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Lizard burrows association with successional stages of biological soil crusts in an arid sandy region

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We study the relationship between the successional stages of biological soil crusts and the distribution of lizards in the 'Arava Valley (eastern Negev Desert). In the dry sandy habitat, four stages of the biological soil crust succession can be characterized by the degree of soil surface compaction. Both the geckos (*Stenodactylus doriae*) and the diurnal lizards (*Acanthodactylus* spp.) strongly preferred the fragile crust, where they dug 80% and 94% of their burrows, respectively. Land conservationists and managers should take these results into consideration when management plans for natural habitats and nature reserves are evaluated.

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Introduction

One of the major components in undisturbed drylands ecological systems are biological soil crusts (Friedmann & Galun, 1974; Skujins, 1984; Evenari, 1985; West, 1990; Johansen, 1993; Eldridge *et al.*, 1995). This 'cryptogamic' or 'microphytic' crust community varies markedly from typically 2 mm thick relatively homogeneous cyanobacterial crusts to complex crust community about 15 mm thick (Zaady *et al.*, 1997). In the successional pathway of the crust communities, the pioneers in colonizing the soil surface after disturbance are the cyanobacteria, which are followed by green algae, mosses and lichens (Rayburn *et al.*, 1982; West, 1990; Johansen, 1993; Eldridge *et al.*, 1995; Zaady *et al.*, 2000). Different factors can modify successional pathways from the same initial state of the system. Physical influences such as soil structure and types, radiation intensity, and topographic traits influence the

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successional pathways and the soil crust community. For example, the slope aspect affects water availability and soil moisture. When physical conditions are the same, disturbances are the key factors that determine a specific successional stage (Zaady *et al.,* 2000).

Sand dune areas are considered dry habitats and are characterized by their extremely low cohesion. As a result, grains of sand on the surface are loose and are easily transported by wind (Tsoar & Möller, 1986; Tsoar, 1990). Stabilization of sand dunes occurs after colonization by filamentous cyanobacteria, which may constitute a prominent crust (Danin, 1996). Because crust organisms have the ability to activate their photosynthetic system in short periods, even at low levels of water availability, such as fog, dew and atmospheric water vapor (Lange *et al.,* 1994), they are often the first organisms to colonize sand dune environments. The polysaccharides that are produced by these cyanobacteria and by soil algae (Bertocchi *et al.,* 1990), form a mucilaginous sheath on the soil surface that lightly binds the soil surface particles (Baily *et al.,* 1973; Metting, 1981; Metting & Rayburn, 1983). The polysaccharides glue the sand particles together (Bailey *et al.,* 1973; Schulten, 1985) and thus play an essential role in sand stabilization and in preventing water and wind erosion (Friedman & Galun, 1974; Neuman *et al.,* 1996; Eldridge & Kinnell, 1997). High holding capacity of moisture, typical to polysaccharides, enhances further crust development and facilitates colonization by other organisms such as above-ground cyanobacteria, soil algae, mosses and lichens. The successional development of these components of the soil crust depends on the rainfall regime (Zaady *et al.,* 1997).

In the 'Arava Valley (with less than 75 mm mean annual rainfall), only 1–2 mm thick cyanobacterial crusts are formed. Soil crusts in sandy areas which play an important role in these ecosystems have been discussed in several contexts: dune stability (Danin, 1996; Tsoar, 1990), prevention of erosion (Eldridge & Greene, 1994; Belnap & Gillette, 1998) water regime (Jeffries *et al.,* 1993*a*,*b*) primary productivity (West, 1990) and plant succession (Danin, 1996).

Reptile species diversity in arid lands is determined or influenced by a variety of abiotic, biotic and anthropogenic factors (Bouskila & Dickman, 2001). Substrate contributes to the diversity of desert lizards, and sandy soils in particular seem to enable the coexistence of more species than other habitats, due to the different life styles that may coexist in this habitat (Disi, 1987; Seeley, 1991; Yom-Tov & Werner, 1996).

The ground gecko *Stenodactylus doriae* is a large nocturnal gecko found in relatively dense populations in sandy areas of the 'Arava Valley, eastern Negev desert, Israel (Amitai & Bouskila, 2001). *Stenodactylus doriae* is active only during the night (Frankenberg, 1978) and spends the day in small burrows that it digs and blocks with sand (Bouskila, 1987, 1988). During daytime, the gecko must stay sheltered in a burrow to avoid predators and extremely high temperatures on the surface of the sand. *Stenodactylus doriae* often has several burrows in its home range, and after spending several successive days in the same burrow it switches to one of the alternative burrows (Bogin, 1999). The two additional lizards investigated in this study, *Acanthodactylus boskianus* and *A. opheodurus*, are diurnal lizards that except for a few hours of above-ground activity, remain concealed in their burrows. These lizards use the burrows as shelters from predators and as a refuge from temperatures that may be too high or too low for their activity on the sand surface.

