# Spatial and temporal distribution of tenebrionid species (Coleoptera) in the Negev Highlands, Israel

Y. Ayal* & O. Merkl†

*\* Mitrani Center of Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University, Sede Boker Campus 84990, Israel*
*† Zoological Department, Hungarian Natural History Museum, H-1088 Budapest, Baross u. 13, Hungary*

Tenebrionid species composition and activity level were studied, using pitfall traps, in two sandy (dune and stabilized sand field) and four compact soil (*wadi*, north- and south-facing slopes, and loess plain) habitats in the Negev Desert Highlands, Israel. Each soil type had a distinctive species composition but habitats within soil types were similar both in species composition and phenologies. The number of species was not correlated with habitat primary production; it was low in sandy habitats (19 spp.) and high in compact soil (33 spp.) habitats. Within the compact soil habitats, large-size species were abundant only in the high plant-cover *wadi*, and the low plant-cover slopes and plain were dominated by smaller species. We suggest that low plant cover on the slopes and plain exposes large tenebrionids to predation by birds and limits them to the *wadi* where they are concealed and find refuge in the plant cover.

**Keywords:** Tenebrionidae; habitat segregation; desert; Negev; predation; birds; *Ciconia alba*; refuge

## Introduction

Darkling beetles (Tenebrionidae) are a conspicuous element of hot desert habitats. The adults are mostly black, seasonally common ground dwellers and, in many species, of a considerable size. They are detritivores, feeding mainly on dead plant material (Kramm & Kramm, 1972; Alsopp, 1980), and exhibit a wide variety of morphological (e.g. Medvedev, 1965) and physiological (e.g. Slobodchikoff, 1983; Seely *et al.*, 1988) adaptations to desert conditions. However, in spite of considerable effort to determine the factors affecting tenebrionid abundance in desert habitats (Wise, 1981; Thomas, 1983; Parmenter & MacMahon, 1988; Parmenter *et al.*, 1989) there is no agreement on the relative importance of abiotic and biotic factors in this respect (*see* Crawford, 1991 for review).

The present study examined tenebrionid distribution in the main habitat types of the Negev Desert Highlands, Israel with the following questions in mind: (1) What are the daily and yearly activity cycles of adults? (2) Does species diversity correlate with habitat features such as productivity of plant cover? (3) To what extent do the species overlap in their habitat use? (4) What are the possible factors which determine species composition and abundance in the study habitats?

## Methods

### Study area and habitats

The study was carried out from May 1989 to May 1992 in the central Negev Desert Highlands, Israel. The Negev is a part of the Palaearctic desert belt and has a typical Mediterranean climate with cold, rainy winters (November–April) and hot, dry summers (May–October). The main habitat types in the region are low rocky ridges, loess plains and sands. Study sites were located in the vicinity of Sede Boker (30°52′50″N, 34°47′50″E), and in the Mashabim Sands nature reserve, about 15 km north-west of Sede Boker. The Sede Boker study site included four habitat types on compact soil while two sand habitat types were studied at Mashabim.

The Sede Boker area is about 500 m above sea level and mean annual precipitation is 97 mm and ranges between 31 to 184 mm. Mean minimum winter temperature (January) is 3·6°C, and mean maximal summer temperature (July–August) is 32·2°C. In each of two rocky ridges (Hatira Ridge and Halukim Ridge) we studied three habitats: north- and south-facing slopes and *wadis* (dry drainage beds). The slopes include exposed rocky surfaces as well as alluvial areas with abundant loose stones and shallow soil. On the north-facing slope, total vegetation cover is about 10% and *Artemisia sieberi* Besser (= *herba-alba* Asso) is the dominant perennial. On the south-facing slope, total vegetation cover is about 5% and *Zygophyllum dumosum* Boiss. is the dominant perennial. Ephemeral vegetation adds 5–15% cover during late winter and spring. *Wadi* beds have deeper soil with low stone cover and relatively rich perennial and annual vegetation with a total cover range between >70% in spring and about 20% in summer. The fourth habitat type at Sede Boker, the Sede Zin loess plain, is poor in stone cover. The perennial vegetation is dominated by *Hammada scoparia* (Pomel) Iljin and a few *Z. dumosum* shrubs with <5% total cover. Ephemeral vegetation cover in the spring ranges between 5 to 50% depending on annual precipitation level. Mashabim sands are about 300 m above sea level at the eastern margin of the northern Sinai sand dunes. Mean annual precipitation is 110 mm and ranges between 30 and 200 mm (no data are available on temperature ranges but they are similar to those of Sede Boker). Two habitat types were studied: sand dunes and stabilized sand fields. Sand dunes are crests of less than 1 ha area and a few metres in height. They are dominated by the shrub *Artemisia monosperma* Delile with total cover <5% and a sparse annual cover during late winter and spring. Stabilized sand fields cover most of the site area, have a thin loess-biogenic crust and 10% cover by the shrubs *Retama raetam* (Forssk.) Webb, *Lycium schweinfurthii* Dammer, and *Helianthemum sessiliflorum* (Desf.) Pers. Cover of annual plants during the spring is 20–50%.

### Pitfall traps

Tenebrionid activity levels were monitored with pitfall traps. The traps were plastic cups with 10 cm diameter opening, 11 cm deep and 600 cm$^3$ volume. The opening was level with the soil surface. We used a grid of 67 traps in each of the three habitats in Halukim and Hatira Ridges, 100 traps in each habitat in Mashabim, and 200 traps in two grids of 100 in Sede Zin, for a total of 200 traps per site. Grid rows were 4 m apart and traps were 3 m apart within rows. The number of traps in a row and number of rows in a grid were adjusted to the habitat geography.

