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# Body size, sexual dimorphism and ecological succession in grasshoppers

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## Abstract

We studied 12 species of Acrididae (4 Oedipodinae and 8 Gomphocerinae) associated with three ecological stages of succession in herbaceous environments in mine tailings near Limoges, France. The pioneer, medium and late stages of succession each contained four different dominant grasshopper species. We measured morphometry variables possibly linked with displacement (locomotory) capacities, taking advantage of previous analyses on walking and jumping-flight performances on the same species.

Early succession species were characterized by long hind and fore wings and a wider pronotum. Their wings also exhibited greater sexual dimorphism in length than grasshopper species from middle or late successional stages. These morphological characters are associated with jumping-flight performances and walking speed, because the best jumpers are the best walkers. Although the ratio of wing length to body length decreases with succession, the overall body size does not, and overall body size is not correlated with displacement performance.

## Résumé

A l'intérieur d'une succession écologique primaire dans des milieux herbacés peuplant des stériles miniers près de Limoges (France), nous avons étudié 12 espèces d'Acrididae (4 Oedipodinae et 8 Gomphocerinae). Les sères pionnière, moyenne et tardive comprennent chacune 4 espèces. Des variables morphométriques en relation possible avec les capacités de déplacement ont été mesurées, bénéficiant de travaux précédents sur l'analyse de la marche et des sauts volants sur les mêmes espèces.

Les espèces pionnières sont caractérisées par des ailes antérieures et postérieures longues, ainsi que par la grande largeur de la métazone du pronotum. Leurs ailes présentent également un dimorphisme sexuel plus affirmé que les espèces des sères moyenne et tardive. Ces caractères sont associés aux performances de saut volant, mais de manière inattendue, à la vitesse de marche, sachant les espèces qui volent le mieux sont aussi celles qui marchent le plus vite. La taille globale du corps ne varie pas significativement avec l'ordre de succession, ni avec les performances de déplacement.

## Key words

primary succession, grasshopper, morphometry, body size, sexual dimorphism, displacement capacities

## Introduction

During the course of primary succession, organisms settle on a new area resulting from changing ecological conditions, ecosystem destruction, or the addition of new land. Mine tailings are excellent sites to study environmental succession, because new mine tailings are always being produced, and scientists can know their exact time of creation. Also, mine tailings begin devoid of virtually all macrobiota. This allows researchers to examine dispersal, immigration, establishment and succession, starting from the very beginning (Parmenter *et al*. 1991, refs in Picaud & Petit 2007a).

Insects are a good model to study succession and to test hypotheses related to succession and community structure. Empirical and theoretical studies suggest that early-succession (pioneer) insect species have high dispersal abilities, fecundity, and resistance to variable conditions. In contrast, late-succession species appear to be better competitors, due in part to greater offspring and adult body size (Brown 1982, Brown & Southwood 1987, Simberloff & Wilson 1969, Majer 1989).

We have been studying succession in uranium mine tailings, in the west edge of Massif Central, France (Picaud & Petit 2007a,b). Seven sites (ranging from 0 to 9 years of age) in Haute-Vienne, near Limoges, have been followed for three years. These sites display distinct successional differences in Caelifera species, which can be assigned to early, medium and late stages of succession. In contrast, Ensifera species are more closely related to vegetation structure itself, more or less independently of the age of the site. Our studies also show a strong correlation between jumping-flight performances and the order of succession of Caelifera. In contrast, walking does not appear to play a significant role in succession, except for species in which the female has reduced wings. Although body size for some organisms appears to be correlated with successional stage, it is unknown if succession in Orthoptera communities is linked to body size.

The aim of this work is to test if there are relationships between the succession order of Caelifera and morphometric variables linked to displacement capacities of the different species (Picaud 1998, El Ghadraoui *et al*. 2008). We focused on overall body size, wing to body ratios, and sexual size dimorphism of different characters.