The goal of this study was to investigate the relationship between the successional stage of the biological soil crusts in sand dune areas and their effect on desert lizards distribution. In addition, we discuss the possibility that the process of land management of a sandy area affects the distribution and density of these species within this area. We measured physiological and geomorphological characteristics of the crusts and compared the distribution of lizard burrows among different crust types to the distribution of available sites in the study site.

Study site

The study site (30°87′N: 35°14′E) is a sandy area near Hazeva in the northern' Arava Valley of the eastern Negev desert, Israel (Fig.1) (USA classification: sand dune soil texture, Typic Torripsamment [Dan *et al.,* 1977]). The region is an extreme desert (Bouskila, 1986; Stern *et al.,* 1986). Mean annual rainfall at Hazeva is 71 mm (Katsnelson, 1966). The dunes are covered with patches of perennial shrubs (most of them 40–140 cm high), and a few Acacia trees (*Acacia tortilis* (Forssk.) Hayne and *A. raddiana* Savi). The main perennial shrubs *Nitraria retusa* (Forssk.) Ascherson, *Traganum nudatum* Delile, and *Hammada salicornica* (Moq.) Iljn), depend on below-ground water, that are usually evenly distributed (Feinbrun-Dothan & Danin, 1991).

Following winter rains (November–March), the interspace between shrubs is covered with cyanobacterial crusts. In the dry season, in unprotected areas, most of the new crusts eventually disintegrate, due to burrowing by rodents, trampling by gazelles, humans, livestock and other wildlife (Bogin, 1999). In areas that were not disturbed for several years, the interspace between the shrubs is covered with hard crusts.

Methods

In order to determine the frequency of different soil surfaces in the study area, we selected 79 random locations (using random lists of directions and distances) and tested the soil surface compaction with a penetrometer (Pocket Pentrometer, Forestry

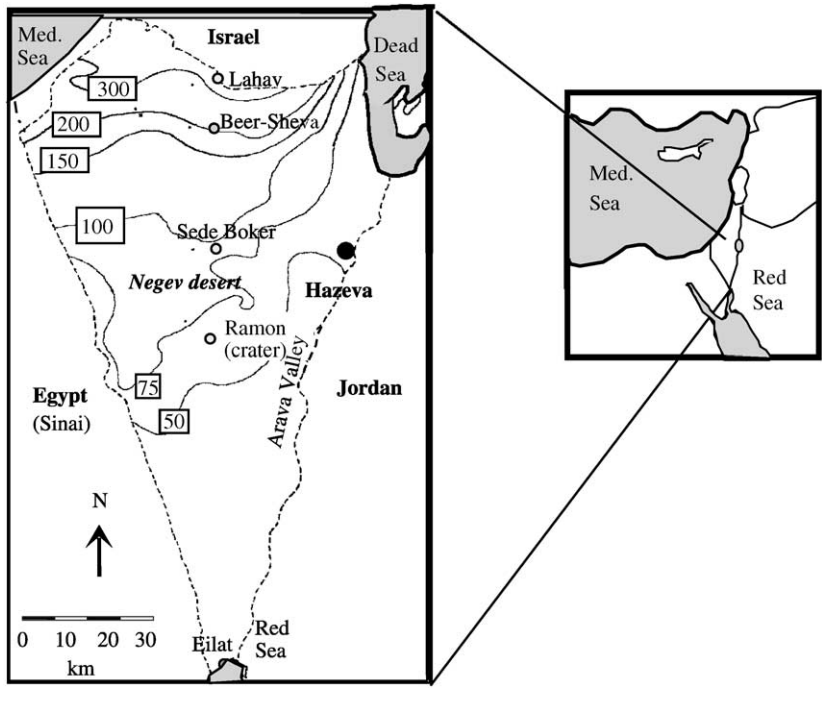


Figure 1. Location of Hazeva, northern 'Arava Valley of the eastern Negev desert, Israel (modification from Stern *et al.*, 1986). The lines indicate the rainfall gradient along the Negev desert.

