Beitr. Ent.	Keltern	ISSN 0005 - 805X
52 (2002) 1	S. 241 - 253	31.08.2002

Increased dispersal rates and distances in density-stressed bush crickets (*Metrioptera brachyptera* (L., 1761)). (Saltatoria: Tettigoniidae)

With 1 table and 4 figures

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Summary

The limitation of dispersal due to habitat fragmentation is considered as one key factor for an increasing risk of extinction especially in sedentary species with low dispersal ability. A few studies on grasshoppers and crickets indicate that dispersal ability even of sedentary species may have been underestimated in the past. It is argued that certain environmental conditions can trigger and increase dispersal in such species. In a first set of experiments emigration rates of the bush cricket *Metrioptera brachyptera* (L., 1761) were recorded in "microcosms" (cage-populations) with various „population“ densities. The proportion of emigrants was correlated with increasing densities. In a second set of experiments individuals stressed by high densities as well as individuals that were not submitted to this stress were released on a soccer field and dispersal patterns of both groups were recorded. Stressed individuals dispersed significantly faster and further than unstressed ones. The results indicate that dispersal is induced by certain environmental conditions suggesting episodic colonization patterns which occur even in sedentary species.

Zusammenfassung

Der infolge der Habitatfragmentierung eingeschränkte Individuenaustausch zwischen Populationen gilt als einer der Hauptgründe für ein erhöhtes Aussterberisiko insbesondere bei standorttreuen Arten mit geringem Ausbreitungspotential. Einige Untersuchungen an Heuschrecken deuten jedoch an, dass das Ausbreitungsvermögen standorttreuer Arten bisher möglicherweise unterschätzt worden ist. Es wird angenommen, daß bestimmte Umweltbedingungen bei diesen Arten Ausbreitungsverhalten auslösen und ihr Ausbreitungsvermögen erhöhen kann. An der Kurzflügeligen Beißschrecke *Metrioptera brachyptera* (L., 1761) wurden in einem ersten Schritt die Emigrationsraten bei verschiedenen Populationsdichten in "Mikrokosmen" (Käfigpopulationen) untersucht. Der Anteil der Individuen, die aus den Käfigen auswanderten, war positiv mit der Individuendichte in den Käfigen korreliert. In einem zweiten Schritt wurden sowohl Indivduen, die unter Dichtestress gehalten wurden, als auch Tiere, die keinen hohen Individuendichten ausgesetzt waren, auf einem Fußballplatz freigelassen und ihr Ausbreitungsmuster untersucht. "Gestresste" Individuen dispergierten signifikant schneller und weiter als "ungestresste". Die Ergebnisse weisen darauf hin, dass Ausbreitungsverhalten induzierbar ist und auch bei standorttreuen Arten auftreten kann. Es ist bei diesen jedoch keine regelmäßige Erscheinung, sondern besitzt Ausnahmecharakter.

Keywords

Dispersal, emigration, experimental approach, metapopulation, microcosm

DOI: 10.21248/contrib.entomol.52.1.241-253

Introduction

The limitation of dispersal due to habitat fragmentation is considered one of the key factors for the increasing risk of extinction of populations and metapopulations (SOULÉ 1986, GILPIN & HANSKI 1991, PRIMACK 1993). Inter-patch dispersal, i.e. the movement of individuals between discrete patches of suitable habitat, is essential for colonization of vacant patches and is therefore of basic importance for metapopulation models (e.g. HANSKI 1985, HANSKI & THOMAS 1994). One question arising from this concept is how to assess the contribution of single local-populations towards the persistence of the whole metapopulation and whether large or small local-populations provide more individuals for interpatch dispersal. Therefore, many studies focus on dispersal behaviour and both emigration- and immigration patterns of metapopulations (THOMAS et al. 1992, HANSKI et al. 1994, 1995, KINDVALL 1996). Recent studies reveal underestimations of both patch occupancy and dispersal distances even in sedentary species (HILL et al. 1996, LEWIS et al. 1997, KINDVALL 1999). Regarding this, possible differences in motivation of individuals to disperse which are emphasized by HANSSON (1991), may generate a bias in such estimations. Dispersal motivation may be affected by population density but usually emigration- and immigration rates are assumed to be independent of patch sizes and population densities (e.g. HANSKI & THOMAS 1994). Recently, these basic parameters of metapopulation modelling have been discussed as being variable and dependent on population density, habitat quality and spatial features of the landscape (KUUSSAARI et al. 1996, BAGUETTE et al. 1998, KINDVALL et al. 1998, KINDVALL 1999). The triggers of emigration and dispersal, respectively, seem to be of crucial importance for mobility patterns (BAKER 1984).