## Material and Methods

*Acridid species*.—We chose to study 12 grasshopper species, based on previous studies on post-mining sites in the Limoges region (Haute-Vienne, France). Our species included four Oedipodinae [*Oedipoda caerulescens* L., *Aiolopus strepens* (Latreille), *A. thalassinus* (F.), and *Stethophyma grossum* (L.)] and eight Gomphocerinae [*Chorthippus albomarginatus* (De Geer), *C. biguttulus* (L.), *C. brunneus* (Thunberg), *C. dorsatus* (Zetterstedt), *C. parallelus* (Zetterstedt), *Omocestus rufipes* (Zetterstedt), *Chrysochraon dispar* (Germar), and *Euchorthippus declivus* (Brisout)]. These 12 species were divided into three successional stages (early, medium, and late) (Table 1). Although *C. albomarginatus* can be common in late succession (Picaud & Petit 2007a), it is generally more common in mid-succession, and for this work, was placed in succession stage two, in order to balance our design of



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**Table 1.** Distribution of grasshopper species according to successional stage in mine tailings in central France (see Picaud & Petit, 2007a and b).

Early successional stage:
*Aiolopus thalassinus*
*Aiolopus strepens*
*Chorthippus brunneus*
*Oedipoda caerulescens*

Middle successional stage:
*Chorthippus biguttulus*
*Omocestus rufipes*
*Stethophyma grossum*
*Chorthippus albomarginatus*

Late successional stage:
*Chorthippus dorsatus*
*Chorthippus parallelus*
*Euchorthippus declivus*
*Chrysochraon dispar*

four species per stage. For each species, 20 males and 20 females were measured, as follows: body length (from the summit of vertex to end of abdomen), hind wing length, tegmina length, hind femur length, prozona width at its maximum, width of principal pronotum sulcus, metazona width at its maximum, head width (vertex side), pronotum length (seen from above), and abdomen length (seen from above). Measurements were taken from drawings made with a stereo microscope equipped with a camera lucida, and were accurate to 0.01 mm.

Estimation of displacement (locomotory) capacities of each species is described in Picaud & Petit (2007b). Walking performance was assessed by calculating the variance of the distances moved by more than 50 individuals of each species, within a 20 m-long tent, with tall grass (about 45 cm height) or short grass (about 5 cm height) on the ground. Jumping flights were estimated by calculating the mean distance moved by an individual during several successive jumps, upon escape instigated by the experimenter. Ten to twenty adults of each sex and of each species were measured. We analyzed the males and the females of each species separately. Nine species were studied for jumping flights, seven for walking on tall grass and six walking on short grass.