Traps were left open and checked daily for 5 consecutive days each month during May–October, and left open continuously and checked once a week during November–April. During May–October 1989, traps were checked at dawn and dusk for diurnal and nocturnal activity. At all other times, traps were checked only early in the morning. Additional data on activity time were noted by direct observations during all seasons. All trapped animals were released except a few taken for reference and identification. Animals

were identified using the tenebrionid collection of the Hungarian Natural History Museum, Budapest, where specimens are deposited.

## Catch standardization and indices

The use of pitfall traps to estimate species abundance has many shortcomings since the number of individuals trapped is affected by environmental and species-specific factors, and trap arrangement (see Ahearn, 1971; Parmenter et al., 1989 and references therein). Within these limitations, trapping results are useful for comparing activity level (a combined effect of animal density and daily movement rate) within species (at different times or among habitats) and between species (at the same time and in the same habitat). To minimize the effect of environmental factors, we considered cold rainy days in spring as non-trapping days, and for each trapping event we calculated the number of non-effective traps (as a result of burial in sand, flooding or damage by animals). We then expressed activity level as the number of individuals trapped per effective trap per trap day (Ind/Tr*Day) in each month.

Because no complete data are available for all years, we used the mean monthly activity level over the 3 years of the study to describe the phenology of each species. The sum of these means over the year gives the species' annual activity level, which is an estimate of its relative abundance in a given habitat. The sum of the species' monthly and annual activity level in a habitat is used as an estimation of the monthly and yearly total abundance of tenebrionids, respectively. The relative abundance of a species $i$ in a habitat $(p_i)$ was calculated as the proportion of the species' monthly activity level out of the sum for all species in the habitat for that month. We used these proportions to calculate the Shannon–Wiener diversity index:

$$H' = - \sum_i^n p_i \ln (p_i)$$

and its evenness index, $J' = H'/H_m$ ($H_m = \ln S$, where $S$ is the number of species in the habitat). We used the species annual activity levels in each habitat to calculate Morisita's index for similarity between habitats (Krebs, 1989).

## Results

Forty-eight species belonging to 27 genera were recovered during the study (Appendix). These species can be divided into those inhabiting sandy soils and those inhabiting compact soils. The few species which were found in both soil types were always rare in one of them. Therefore, we will discuss each of the two soil types separately. Within each soil type, species phenologies were highly correlated among habitats (Kendall Coefficient of Concordance $>0.70$, $p < 0.05$). Therefore, phenologies for each species were averaged over habitats within soil types. In contrast, total tenebrionid activity over the year did differ among habitats (see below), so these data are shown separately for each habitat.

### Sandy habitats

*Yearly phenology*
The two sandy habitats were inhabited by 19 species belonging to 13 genera (Appendix). Of these, only nine species were common (annual activity level $>0.05$ Ind/Tr*Day) in at least one of the two habitats. These nine species comprised about 90% of all individuals
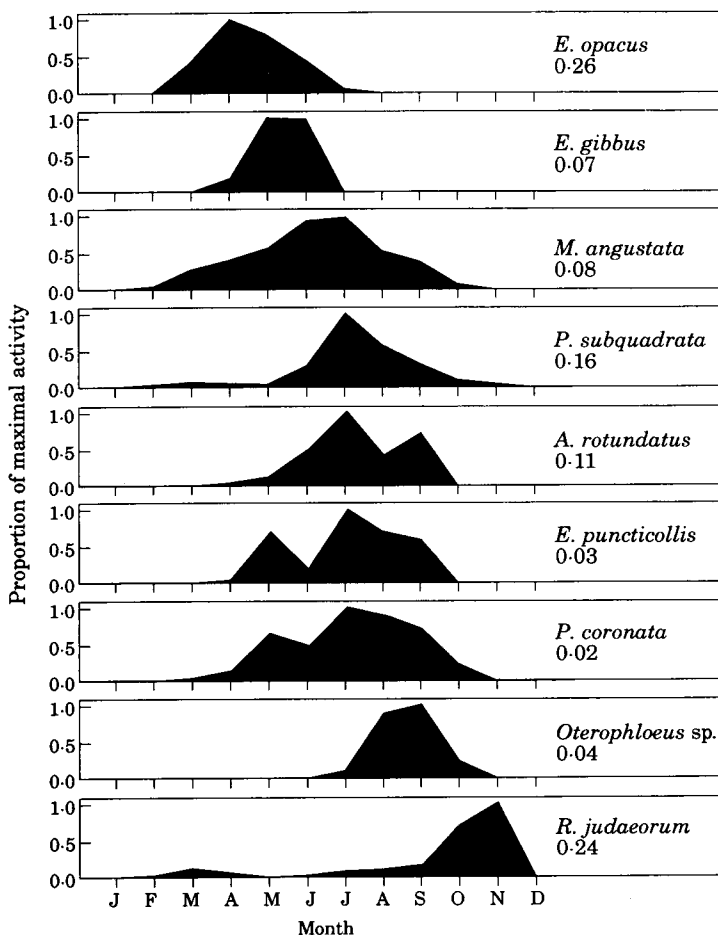
**Figure 1.** Monthly activity levels as a proportion of maximal activity level observed for that species for common (annual activity level >0·05) tenebrionid species of sandy habitats. Figures below species' names are maximal activity levels.

captured in both habitats and their phenologies averaged over the two habitats are shown in Fig. 1.

Two *Erodius* species, *E. opacus* and *E. gibbus*, were active during the spring and early summer. *Erodius opacus* activity started in March, peaked in April and terminated in June. *Erodius gibbus* activity started in April, lasted only 2 months and terminated in June. A third species, *Mesostena angustata*, also became active in March but continued all through the summer; it peaked during June–July and terminated in October. The other six species were mainly summer and autumn active. Of these, three species exhibited short activity periods; *Pimelia subquadrata* was active mainly during July–August, *Oterophloeus* sp. during August–September, and *Blaps judaeorum* during October–November. The three remaining species, namely *Prionotheca coronata*, *Erodius puncticollis* and *Arthrodeis rotundatus*, were active throughout the summer.