High population densities are reported to play an important role in inducing dispersal of grasshoppers and crickets (AIKMAN & HEWITT 1972, SÄNGER 1984, LAUß MANN 1998). Nevertheless, JOERN & GAINES (1990) assume a genetically fixed dispersal behaviour that possibly is connected with invariable emigration rates. Density-dependent dispersal indicates that individuals, parts of populations or even entire species can switch from „sedentary“ to „mobile“ in a „facultative migration“ (SOUTHWOOD 1962) as a reaction to environmental adversities (JOHNSON 1969).

The above mentioned aspects led to the following hypothesis of the present study:

Even very sedentary species are able to cover great distances and cross so-called dispersal barriers under certain environmental conditions. These patterns, however, occur only occasionaly at times when individuals of these species are forced to emigrate. Both emigration rates and dispersal ability are assumed to be positively correlated with population density. Therefore, density-stressed populations are thought to produce a higher proportion of emigrants that cover great distances.

The aim of the study is to show that emigration rates can increase with population density and to reveal a shift from sedentary to dispersive in individuals of the bush cricket *Metrioptera brachyptera* exposed to different density stress.

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Methods

Microcosm-experiments to measure emigration rates at different densities

Eight acrylic glass cages (160 x 60 x 40 cm) housed eight „model-populations" of *M. brachyptera* in „microcosms" (cf. FRASER and KEDDY 1997). To provide comparable „habitat conditions" between cages, the cages had an identical setup: each had a three to five cm litter layer, two flower pots (20 cm in diameter) and was covered with gauze (Fig. 1). The flower pots were planted with *Molinia caerulea* which was the predominant species in the habitat where *Metrioptera*-individuals had been collected (wet heathland and bog margins). A 20 cm long rectangular plastic nozzle (20 x 6 cm) was fixed in a 45° angle to a rectangular hole in the front side of each cage acting as an exit similar to a fish trap (see fig. 1). A transparent plastic bag was attached to the end of the nozzle.

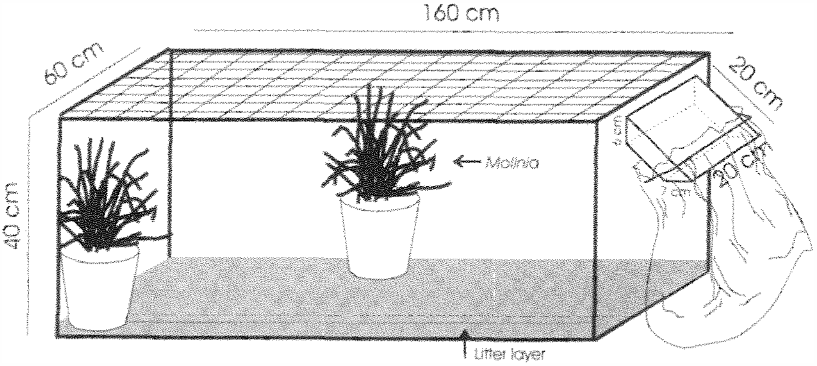

Fig. 1: Model-habitat of *Metrioptera brachyptera* used in the density-dependent emigration experiments. In each experimental replicate eight acrylic glass cages housed eight «model-populations» of *M. brachyptera*. To provide comparable «habitat conditions» between cages, the cages had an identical setup: each cage had a three to five cm litter layer, two flower pots and was covered with gauze. The flower pots were planted with *Molinia caerulea* which was the predominant species in the habitat the *Metrioptera*-individuals had been collected (see methods).