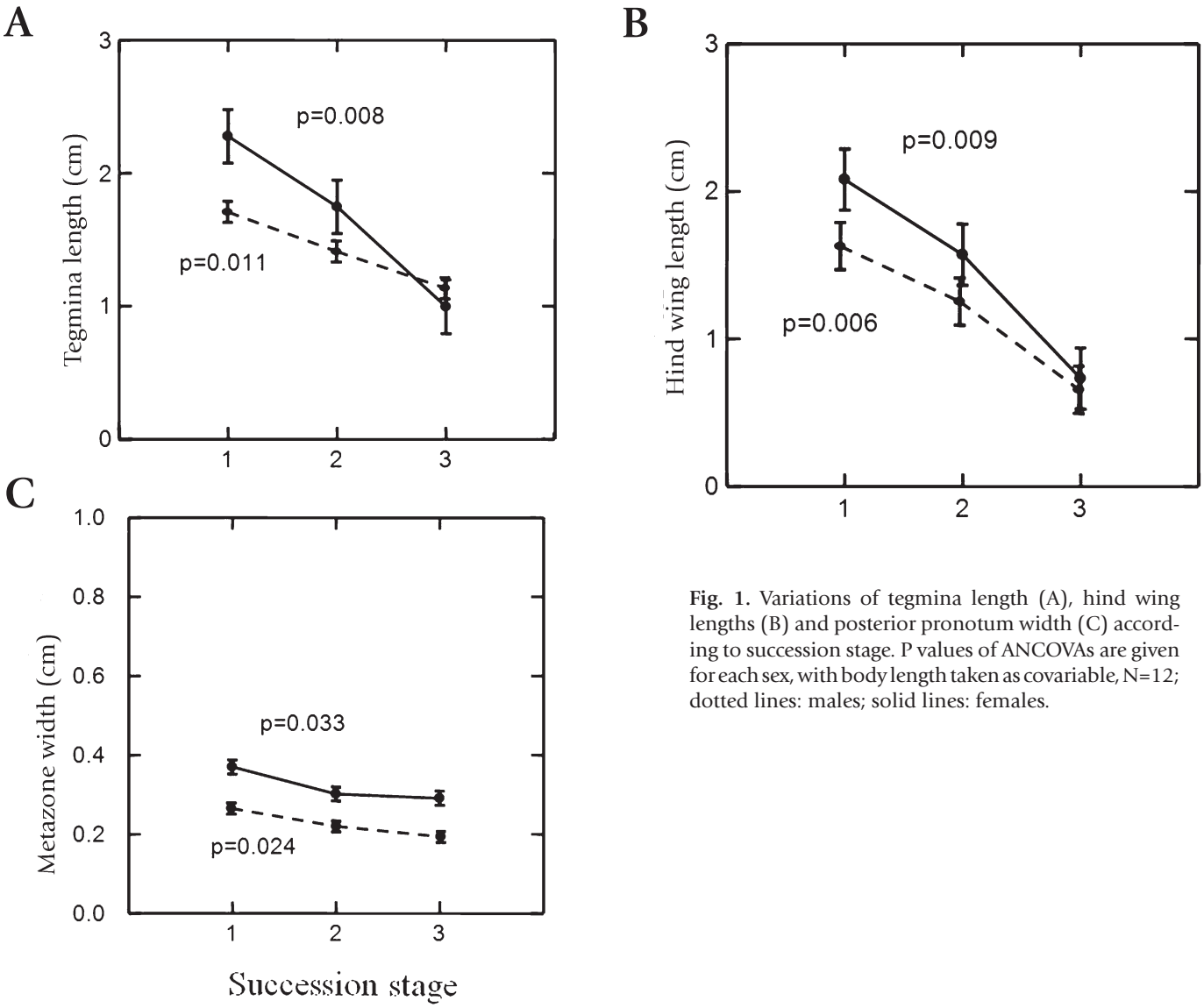



**Fig. 1.** Variations of tegmina length (A), hind wing lengths (B) and posterior pronotum width (C) according to succession stage. P values of ANCOVAs are given for each sex, with body length taken as covariable, N=12; dotted lines: males; solid lines: females.



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**Table 2.** Correlations between body length and other morphometric variables (N=12). Data represent means from 20 individuals of each sex and species.

| | Females | | Males | |
|---|---|---|---|---|
| Morphometric variable | Pearson | p Bonferroni | Pearson | p Bonferroni |
| Hind wing length | 0.46 | 0.13 | 0.62 | 0.033 |
| Tegmina length | 0.53 | 0.075 | 0.76 | 0.004 |
| Hind femur length | 0.97 | <0.001 | 0.96 | <0.001 |
| Max. prozona width | 0.94 | <0.001 | 0.96 | <0.001 |
| Principal sulcus width | 0.95 | <0.001 | 0.93 | <0.001 |
| Max. metazona width | 0.84 | 0.001 | 0.78 | 0.003 |
| Head width | 0.85 | <0.001 | 0.79 | 0.002 |
| Pronotum length | 0.95 | <0.001 | 0.95 | <0.001 |
| Abdomen length | 0.96 | <0.001 | 0.97 | <0.001 |

*Data treatment*.—The means for morphometric variables were calculated for each sex and each species, and considered as quantitative variables in ANOVA and ANCOVA, with successional stage as a factor. Sexual dimorphism was determined by the difference between the mean values in females and in males, for each character and each species. When the difference for a character is correlated to the mean value for males and females, which is frequent as pointed out by Teder & Tammaru (2005), an ANCOVA was conducted, the mean value taken as a covariable, and the succession stage as a factor. This method avoids the flaws in using organ-length ratios (male against female), following Ranta *et al.* (1994). All variance analyses were conducted with SYSTAT vers. 7.0 ™ (SPSS Inc., 1997), while the correlations were calculated with PAST vers. 1.70 (Hammer *et al.*, 2001).