The highest number of co-occurring species was found during May–June, when spring species and late summer species overlapped (see below). This included seven out of the nine common species and five of the less common ones, for a total of 12 co-occurring species.

*Daily activity patterns*
The species' daily activity pattern depended on their activity period within the year (Ayal, pers. obs.). Species which were active in early spring (e.g. *E. opacus*, *E. gibbus* and *M. angustata*) were diurnal. However, they shifted their activity from mid-day during March to early morning and late afternoon as daily temperatures increased during late April and May. Moreover, *M. angustata*, which was active during the day in spring, shifted to a nocturnal-crepuscular activity during June–September. All summer-active species exhibited a nocturnal-crepuscular activity pattern. However, *Blaps judaeorum* shifted its activity to the early morning and late afternoon during October–November.

*Seasonal patterns of tenebrionid total activity and diversity*
The same five species, namely *E. opacus*, *P. subquadrata*, *M. angustata*, *A. rotundatus* and *B. judaeorum*, were dominant, although in different relative abundances, in both sandy habitats (Fig. 2). Another species, *E. gibbus*, was common only in the stabilized sand. Total activity patterns reflected activity of the dominants. Therefore, the differences in species activity levels between these two habitats also resulted in differences in the pattern of tenebrionid total activity level between them. In both habitats, *E. opacus* was the commonest species from March to May. High abundances of this species and *E. gibbus* in the stabilized sand resulted in a peak of total activity level in this habitat in May. From June onwards, total activity level in the stabilized sands decreased steadily. *Mesostena angustata*, *Arthrodeis rotundatus* and *Pimelia subquadrata* were equally dominant and comprised about 85% of the tenebrionid total activity in this habitat from June to September. Low abundances of *E. opacus* and *E. gibbus* in the dunes resulted in low total activity level during April. The peak of total tenebrionid activity in the dunes in July was due to the high activity level of *Pimelia subquadrata* in this habitat which comprised about 50% of the habitat's tenebrionid summer activity. *Blaps judaeorum* was the dominant species in both habitats during October–November. Its higher abundance in the dunes resulted in a higher activity level in this habitat than in the stabilized sand during these 2 months. The number of active species (Fig. 3a) and species' evenness (Fig. 3b) exhibited similar trends in both sand habitats during the year. Although the number of active species increased from January to April, species evenness decreased during this period as one or two species dominated in both habitats in the spring (see above). Species' evenness increased during the summer and then decreased sharply during October and November when *B. judaeorum* dominated both sand habitats.
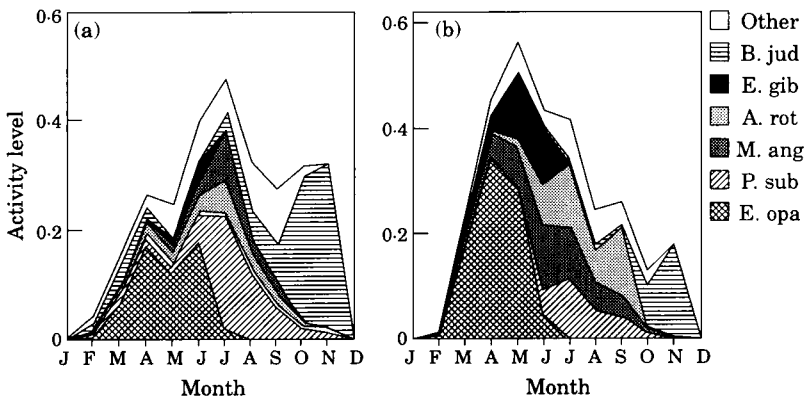


**Figure 2.** Monthly activity levels of the six dominant species of sandy habitats as part of the tenebrionid total activity level in (a) dunes and (b) stabilized sand field. E. opa, *E. opacus*; E. gib, *E. gibbus*; P. sub, *P. subquadrata*; M. ang, *M. angustata*; A. rot, *A. rotundatus*; B. jud, *B. judaeorum*; Other, all other species combined.

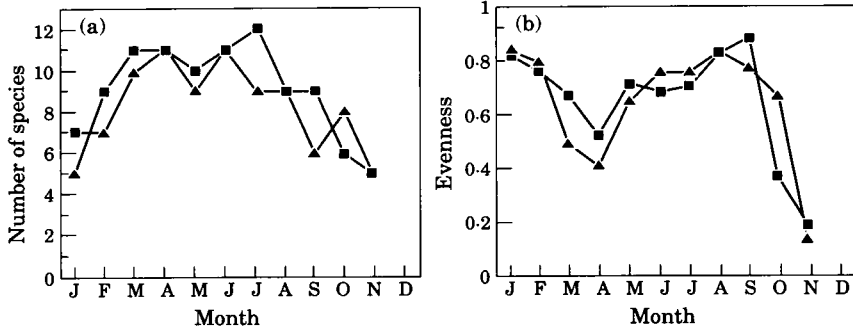**Figure 3.** Diversity of tenebrionid communities in sandy habitats. (a) Number of co-occurring active species. (b) Shannon–Wiener evenness index $J'$. ■, Dune; ▲, stabilized sand field.

On an annual basis, the two sand habitats exhibited high similarity in species composition and abundances (Morista's similarity index = 0·8). Nevertheless, the two sand habitats did differ in some aspects of their tenebrionid species composition. In the stabilized sand, considerable numbers of the compact-soil species *Mesostena puncticollis* were captured (maximal mean monthly activity level of 0·008 Ind/Tr*Day, total yearly activity level = 0·04). Furthermore, a few individuals of five other compact-soil species, namely *Pimelia boehmi*, *Pimelia* sp., *Sepidium tricuspidatum*, *Adesmia dilatata* and *Adelostoma grande*, were also recovered in this habitat.