In the cages, different numbers of individuals were kept at an approximately even sex ratio ranging from five to 40 individuals per cage (5, 10, 15, 20 etc.). A total number of 180 individuals for each replicate was collected on the day prior to the experiment and transported in separate cigarette boxes. For each replicate new individuals were caught in the field. During the seven days of each experimental replicate all individuals found to have emigrated into the plastic bags were counted twice a day (11:30 h and 17:00 h) by closing the bags below the nozzle exit and removing it with the enclosed individuals. These were then released to a holding cage and a new bag was then fixed to the nozzle. After the 11:30 h counting, each „model-population" was provided with six flowers of *Leontodon autumnalis* or *Sonchus arvensis* as a food supply in addition to *Molinia caerulea*. The cages were exposed on the roof of the institute building and after one replicate, each cage was moved to the former position of another one. Three of the replicates were carried out in 1997 followed by two in 1998 for both males and females:

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Aug. 5 – Aug. 11, 1997 (juvenile/adult)
Aug. 15 – Aug. 21, 1997 (juvenile/adult)
Aug. 29 – Sep. 4, 1997 (adult)
Aug. 5 – Aug. 11, 1998 (adult)
Aug. 21 – Aug. 27, 1998 (adult)

The same experimental design was used in a sixth replicate (Aug. 14 – Aug. 20, 1998) to measure density-dependent emigration exclusively for females. All replicates were carried out at comparable weather conditions favourable enough to allow behavioural patterns like mating and egg-laying.

Release-experiments with individuals exposed to different densities

To investigate whether population density has an impact on dispersal behaviour, the mobility patterns of individuals which experienced no density-stress were compared to „stressed" individuals (taken from the high-density-cages of the microcosm-experiments). This was done by releasing the two groups simultaneously on the lawn of a soccer field (100 x 62 m). This location was chosen to increase resight probability. The 130 „stressed" individuals were released at one intersection of the centre circle with the centre line whereas the 224 „unstressed" individuals were released at the other intersection of the centre circle and the centre line of the soccer field. The two groups of individuals were tagged differently either with a silver permanent marker („unstressed") or with a white one.

The experiment lasted for 16 days and eight control walks were conducted either at 10:00 h, 16:00 h or 20:00 pm depending on weather conditions. No control walks were carried out during rainfall. Each resight session lasted 90 minutes and was performed on transects in a minimum intertransect distance of three meters. The transects extended to a maximum of 50 meters beyond the margin of the soccer field.

Each day, the distances between release and resight point were measured for both „stressed" and „unstressed" individuals. Thus, the number of recorded distances of one day corresponds to the number of resighted individuals of that particular day. The number of recorded distances of different days can, however, stem from the same individuals.

Results

In the five replicates carried out with males and females, a significant positive correlation (Pearson, R=0.96, p 0.001, n=40) between the density of stocked individuals and the proportion of emigrants was found (Fig. 2a). The difference in the proportion of emigrants was significant between the cage stocked with five individuals and that stocked with 10 bush-crickets (p 0.05), and it was highly significant between the former cage and all cages with 15 individuals or more (p 0.001, ANOVA, post-hoc-test Bonferroni). Differences between cages with more than five individuals were not significant. Thus, the density-dependent increase of emigration rates seems to be between the cage holding five individuals and the one holding 10 individuals. In order to detect sex-related differences in emigration rates, the proportion of emigrants in both sexes was analyzed seperately (Fig. 2b). In males as well as in females the proportion of emigrants was positively correlated with density (males: Pearson, R=0.693, p 0.001, n=40; females: R=0.4913, p 0.001, n=40), but between the sexes no significant difference in the pro-