## Results

An overall examination of the different measured variables reveal that they are all significantly related to body length (Table 2), except for the hind wings and, to a lesser extent, the tegmina of the females.

**Table 3.** Variance analyses of sexual dimorphism and stage of succession (N=12). The differences were calculated from the mean measures taken on 20 males and 20 females of each species, with four species per successional stage.

| Morphometric variable | Fr (ANOVA) | p | Fr (ANCOVA) | p |
|---|---|---|---|---|
| Body Length | 0.1146 | 0.89 | | |
| Hind wing length | 7.32 | 0.013 | - | - |
| Tegmina length | 6.49 | 0.018 | - | - |
| Hind femur length | 0.613 | 0.56 | - | - |
| Max. prozona width | 0.358 | 0.71 | 3.812 | 0.069 |
| Principal sulcus width | 0.306 | 0.74 | 2.304 | 0.16 |
| Max. metazona width | 1.09 | 0.94 | 1.763 | 0.23 |
| Head width | 0.183 | 0.84 | 2.345 | 0.16 |
| Pronotum length | 0.541 | 0.60 | 0.059 | 0.94 |
| Abdomen length | 0.132 | 0.88 | - | - |

*The relationships between succession and morphology*.—The first test of the influence of succession stage on morphological variables showed contrasting results. Overall body length does not vary significantly with successional stage, neither for females (Fr = 0.452, p = 0.65, N = 12), nor males (Fr = 0.626, p = 0.557, N = 12). We therefore conducted ANCOVAs with body length as a covariable, and tested for links between the succession stage of the 12 species and the other variables. Three morphological traits varied significantly according to succession stage: tegmina length (p<1%), hind wing length (p<1%) and maximum prothorax (metazona) width (p<5%), in both sexes (Fig. 1). More precisely, both wing length and metazona width decreases in later successional stages. The remaining variables showed no significant differences according to succession (p>15%).

*Order of succession and sexual dimorphism of morphometric variables*.—We tested if succession stage influenced the sexual differences between character values. Table 3 shows that hind and fore wings of the females are significantly larger than those of the males, and that these differences decrease with the later succession stages (Fig. 2). Because mean body length differences between males and females are positively correlated to sexual differences of several characters, we performed ANCOVAs with mean body length as a covariable. This approach added no new character presenting a sexual dimorphism which differed significantly according to succession stage.