### Compact soil habitats

*Yearly phenology*

Thirty-six species belonging to 22 genera were recovered in the four compact soil habitats (Appendix). Of these, 11 species were too rare (total activity level <0·05) to analyse their year-round activity patterns. The remaining 22 species can be divided into two groups according to the time of adult activity: spring-active (Fig. 4a), and summer- and autumn-active species (Fig. 4b).

Adults of spring-active species exhibited short activity periods. Although four species started activity in February (Fig. 4a), most spring-active species started in March, and all reached peak activity during March–April (Fig. 4a). Adults of *Adesmia metallica* and *Sepidium tricuspidatum* terminated their activity at the beginning of May and those of most other species at the end of May. *Zophosis punctata* was the only species which was highly active both in spring and summer; it started its activity in March, was highly active during April–August, and terminated its activity in late September. *Scleron andreinii* and *Gonocephalum perplexum* exhibited low activity levels during the summer. A few *A. dilatata*, *Pimelia boehmi* and *S. tricuspidatum* were active during the autumn. Such activity was especially noticed in *S. tricuspidatum* following 17-mm rainfall in the autumn of 1991.

Adults of summer-active species had longer activity periods that, in some species, were extended into the autumn. Most of them began activity in April or later and they exhibited more diverse activity patterns than spring-active species. Many exhibited high activity levels during 1 or 2 months and low activity levels in all other months. Peak activity occurred as early as June in *Mesostena puncticollis* and *Adelostoma grande*; during July–August in *Trachyderma philistina*, *Pimelia canescens* and *P. grandis*; and late October in *Hionthis tentyrioides*, *Akis elevata*, *Gedeon hierichonticus*, *Blaps sulcata* and *B. wiedemanni*. *Zophosis complanata* did not exhibit a clear activity peak but spread its activity evenly along several months, similar to *Z. punctata* mentioned above.
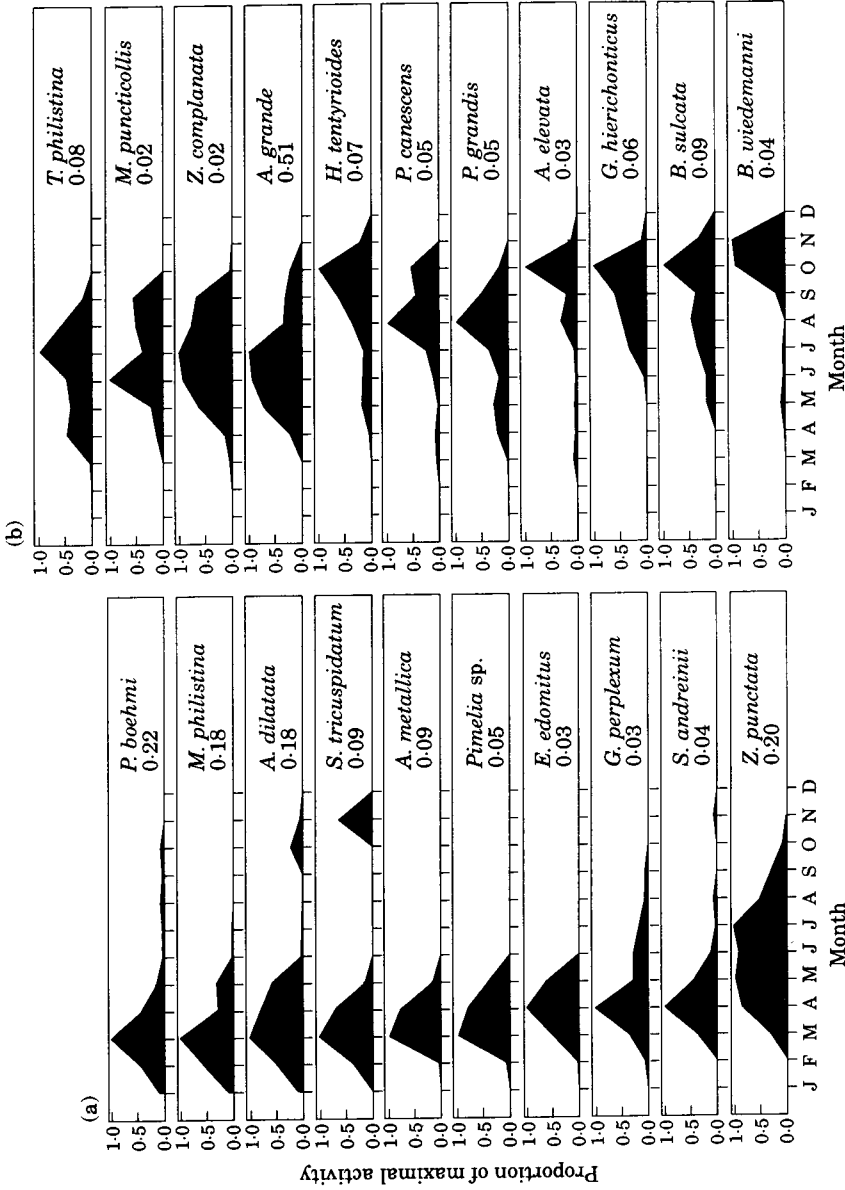
**Figure 4.** Monthly activity levels as a proportion of the maximal activity level observed for that species for common (annual activity level >0·05) tenebrionid species of compact-soil habitats. (a) Spring-active species. (b) Summer- and autumn-active species. Figures below species names are maximal activity level.

*Daily activity patterns*

All spring species were active during the day (Ayal, pers. obs.). During February and March when daytime temperatures were rather low the adults were active during the warm midday hours. During April when daily temperatures started to reach high levels, most species began to exhibit bi-modal activity patterns, being active during early morning and late afternoon, but avoiding activity during hot midday hours.