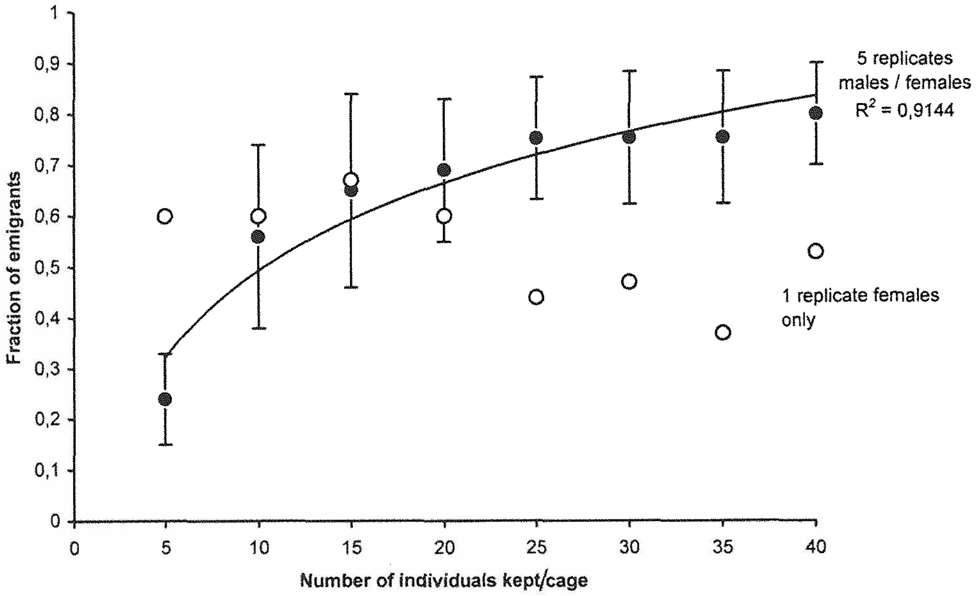

Fig. 2a: Positive correlation between density and emigration rate. Regression, mean and standard deviation of the five replicates (each with eight cages) with males and females (black dots) and one replicate carried out exlusively with females (circles). For levels of significance see text.

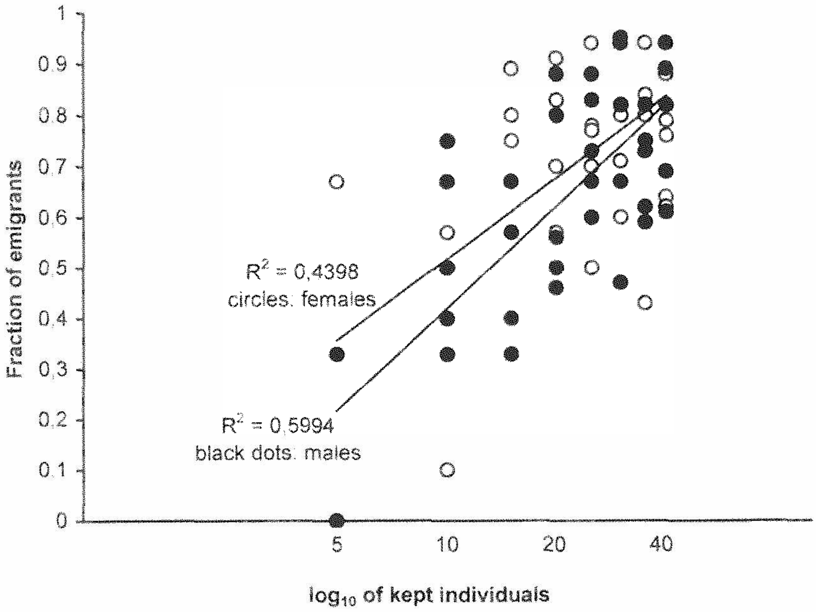

Fig. 2b: Regressions of density and emigration rates of males and females analyzed seperately. In both sexes a positive correlation could be detected without significant sex-related differences in the proportion of emigrants. For levels of significance see text.

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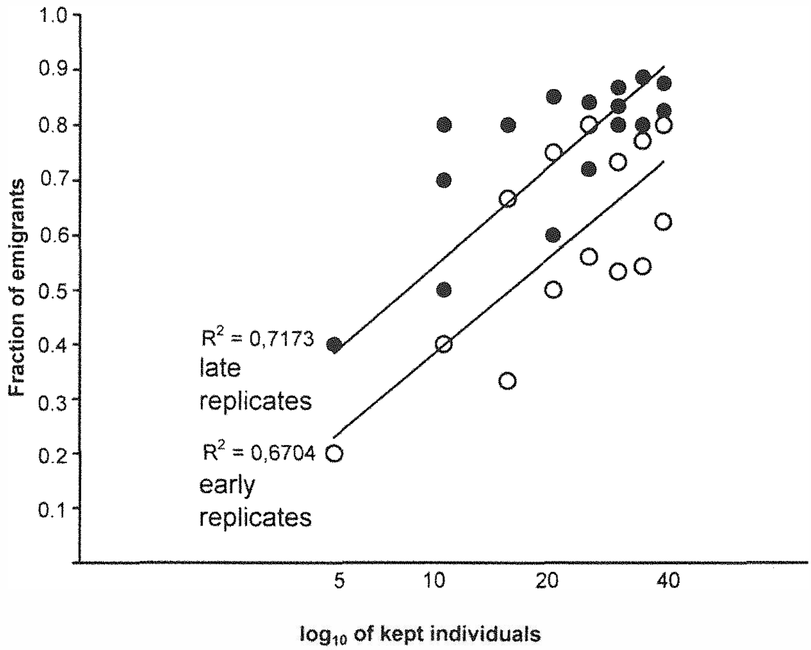

