-Gattung *Tomocerus* (Collembola: Tomoceridae). Ent. Germ. **4**, 55—83.

— & S. ULMER, 1978. Zur Funktionsmorphologie des Sprung-Apparates der Springschwänze am Beispiel von Arten der Gattung *Tomocerus* (Collembola: Tomoceridae). Entomologia Generalis **5**, 035—055.

EVANS, M. E. G., 1973. The jump of the click beetle (Coleoptera, Elateridae) — energetics and mechanics. J. Zool. **169**, 181—194.

— 1975. The jump of *Petrobius* (Thysanura, Machilidae). J. Zool. **176**, 49—65.

HEITLER, W. J., 1974. The Locust Jump. J. comp. Physiol. **89**, 93—104.

HINTZPETER, U. & TH. BAUER, 1986. The antennal setal trap of the Ground beetle *Loricera pilicornis* FABRICIUS, 1775: a specialization for feeding on Collembola. J. Zool. **208**, 615—630.

PALISSA, A., 1964. Apterygota — Urinsekten. In: BROHMER, P., P. EHRMANN & G. ULMER, (Hrsg.): Die Tierwelt Mitteleuropas **4**, (1a); Quelle & Meyer Verlag, Leipzig.

PISTOR, D., 1955. Die Sprungmuskulatur der Collembolen. Zool. Jb. Syst. **83**, 511—540.

SCHALLER, F., 1970. Collembola (Springschwänze). In: HELMCKE, J.-G., D. STARCK, & H. WERMUTH, (Hrsg.), Handbuch der Zoologie **4**, (2) 2/1, 1—72.
STACH, J. 1947—1960. The apterygotan fauna of Poland in relation to the world fauna of this group of insects. 8 Teile. Kraków.

Address of the authors: THOMAS BAUER, Tierökologie I, Universität, Postfach 10 12 51, D - 8580 Bayreuth (FRG), and ERHARD CHRISTIAN, Institut für Allgemeine Biologie, Universität, Schwarzspanierstr. 17, A - 1090 Wien (Austria).

Synopsis: *Original scientific paper*

BAUER, TH., & E. CHRISTIAN, 1987. Habitat dependent differences in the flight behaviour of Collembola. Pedobiologia **30**, 233—239.

Observation of the flight behaviour of springtails from different habitats led to the following hypothesis: Atmobiotic species should escape by a single long distance, rapid jump that catapults them out of the range and field of view of an attacker. Litter-inhabitants, on the other hand, execute short jumps but more jumps per unit time. Eight out of nine species from the Fam. Entomobryidae behaved as predicted in the experiments. *Entomobrya dorsalis*, for example, a typical atmobiotic species, leaps about 4 times further than epedaphic species of similar size but performs only half of the jumps per unit time. Only the bark-inhabiting *Entomobrya corticalis* behaved differently. Even when touched it escapes by running quickly and only very rarely employs a short jump.

Tree inhabitants are characterized by greater resistance to desiccation while inhabitants of deeper litter layers show low resistance. Among species that live on or in the uppermost litter layer there is no conspicuous difference in resistance to dryness between long distance and short distance jumping species.

The adaptative value of different flight mechanisms in different habitats and the possible underlying physiological mechanisms are discussed.

Key words: Collembola, flight behaviour, habitat dependence, adaptation.