Most summer active species were crepuscular and nocturnal and use burrows, stone undersides, rock fissures and plant cover for hiding during day time (Ayal, pers. obs.). Only the two *Zophosis* spp. were observed being active during the day. However, during hot summer days they avoided being active during the hottest midday hours and were mainly active in the morning or afternoon.

*Seasonal patterns of tenebrionid total activity*

Total tenebrionid activity was highest in the highly productive *wadi* (Fig. 5a). Of the remaining three habitats activity was higher on the south slope than the north slope and
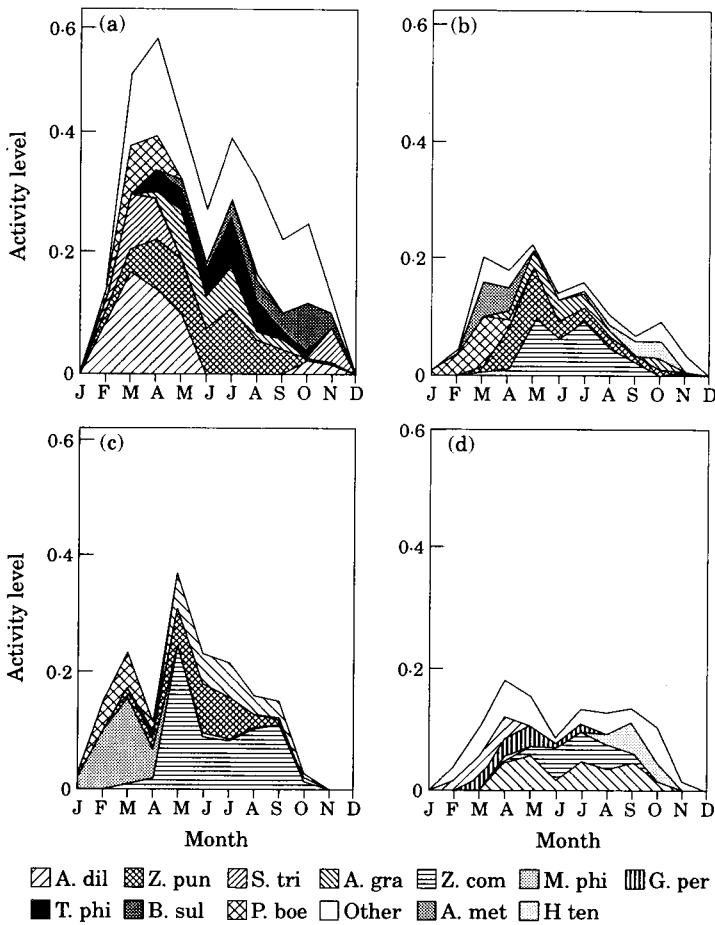


**Figure 5.** Monthly activity levels of the 13 dominant species of compact-soil habitats as part of the tenebrionid total activity level in the (a) *wadi*, (b) north-facing slope, (c) south-facing slope and (d) loess plain. A. dil, *A. dilatata*; A. met, *A. metallica*; Z. pun, *Z. punctata*; Z. com, *Z. complanata*; B. sul, *B. sulcata*; S. tri, *S. tricuspidatum*; P. boe, *P. boehmi*; A. gra, *A. grande*; M. phi, *M. philistina*; T. phi, *T. philistina*; C. per, *G. perplexum*; H. ten, *H. tentyrioides*; Other, all other species combined.

loess plain (Fig. 5b–d), even though the loess plain was the most productive of the three (Ayal, per. obs.). In the *wadi*, a prominent peak in tenebrionid activity occurred during March–April due to the high abundances of the four spring species *A. dilatata*, *Z. punctata*, *P. boehmi*, and *S. tricuspidatum* (Fig. 5a). During May–September, *Z. punctata*, *A. grande*, *T. philistina*, and *B. sulcata* were highly active in this habitat. *Blaps sulcata* dominated the *wadi* during October. In the north-facing slope, *A. metallica* and *P. boehmi* dominated during March–April; *Z. punctata*, *Z. complanata* and *A. grande* during the summer; and *H. tentyrioides* during October (Fig. 5b). On the south-facing slope, peak spring activity occurred as early as March due to the high activity level of *Micipsa philistina* and *P. boehmi* (Fig. 5c). In the summer, peak activity occurred in May due to the high abundance of *Z. complanata*, which together with *Z. punctata* and *A. grande* dominate this habitat. In the loess plain, *S. tricuspidatum*, *A. dilatata* and *G. perplexum* dominated in the spring; and *A. grande*, *Z. complanata* and *H. tentyrioides* in the summer (Fig. 5d).

The *wadi* had the highest number of species, with 15–20 co-occurring species during most of the year (Fig. 6a). Species' evenness in the *wadi* and on the slope increased in general from February onwards, whereas in the loess plain, it fluctuated all through the summer (Fig. 6b).

### Comparison of tenebrionid species composition

The four compact-soil habitats exhibited different degrees of similarity in their species composition and abundances. The three low productivity habitats (slopes and plain) were extremely similar to each other (Morisita's index = 0·65–0·87) and even the *wadi* was quite similar (Morisita's index = 0·52–0·58) to two of the three other habitats. Only the most productive *wadi* and the least productive south slope were strongly dissimilar (Morisita's index = 0·36). Most species were found in at least two or three of the four habitats. However, there were exceptions: *Blaps sulcata*, *Gedeon hierichonticus* and *Trachyderma philistina* were common *wadi* species that were rarely found or absent from all other habitats. In the south-facing slope, *Micipsa philistina*, *Akis elevata* and *Amnodeis confluens* were relatively common species that were absent or rare in all other three habitats whereas *Gonocephalum perplexum* was common in the Zin loess plain and rare in other habitats.