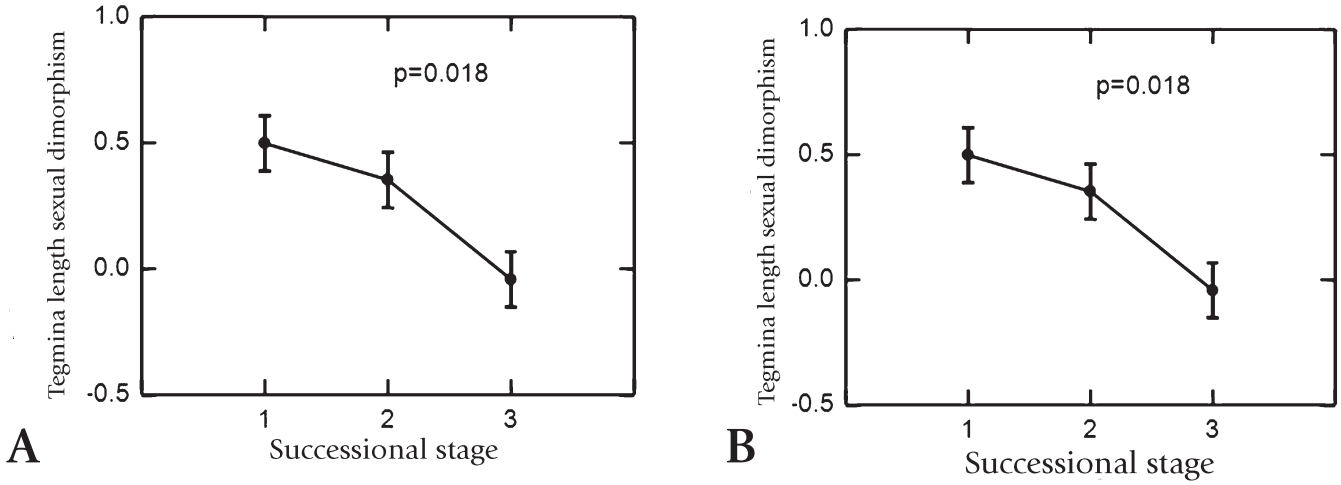



**Fig. 2.** Variations of sexual dimorphism associated with tegmina length (A) and hind wing length (B) according to succession stage (p values are given for ANOVAs, N=12).



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**Table 4.** Correlations between morphometric measures and locomotory performances. Jumping flights are expressed as the log of mean distances in m, and walking by the variance of distance (in m) moved during 24 h. For example N=18 means that 9 species of each sex have been tested for jumping flight. The morphometric measures for each species were taken as the means of 20 individuals of each sex.

| | Jumping flight (log) | | Walking in tall grass | | Walking in short grass | |
|---|---|---|---|---|---|---|
| | r Pearson | p (N=18) | r Pearson | p (N=14) | r Pearson | p (N=12) |
| Body Length | 0.17 | 0.501 | 0.08 | 0.79 | 0.31 | 0.33 |
| Hind wing length | 0.68 | 0.002 | 0.46 | 0.10 | 0.60 | 0.04 |
| Tegmina length | 0.71 | 0.001 | 0.48 | 0.08 | 0.61 | 0.03 |
| Hind femur length | 0.08 | 0.763 | 0.07 | 0.80 | 0.31 | 0.33 |
| Max. prozona width | 0.03 | 0.919 | 0.12 | 0.68 | 0.42 | 0.18 |
| Principal sulcus width | 0.18 | 0.470 | 0.31 | 0.29 | 0.52 | 0.08 |
| Max. metazona width | 0.496 | 0.036 | 0.54 | 0.049 | 0.67 | 0.018 |
| Head width | 0.12 | 0.635 | -0.08 | 0.77 | 0.18 | 0.59 |
| Pronotum length | 0.33 | 0.180 | 0.14 | 0.64 | 0.42 | 0.17 |
| Abdomen length | 0.13 | 0.618 | 0.11 | 0.71 | 0.30 | 0.35 |

*Relationships between morphology and displacement capacities*.—The ability to move via jumping flight and walking was significantly correlated with lengths of both fore and hind wings and metazona width, with one exception. The strongest Pearson's correlations associated with jumping flights were of wing length, ($p<0.002$). These organs were less significantly associated with walking in short grass ($p<0.05$), whereas, metazona width was better linked to walking in short grass ($p<0.02$) than in tall grass or to jumping flight ($p<0.05$).

## Discussion

In our study, grasshopper morphology was related to different successional stages in a mine-tailings habitat. Early succession, pioneer, species have long fore and hind wings, and a large pronotum (metazona) width. This last character corresponds to a strong bending of lateral carinae, diverging in the pronotum metazona, and is a character used to distinguish *C. brunneus* (early succession) from *C. biguttulus* (late succession). The significance of this syndrome is its apparent link to both flight and walking ability (El Ghadraoui *et al*. 2008). We hypothesize that the thoracic muscles situated under the enlarged metazona are involved in the movement of both wings and legs.