Fig. 2c: Regressions of density and emigration rate of mixed-sexes replicates carried out at the end of the season between Aug. 15. and Sep. 4. (black dots) and two mixed-sexes replicates performed early in the season Aug. 5 – Aug. 11. (circles). «Early» replicates exhibit significantly lower overall emigration than «date» replicates (*t*-test, *t*=-2.573, p 0.05, n=24 or 16, respectively).

portion of emigrants could be detected (*t*-test, t=1.558, p=0.123, n=40). In the „early" mixed-sex-replicates (1. and 4.: Aug. 5 – Aug. 11) lower overall emigration rates than in the three later ones were found (3. – 5.: Aug. 15 – Sep. 4) (Fig. 2c).

The emigration rates of the sixth replicate (exclusively with females) differed considerably from the replicates with both males and females (see fig. 2a). Here, even the low-density cages had a high proportion of emigrants. Furthermore, the emigration rates tend to decrease with an increasing density of stocked individuals.

During the eight resight sessions of the release-experiment on the soccer field, 62 distances of at least 42 unstressed individuals and 72 distances of at least 40 stressed individuals were recorded (Resighting proportion: 28% vs. 55%; unstressed vs. stressed). Although the released specimens were not marked individually, the minimum number of resighted specimens could be obtained from specific characteristics (sex, colour, injuries) and by the number of simultaneously resighted individuals of the same day.

The stressed individuals covered significantly higher distances in significantly less time than the unstressed ones (Mann-Whitney-U-test, U=1231.0, Z=-4.493, p 0.001, n=132) (Fig. 3). Dispersal distances increased rapidly until the third day after the release but started to slow down after the third day. On the 11th day after the release the maximum distance of 75 m from the release point was observed in a stressed individual far beyond the margin of the soccer field. A linear increase of distances with time was found in unstressed individuals. Therefore, the maximum distance from the release point of an unstressed individual (57 m) could be only recorded on the 16th day after the release.

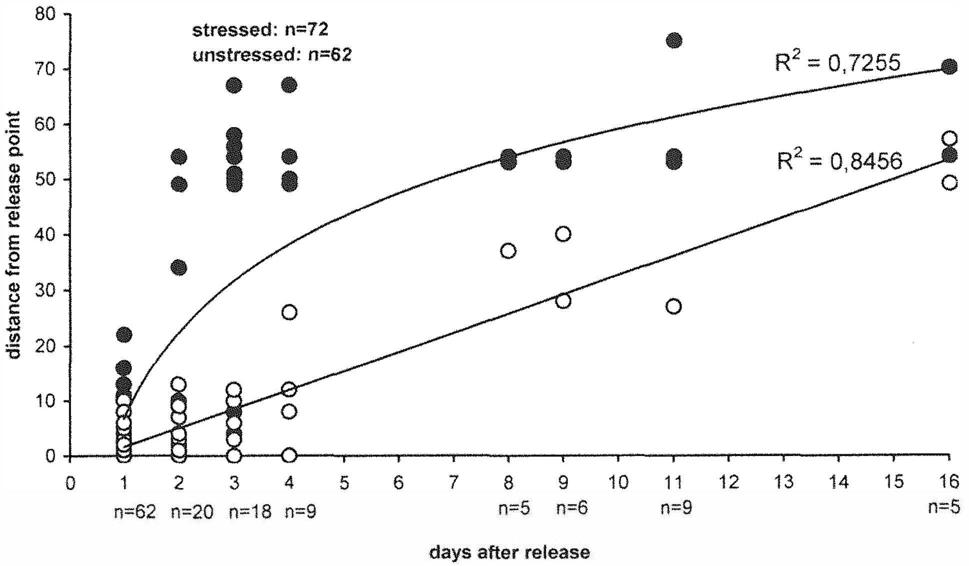

Fig. 3: Dispersal distances recorded for individuals stocked at high densities («stressed», black dots) and individuals which were not exposed to high densities («unstressed», circles). Distances covered were significantly higher in «stressed» individuals (for levels of significance see text).