The species that were rare in the less productive habitats were generally the larger species. Figure 7 shows the yearly total activity level of the 16 species with activity levels ≥0·1 Ind/Tr*Day in at least one of the four habitats, when these species are ranked by sizes. In the *wadi*, species of all sizes were abundant (Fig. 5). However, large species were abundant only in the *wadi*. The largest abundant species on the slopes were *Pimelia boehmi* (10th in rank) and *A. metallica* (8th in rank, N slope only) (Fig. 5). The most abundance species in the open habitats were all relatively small species: *Zophosis complanata* (6th in
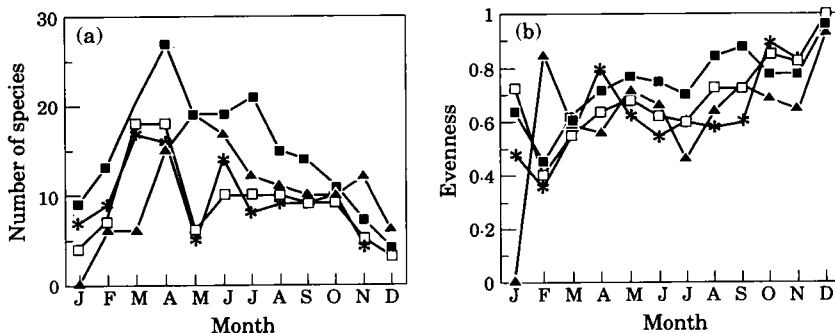


**Figure 6.** Diversity of tenebrionid communities of compact-soil habitats. (a) Number of co-occurring active species. (b) Shannon–Wiener evenness index *J'*. ■, *Wadi*; □, north-facing slope; *, south-facing slope; ▲, loess plain.
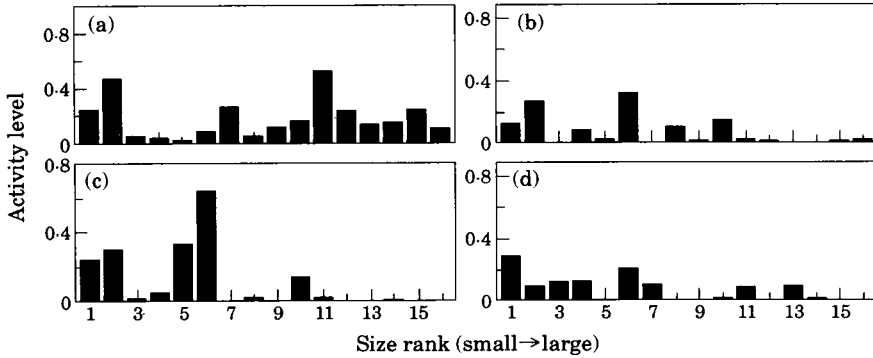
**Figure 7.** Yearly total activity levels of the 16 common species (total activity level $>0.1$ in at least one habitat) in each of the four compact-soil habitats: (a) *wadi*, (b) north-facing slope, (c) south-facing slope and (d) loess plain. Species are ranked by size from smallest (1) to largest (16). Species names: 1, *A. grande*; 2, *Z. punctata*; 3, *G. perplexum*; 4, *H. tentyrioides*; 5, *M. philistina*; 6, *Z. complanata*; 7, *S. tricuspidatum*; 8, *A. metallica*; 9, *P. canescens*; 10, *P. boehmi*; 11, *A. dilatata*; 12, *B. sulcata*; 13, *P.* sp.; 14, *G. hierichonticus*; 15, *T. philistina*; 16, *P. grandis*.

size rank), *Micipsa philistina* (S slope only, 5th in size), and *Zophosis punctata* and *Adelostoma grande* (ranked 2nd and 1st respectively). The last two species are also common in the *wadi*.

### Tenebrionid predation by birds

With the exception of species of the genus *Blaps*, all other adult tenebrionids of the Negev seem to lack the chemical defences against predators that are common among tenebrionids in other regions (Eisner & Meinwald, 1966; Tschinkel, 1975). Hence, tenebrionids of the Negev Highlands are presumably very vulnerable to predation and may form an important food resource to many bird species. A prominent example is the white stork *Ciconia alba* during its spring migration from Africa to Europe. The Negev Desert is major route for its spring migration, which takes place from mid-March to the end of April and coincides with the peak abundance of spring-active tenebrionids. During this period thousands of storks pass through the Negev feeding on every arthropod species of considerable size.

**Table 1.** *Contents of 23 pellets of White Stork collected during the spring migration in the Sede Boker area*

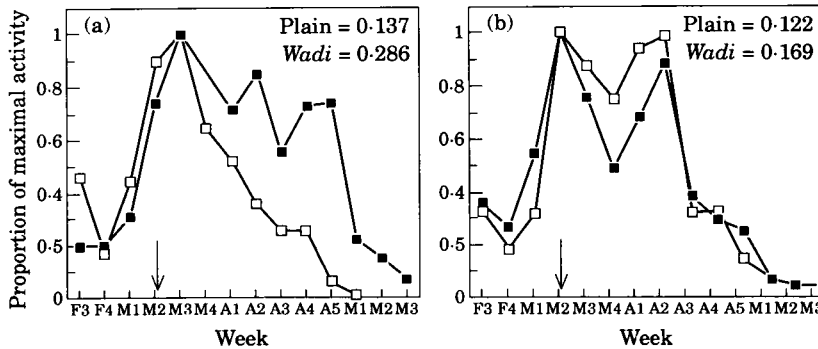| Species | No. of individuals | Per cent of total |
|---|---|---|
| *Adesmia dilatata* | 356 | 24·4 |
| *Adesmia abbreviata* | 242 | 16·6 |
| *Pimelia boehmi* | 190 | 13·0 |
| *Pimelia* sp. | 150 | 10·3 |
| *Pimelia grandis* | 35 | 2·4 |
| *Sepidium tricuspidatum* | 170 | 11·6 |
| *Erodius edomitus* | 86 | 5·9 |
| Other tenebrionids | 51 | 3·5 |
| Other arthropods | 182 | 12·5 |
| Total | 1462 | |

**Figure 8.** Weekly changes in activity level as a proportion of the maximum for (a) *A. dilatata* and (b) *S. tricuspidatum* during spring 1992 in the *wadi* (■) and the loess plain (□). Figures are values of weekly maximal activity levels for each species in each habitat. The arrows indicate the arrival time of the storks. F3, 3rd week of February; F4, 4th week of February, etc.