Grasshoppers common in late succession, in contrast, share reduced fore and hind wings, and generally display parallel or subparallel lateral carinae in the metazona. These characters are presumably associated with poor flying ability. Reduced locomotory ability may be associated with enhanced fecundity, because such species may allocate proportionally more resources to reproduction than locomotion. However, this needs to be tested in our system, because the abdomens (which, in females contain the ovaries) of late-succession grasshopper species were not significantly longer than those of early succession species.

Our study did not find an association between succession stage and overall grasshopper body length. However, in every species, female body size was larger than male body size. This may be explained by any number of proximal and evolutionary mechanisms, including the fact that in some species, females have an additional instar (see Esperk *et al*. 2007 for review, and Hassal & Grayson 1987 and Willot & Hassal for the example of *C. brunneus*).

Greater female size has important consequences and it is interesting to compare the sexual dimorphism of jumping-flight performances to the sexual dimorphism of certain morphological characters (specifically fore and hind wing length, and metazona width). As the females are always longer than the males, the dimorphism concerning these three characters goes in two opposite directions. In the pioneer species, the longer flight organs in females ensure better performances and reduce the handicap of their weight relative to males. For example, *Oedipoda caerulescens*, from the early successional stage, shows the greatest sexual differences for these characters. These differences are sufficient to allow the heavier females to perform flying jumps equal to that of males. In contrast, for species inhabiting late successional stages, the wings of the males are often longer than those in females (Table 5). In this case, there is no compensation for the superior weight of the female, but rather the contrary. This exaggerates the difference in displacement ability between both sexes, to the advantage of males.

In this study, we must note that the size of individuals may vary within a given species, according to the number of generations that have settled in a colonized area, because of successional changes in host-plant species, quality and abundance. However, our approach, based on interspecific comparisons of morphological measures,

**Table 5.** Sexual dimorphism of morphometric measures and of jumping-flight performances Abbreviations: B Lgth: body length; HW Lgth: hind wing length; T Lgth: tegmina length; Mz W: metazona width; JFp: jumping flight probability of ANOVA. For each character, the dimorphism for a given species is calculated from the mean values in females, less the mean values in males. The sexual dimorphism for jumping flight is assessed by the probability associated by ANOVA on distances moved by males and females (Table 1 in Picaud & Petit, 2007b).

| Species | Succ. stage | B Lgth | HW Lgth | T Lgth | Mz W | JFp |
|---|---|---|---|---|---|---|
| *A. thalassinus* | 1 | 0.82 | 0.56 | 0.60 | 0.11 | 0.004 |
| *C. brunneus* | 1 | 0.59 | 0.32 | 0.34 | 0.08 | 0.005 |
| *O. caerulescens* | 1 | 0.94 | 0.64 | 0.71 | 0.15 | 0.22 N.S. |
| *C. albomarginatus* | 2 | 0.78 | 0.38 | 0.36 | 0.06 | 0.6 N.S. |
| *C. biguttulus* | 2 | 0.48 | 0.33 | 0.35 | 0.06 | <0.001 |
| *O. rufipes* | 2 | 0.55 | 0.29 | 0.30 | 0.06 | 0.09 N.S. |
| *C. parallelus* | 3 | 0.55 | -0.08 | -0.32 | 0.06 | <0.001 |
| *C. dispar* | 3 | 0.95 | -0.02 | -0.30 | 0.13 | <0.001 |
| *E. declivus* | 3 | 0.55 | 0.12 | 0.09 | 0.07 | 0.001 |



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showed that the overall size of grasshopper species does not vary significantly during the course of succession. This contrasts with the findings of Siemann *et al*. (1999) who showed that among 718 arthropod species studied in an old-field succession, body size significantly decreased with age of successional stage. Differences between Siemans's study and ours may be due to number of species studied (12 *vs* 718). Alternatively it may be because in the grasshoppers we studied, there is no progressive feeding specialization during succession: diet is rather uniform, ranging from oligophagous (mainly Poaceae) or polyphagous (Dicots and Poaceae) (El Ghadraoui *et al*. 2001).