Discussion

Triggers of emigration

The results of the cage-experiments suggest a positive correlation between density and emigration rates, at least in the model-populations of *M. brachyptera* examined. The main increase of emigration rates between five and 10 individuals per cage indicates that the resource supply (respectively the „habitat quality") of the cages may be sufficient for a density of about five individuals. The non-linear regression suggests that a certain threshold (i.e. a „carrying capacity" of the cages) has to be exceeded before density-dependent emigration is induced. Density-dependent emigration in grasshoppers and crickets is reported by SÄNGER (1984), REMMERT (1992) and KINDVALL et al. (1998).

Since the later replicates show a higher overall proportion of emigrants, „older" individuals seem to be more sensitive to density-stress. Similarly, males of *Metrioptera bicolor* move longer distances per day later in the season (KINDVALL, pers. com.).

It is known that the intensity of male stridulation e. g. the number of stridulating males act as a trigger of emigration (MCHUGH 1972, REMMERT 1992). ARAK et al. (1990) suggest that mating success of male *Tettigonia viridissima* will be maximized when singing males space out as far as possible. In butterflies, an increase of male harassment on mated females or an increase of territorial fights at high population densities leads to emigration (e. g. WICKMAN & WIKLUND 1983, WICKMAN 1986, BAGUETTE et al. 1998, BRUNZEL 1999). The replicate carried out exclusively with females revealed no positive correlation of emigration rates with density and thus, it supports the hypothesis of an acoustic trigger for emigration.

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Although carried out only once, the high emigration rates of the low-density cage in the female replicate seem to contradict a positive correlation between emigration and density. But it may, however, point at an increase of emigration rates at very low densities as well as at high densities in the mixed-sex-replicates. The low female density with absent males may be interpreted (by the female) as a sign of bad habitat quality (e.g. bad egg-laying conditions) and thus induce emigration. This is supported by the high emigration rates at very low densities as was shown for butterflies (KUUSSAARI et al. 1996), an effect that was possibly caused by a lack of conspecific attraction.

Although the mixed-sex-replicates reveal no different emigration rates of males and females, the female replicate suggests - at least under certain circumstances (e.g. male absence) - sexual differences in the response to high densities. However, no differences were detected under the more or less equal sex ratio given in the mixed-sex-replicates. Nevertheless, sexual differences in the emigration behaviour may occur, if, for instance, the operational sex ratio shifts towards a dominance of one sex (e.g. due to the mating status of females). These aspects of different sexual movement patterns need further investigation.

In addition to "running" further and faster, as it may be supposed because of the release-experiments, density-stress provides another way to considerably increase dispersal distances in rather immobile grashoppers and crickets: getting long wings. Increasing population densities („crowding“) lead to the production of certain pheromones in instars of Locustinae-grasshoppers. These pheromones are known to induce a shift from a sedentary to a migratory phase with long wings (NOLTE 1977, DALE & TOBE 1990, LOHER 1990) which then emigrates in the well-known swarms (FARROW 1990). Long-winged macropterous morphs are described from several european crickets and grasshoppers which are usually apterous or mesopterous and therefore rather immobile (Tab. 1). The most impressive example may be the nowadays rare species *Polysarcus denticauda*. This usually apterous cricket is reported to have covered great distances as a long-winged (!) morph in the 1940´s probably due to „crowding“ (EBNER 1950/51, ENGEL 1951). BRUNZEL (1999) observed long-winged morphs also in *M. brachyptera* performing flights of more than 20 meters.