Tenebrionids are one of their common food items (Table 1). During the short period of their spring migration storks may devastate regional tenebrionid populations removing up to 95% of the adults of large-size species (Ayal, pers. obs.). Adult tenebrionids should be more vulnerable to predation in less productive habitats, where large species cannot find refuge under plant cover or in animal burrows. This is suggested by the changes in abundance of *Adesmia dilatata* (Fig. 8a) and *Sepidium tricuspidatum* (Fig. 8b) in the Zin loess plain and the nearby *wadi* during the stork spring migration of 1992. The activity level of *A. dilatata* decreased rapidly in the loess plain, compared with the *wadi* in mid-March when storks arrived to the area. In contrast, the activity level of *S. tricuspidatum* was similar between habitats at the same time. *Adesmia dilatata* is a large (11th in rank; Fig. 7) and conspicuously black species and can be easily located by foraging storks in the low plant cover of the plain, compared to the *wadi*, which was rich in plant cover. The smaller (7th in rank) and grey *S. tricuspidatum* blends better with the loess background and hence should be less exposed to predation by storks (Table 1).

## Discussion

### *Segregation among tenebrionid species*

In accordance with other studies of desert tenebrionids (e.g. Thomas, 1983; Sheldon & Rogers, 1984; Crawford, 1988) our results clearly show that soil type is the main environmental variable affecting the distribution of the Negev Highland tenebrionids. Most species were limited to either sand or compact-soil habitats. The two exceptions were *Arthrodeis rotundatus* (a common stabilized sand species also found in compact-soil habitats) and *Mesostena puncticollis* (a common compact soil species also found in the stabilized sand). However, habitats within a soil type exhibited a remarkable similarity in species composition. The two sand habitats had the same species composition and differed mainly in species' relative abundance despite the differences in their plant communities. High overlap in habitat use was also found among most compact-soil species. Most species were found in all four major habitat types we studied with only a few species confined to only one or two of them. However, the habitats differed in the relative abundance of these species which may, in part, be a result of differences in exposure to predators (see below). The lowest degree in similarity was found between the *wadi* and the south-facing slope with the most extreme difference in productivity.

In both sandy and compact-soil habitats, species segregated into distinct groups of spring- and summer-active species. But within these two groups, species overlapped in their daily activity time; all spring-active species were diurnal and most summer-active species were crepuscular and nocturnal. The only exceptions were the two summer-daily-active *Zophosis* species, but they overlapped widely in their habitat use. However, in all species, daily activity cycles were flexible and species tended to be active during the most benign daily temperatures; they shifted their daily activity during the year according to the timing of the proper temperature. Such shifts have been noted for Judean desert species by Bodenheimer (1934) and some Namib species (Holm & Edney, 1973) although some other Namib species are active on the verge of their upper thermal limit (Seely *et al.*, 1988). Locomotory activity in desert Tenebrionidae has been reviewed by Cloudsley-Thompson & Constantinou (1985); see also Cloudsley-Thompson, 1991.

### Habitat productivity and tenebrionid abundance and diversity

Within compact-soil habitats, diversity as well as total activity level was more or less directly related to productivity — higher in the *wadi* and lowest in the slopes and loess plain (Fig. 5). Sandy soil habitats in deserts generally have higher soil moisture, primary production and plant cover than hard soil habitats (Noy-Meir, 1973; Seely, 1991). Among the compact-soil habitats we studied, only the *wadi* had a level of primary production comparable to the sandy habitats. Indeed, total activity levels in the sandy habitats (Fig. 2) were as high as in the *wadi* (Fig. 5). However, we found many fewer tenebrionid species in sandy habitats (19 with nine abundant) than in the *wadi* (25 with 18 abundant). Instead, the sandy habitats had similar species numbers to those found in the less productive north-facing slope (15 with eight abundant), south-facing slope (22 with seven abundant) and the loess plain (11 with nine abundant). Moreover, the number of co-occurring species at any one time was higher in all compact-soil habitats (Fig. 6) than in both sandy habitats (Fig. 3). One possible reason for this pattern is that the sandy areas of the Negev are at the far eastern end of the Saharan sand dunes which extend into the Negev Highlands through northern Sinai. The tenebrionic fauna may have become depauperate with distance from its distributional centre.

### Habitat change and tenebrionid species composition

The sandy areas of the northern Negev are in the process of stabilization as a result of a decrease in grazing over the past 40 years. This is especially so in the Mashabim sands we studied, where livestock grazing was banned about 15 years ago when the area was allocated as a nature reserve. As a result, the sand over a large portion of the area has stabilized, and a thin loess crust which is kept together by a blue-green algae mat has developed on the surface. Concurrently, plant cover in the stabilized sand area has increased and species composition has changed. In spite of the differences in plant community composition and structure, the differences in the tenebrionid fauna between these two sub-habitats is relatively small and mainly involves changes in relative abundance of the species and not in species composition. This suggests that (a) tenebrionids are less sensitive than plants to changes in their physical environment, including to soil structure which is the habitat variable which most affects their distribution (see above), and (b) that type of food (i.e. plants species) does not much affect species composition. However, the appearance of loess species in the stabilized area may indicate the beginning of a process of faunal changes which will accelerate in the future. The existing low species number in this site may also be a result of species loss following the changes in the habitat physical properties and plant community. Lack of information on

tenebrionid abundance in the area in the past, or similar habitats which are still being grazed, prevent the examination of this possibility.