In conclusion, the grasshopper species in the primary succession studied here appear to have adopted two opposite strategies, both conditioned by a greater size of the females over the males. One important constraint on the pioneer species is long distance displacement, accomplished during sustained jumping flights. Because females weigh more than males, they must have relatively longer flight organs than the males to fly. In contrast, the late-succession species face a different constraint: competition with other settled species. In this case, females decrease their displacement capacities, and we hypothesize that this is selected because it allows females to favor reproduction over dispersal (Picaud 1998).

## References


Brown V.K. 1982. Size and shape as ecological discriminants in successional communities of Heteroptera. Biological Journal of the Linnean Society 18: 279-290.

Brown V.K., Southwood T.R.E. 1987. Secondary succession: patterns and strategies, pp 315-337 In: Gray A.J., Crawley M.J., Edwards D.J. (Eds). Colonization, Succession and Stability. Blackwell Scientific Publications, Oxford.

El Ghadraoui L., Petit D., Picaud F., El Yamani J. 2001. Relationship between labrum sensilla number in the Moroccan locust *Dociostaurus maroccanus* and the nature of its diet. Journal of Orthoptera Research 10: 335-343.

El Ghadraoui L., Petit D., Mokhles R., Azouzi A., Lazraq A. 2008. Situation du criquet marocain *Dociostaurus maroccanus* Thunb. 1815 par rapport aux différentes espèces acridiennes: morphométrie et capacités de déplacements. Afrique Science 4(1) http://www.afriquescience.infodocument.php?id=928

Hammer Ø., Harper D.A.T., Ryan P.D. 2001. PAST (vers. 1.70.) Palaeontological Statistic Software Package for Education and Data Analysis. http://folk.uio.no/ohammer/past. Palaeontologica Electronica 4(1): 9 pp.

Hassall M., Grayson F.W.L. 1987. The occurrence of an additional instar in the development of *Chorthippus brunneus* (Orthoptera: Gomphocerinae). Journal of Natural History 21: 329-337.

Majer J.D. 1989. Animals in Primary Succession. The Role of Fauna in Reclaimed Lands. Cambridge University Press.

Parmenter R.R., McMahon J.A., Gilbert C.A.B. 1991. Early sucessional patterns of Arthropod recolonization on reclaimed Wyoming strip mines: the grasshoppers (Orthoptera: Acrididae) and allied faunas (Orthoptera: Gryllacrididae, Tettigoniidae). Environmental Entomology 20: 135-142.

Picaud F. 1998. Succession écologique chez les insectes orthoptères: application aux haldes de mines. Thèse de doctorat, Université de Limoges, 157 pp.

Picaud F., Petit D. 2007a. Primary succession of Orthoptera on mine tailings: role of vegetation. Annales de la Société Entomologique de France 43: 69-79.

Picaud F., Petit D. 2007b. Primary succession of Acrididae (Orthoptera): differences in displacement capacities in early and late colonizers of new habitats. Acta Oecologica 32: 59-66.

Ranta E., Laurila A., Elmberg J. 1994. Reinventing the wheel: analysis of sexual dimorphism in body size. Oikos 70: 313-321.

Sesperk T., Tammaru T., Nylin S., Teder T. 2007. Achieving high sexual size dimorphism in insects: females add instars. Ecological Entomology 32: 243-256.

Siemann E., Haarstad J., Tilman D. 1999. Dynamics of plant and arthropod diversity during an old field succession. Ecography 22: 406-414.

Simberloff D.S., Wilson E.O. 1969. Experimental zoogeography of islands: the colonisation of empty islands. Ecology 50: 278-296.

Teder T., Tammaru T. 2005. Sexual size dimorphism within species increases with body size in insects. Oikos 108: 321-334.

SPSS, Inc. 1997. SYSTAT vers 7.0. The system for statistics. SYSTAT Inc., Evanston, IL.

Willott S.J., Hassall M. 1998. Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. Functional Ecology 12: 232-241.




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