Impact of density-induced dispersal-patterns on the conservation of populations in fragmented landscapes

The release experiments of this study suggest that individuals which experienced high densities dispersed faster and further than individuals which were not exposed to density-stress. But the significant differences found are linked to faster spreading of stressed indviduals rather than to higher distances covered. The resighted unstressed individuals, although fewer, seem to have covered similar distances but much later than the stressed ones. It took unstressed individuals longer to cover similar distances as stressed ones, resulting in a longer exposure to predators before they reach a new patch. Regarding this, the surprisingly lower resighting-proportion of unstressed individuals (28% : 55%; unstressed : stressed) may in fact be caused by predators: birds were observed preying on released *Metrioptera*-individuals. A constant rate of loss due to predation would inevitably lead to a lower resighting-proportion of slower-spreading individuals. This also would explain the higher proportion of lower dispersal distances which are found in the unstressed individuals: most of them may get lost before being able to cover high distances.

Tab. 1: Macroptery, mean and maximum dispersal ranges of German grasshoppers and crickets (a=only males, females – if reported – lower distances; f=capable of flying; *=distances to nearest populations).

Species	Maximum range	Mean range	Macroptery	References
Polysarcus denticauda	>2000 m	-	+	Ebner 1950/51 Engel 1951
Conocephalus discolor	-	-	+	Ando & Hartley (1982)
Decticus verrucivorus	-	40 m		Hjerman & Ims (1996)
			0	Götz (1970)
Metrioptera bicolor	-	-	+	Kindvall & Ahlen (1992)
	40 m (120 m, unsuit. habitat)	2 m		Kindvall (1999)
Metrioptera brachyptera	75 m	-	+	this study
Metrioptera roeselii	1000 m (larvae)	-	-	De Jong & Kindvall (1991)
			+	Voisin (1982)
Platycleis albopunctata	ca. 2000-5600 m*	-	f	Gottschalk (1996)
Tettigonia viridissima	350 m >2000 m*	-	f	Laußmann (1994) Laußmann (1998)
Acheta domesticus	-	-	+	Patton (1975)
Gryllus campestris	-	-	+	Wallascheck (1991)
Tetrix subulata	80 m	-	f	Laußmann (1998)
Tetrix tenuicornis	-	-	+	Laußmann (1998)
Tetrix undulata	-	-	+	Laußmann (1998)
Chorthippus apricarius	>2000 m*	-	f	Laußmann (1998)
Cho. brunneus	>2000 m*	-	f	Laußmann (1998)
Cho. dorsatus	>2000 m*	-	f	Laußmann (1998)
Chorthippus parallelus	>2000 m*	-		Manzke (1995)
			+	Laußmann (1994)
Chorthippus mollis	>2000 m*	-	f	Laußmann (1998)
Cho. montanus	-	-	+	Laußmann (1998)
Chorthippus pullus	157 m	17 m	f	pers. com. Janßen
Stenobothrus lineatus	88 m^a	18 m^a	f	Samietz et al. (1996)
Chrysochraon dispar	>2000 m*	-		Laußmann (1998)
			+	Hochkirch (1997)
Euthystira brachyptera	>2000 m*	-		Laußmann (1998)
			+	Atzinger (1952)
Oedipoda caerulescens	800 m^a	-	f	Appelt (1996)
	585 m^a	99 m^a		unpubl. Data
Oedipoda germanica	514 m^a	46 m^a	f	Zöller in Wagner & Berger (1996)
	> 200 m			Wagner & Berger (1996)
Psophus stridulus	700 m^a	167 m^a	f	Buchweitz (1993)
Sphingonotus caerulans	3600 m^a	-	f	pers. unpubl. data
Bryodema tuberculata	ca. 900 m	-	f	Reich in Köhler (1996)
Omocestus viridulus	>2000 m*	-	f	Laußmann (1998)
Parapleurus alliaceus	>2000 m*	-	f	Laußmann (1998)

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The hypothesis of a faster spreading of stressed individuals is supported by RIEGERT et al. (1954). They note that density-stressed grasshoppers disperse faster than supposedly unstressed individuals (low density). However, they did not test individuals stocked at low densities. AIKMAN & HEWITT (1972) observed decreasing dispersal speed in the course of a release experiment and linked that to the decreasing density due to the spreading.