To conclude, high diversity of tenebrionids in the Negev Highlands does not rely on fine segregation in either habitat use or activity time. Adult tenebrionids are mainly scavengers of plant material, but they also occasionally consume remains of dead animals, with no apparent specificity between species. Hence, competition for food related to classical niche partitioning does not seem to play an important role in shaping tenebrionid community structure in habitats within the same soil type. However, as the ecology of tenebrionid larvae is largely obscure, the importance of competition in the larval stage cannot be ruled out, although in one case (Wise, 1981) such competition was proved not to be important.

However, the peculiar segregation of the loess-dwelling species by adult size pointed out above (Fig. 6) calls for some explanation. A possible one is predation of the adults by birds (Ayal, 1990). Predation was found to be an important factor limiting arid-land tenebrionid population in North America (Parmenter & MacMahon, 1988) and was suggested as a possible explanation of the diurnal activity of Namib Desert species (Ward, 1991). The white stork is by no means an exception and remains of adult tenebrionids are commonly found in pellets of nocturnal (e.g. the Little Owl *Athene noctua*) or diurnal birds of prey (e.g. the Great Gray Shrike *Lanius excubitor*). The relatively dense plant cover in the *wadi* should make it difficult to detect large tenebrionids from a distance and offers ample refuges from approaching predators to big tenebrionids under plant cover or in burrows. However, on the slopes and loess plain only small species can conceal themselves in small cracks of the soil crust, under stones or at the base of small shrubs. Hence, predation by birds may act as an important factor in the determination of species abundances in different habitats, especially of large species. This possibility needs further study by field experiments, not only for understanding the factors which determine tenebrionid distribution and abundance but also as an important food link by which dead plant material is transferred to higher trophic levels.

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# Appendix

*Tenebrionid species of the Negev Highlands and the habitat type in which they were found*

| Species | Compact soil habitat* | Sand habitat† |
| --- | --- | --- |
| *Erodius edomitus* Koch | Spr, common | |
| *E. gibbus* Fabricius | Spr, uncommon | Spr & Sum, common |
| *E. opacus* Kraatz | | Spr & Sum, common |
| *E. puncticollis* Solier | | Sum, common |
| *Arthroideis rotundatus* Solier | Sum, uncommon | Sum, common |
| *Amnodeis confluens* Miller | Spr, uncommon | |
| *Zophosis punctata* Brulle | Sum, common | |
| *Z. complanata* Solier | Sum, common | |
| *Z. pharaonis* Koch | | Spr & Sum, uncommon |
| *Mesostena puncticollis* Solier | Sum, common | Sum, uncommon |
| *N. angustata* Fabricius | | Spr & Sum, common |
| *Micipsa philistina* Reiche | Spr, common | |
| *M. burtoni* Baudi | | Sum, rare |
| *Hionthis tenmtyrioides* Miller | Sum & Aut, common | |
| *Tentyria discicollis* Reiche & Saulcy | Sum, uncommon | |
| *Oterophloeus* sp. | | Sum, common |

## Appendix (*continued*)

| Species | Compact soil habitat* | Sand habitat† |
|---|---|---|
| *Adesmia metallica syriaca* Baudi | Spr, common | |
| *A. dilatata* Klug | Spr, common | |
| *A. abbreviata* Klug | Spr, uncommon | |
| *Adelostoma grande* Haag & Rutenberg | Sum, common | |
| *Sepidium tricuspidatum* (= *korah*) Fabricius | Spr, common | |
| *S. dathan* Crotch | Spr, rare | |
| *Akis elevata* Solier | Sum & Aut, uncommon | |
| *A. goryi* Solier | Sum, uncommon | |
| *Prionotheca coronata* Ancey | | Sum, common |
| *Trachiderma philistina* Reiche & Saulcy | Sum, common | |
| *Pimelia boehmi* Reitter | Spr, common | |
| *P. grandis* Klug | Sum, common | |
| *P. interpunctata* Klug | | Spr & Sum, rare |
| *P. canescens* Klug | Sum, common | |
| *p. subquadrata* Sturm | | Sum, common |
| *P.* sp. | Spr, common | |
| *Scaurus puncticollis* Solier | Sum, rare | |
| *Gedeon hierichonticus* Reiche & Saulcy | Sum, common | |
| *Pterolasia squalida* Solier | | Spr & Sum, uncommon |
| *Blaps sulcata* Laporte de Castelnau | Sum & Aut, common | |
| *B. wiedemanni* Solier | Aut, common | |
| *B. judaeorum* Miller | | Sum & Aut, common |
| *B. bifurcata* Solier | | Aut, rare |
| *Cheirodes sardoa* Guerin | Sum, rare | |
| *Ch. pilosus* Tournier | | Sum, rare |
| *Gonocephalum soricinum* Reiche & Sailcy | Spr, rare | |
| *G. perplexum* Lucas | Sum, common | |
| *Scleron andreinii* Gridelli | Spr, common | |
| *Eurycaulus hirsutus* Miller | | Sum, uncommon |
| *Dendarus syriacus* Reiche | Spr, rare | |
| *Machlopsis crenatocostata* Redtenbacher | | Sum, rare |
| Totals | | |
| Genera    27 | 22 | 13 |
| Species    48 | 33 | 19 |

Spr, Spring; Sum, summer; Aut, autumn.
* Includes rocky slopes and loess plain habitats.
† Includes sand dunes and semi-stabilized sand fields.