Increasing density in *M. brachyptera* seem to cause a higher proportion of emigrants covering greater distances in shorter time. High population densities in sedentary, immobile grasshoppers can produce macropterous morphs which are known to perform dispersal flights (UVAROV 1977, FARROW 1990). However, RITCHIE et al. (1977) do not consider macroptery as important for dispersal due to the „oogenesis-flight-syndrome“. The results of this study support the hypothesis that dispersal is positively correlated with population density and therefore is condition-dependent, such that gene flow and colonization may be episodic. The higher proportion of stressed emigrants dispersing faster than unstressed individuals could lead to an increase of colonization probability and thus to an expansion of a species (Fig. 4). Environmentally induced episodic dispersal may be the reason for the considerable differences recorded between the mean and the maximum range of species (see tab. 1). This can also be the cause for the expansion of sedentary grasshoppers and crickets (e.g. *Calliptamus italicus*, HARZ 1960, *Oecanthus pellucens*, DORDA 1995, *Chorthippus parallelus*, MANZKE 1995) as well as butterflies (e.g. BRUNZEL & ELLIGSEN 1999) that were observed occasionaly.

The „cage experiments“ are only an approximation of the natural situation of a metapopulation in a fragemented landscape since immigration and re-immigration of already emigrated individuals were not investigated. However, considering emigration rates as a

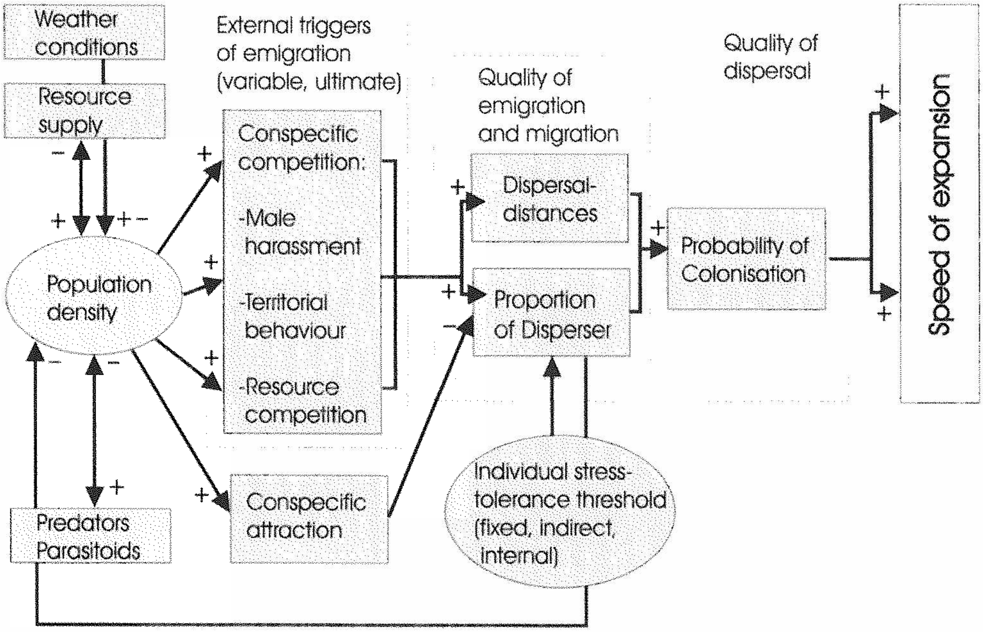

Fig. 4: Model of density-induced dispersal.

basic parameter of metapopulation-modelling, the positive effect of a density-induced increase of emigration rates and dispersal distances on the probability of colonizing vacant patches should be taken into account even in sedentary species. As results of KEAN & BARLOW (2000) suggest, the density-dependence of modelling-parameters has a considerable impact on metapopulation persistence.

Acknowledgements

I would like to thank O. Kindvall for very helpful comments on the manuscript and P. Giere for the stylistical review of the English.

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DOI: 10.21248/contrib.entomol.52.1.241-253

Zeitschrift/Journal: Beiträge zur Entomologie = Contributions to Entomology

Jahr/Year: 2002

Band/Volume: 52

Autor(en)/Author(s): Brunzel Stefan

Artikel/Article: Increased dispersal rates and distances in density-stressed bush crickets {Metrioptera brachyptera (L., 1761)). (Saltatoria: Tettigoniidae) 241-253