Suppliers, Inc.). We report the highest pressure (in units of $kg\,cm^{-2}$) that can be applied to the soil by the penetrometer before the soil surface gives in. Because shrubs are not suitable as burrow locations for the lizards (Bogin, 1999), 11 of the locations that fell on shrub patches were excluded from the analysis, resulting in a total of 68 locations in the sample. From the distribution of measurements we were able to divide the crusts into three different successional stages. We refer to them as fragile crust (the softest, temporary crust, resistance to pressure $<1{\cdot}85\,kg\,cm^{-2}$), medium crust (relatively hard but still temporary, resistance to pressure 1·85–$3\,kg\,cm^{-2}$) and hard crust (permanent, resistance to pressure $>3\,kg\,cm^{-2}$). We refer to a fourth surface type, characterized by a complete lack of crust, as 'loose sand'. Loose sand is very different from any crusted surface and is easy to discern it visually.

Samples were collected at three random locations in each of the four surfaces. We followed the suggestions of Johansen (1993) and West (1990) and evaluated the crusts with several different methods. These methods complement each other and provide a better picture of the processes, which occur in the soil crusts and at the different successional stages. Biophysiological parameters (proteins, chlorophyll and polysaccharide content) and a geomorphological parameter (resistance to pressure) were measured from these samples.

Protein content was measured using the Lowry method (Lowry *et al.*, 1951). The total chlorophyll content was extracted with ethanol and quantified (Lichtenthaler & Wellburn, 1983). The polysaccharides were measured photometerically (Spectronic 21, Bausch & Lomb), using Anthron reagent and Sulfuric acid (Dische, 1962).

Values of resistance to pressure near the roofs of 50 *S. doriae* burrow entrances were measured as described previously for the random points. *Stenodactylus doriae* burrows and their identification are described in details elsewhere (Bouskila, 1987, 1988; Bogin, 1999). To measure resistance near *Acanthodactylus* burrows, we located 50 burrows along transects (10–20 m apart) in the study site. These burrows can be identified precisely by their shape and by the footprints of the lizards near the entrance, however, the distinction between burrows of the two *Acanthodactylus* species is not possible without destroying the burrow and catching the lizard. We thus treated the burrows of the two diurnal lizards together, with no attempt to identify the two species. All measurements near burrows were taken 2–4 cm from the roof of the entrance.

One-way ANOVA, with Duncan New Multiple Range and Scheffe *F*-tests (Sokal & Rohlf, 1995), were used to test differences in parameter means between the sand surfaces. From the frequency of random points in the four surfaces we calculated expected numbers of burrows. We compared these expected numbers with the observed numbers of burrows in each surface type with Chi square test (Zar, 1984). Differences were considered statistically significant if $p<0{\cdot}05$.

Results

Protein content steadily decreases from very hard crust (stable undisturbed crust), to medium crust, fragile crust and to loose sand at the lower point (Fig. 2) ($p<0{\cdot}0001$). Chlorophyll content in the hard crust and the medium crust was similar to each other, but significantly higher than in the fragile crust and in loose sand ($p<0{\cdot}006$) (Fig. 3). Polysaccharides showed a pattern similar to that found in protein content, but not all comparisons were significantly different. Significant differences were found between the hard crust and all other surfaces (Fig. 4) ($p<0{\cdot}0001$). Loose sand was not statistically different from fragile crust but had lower values than the medium crust

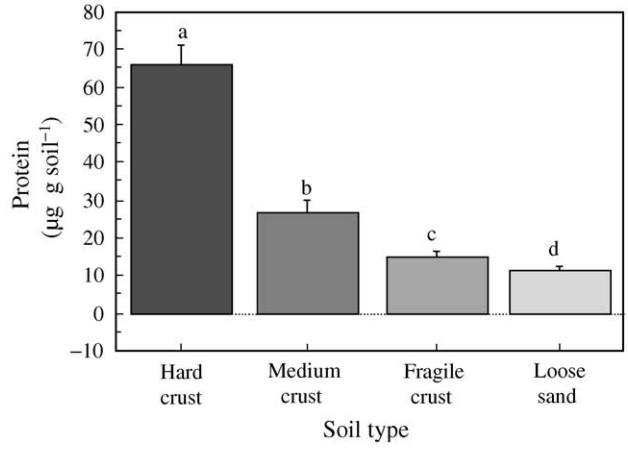


Figure 2. Protein content of the three crust types in comparison to loose sand. Mean ±SE, values with different letters are significantly different ($p<0{\cdot}0001$).

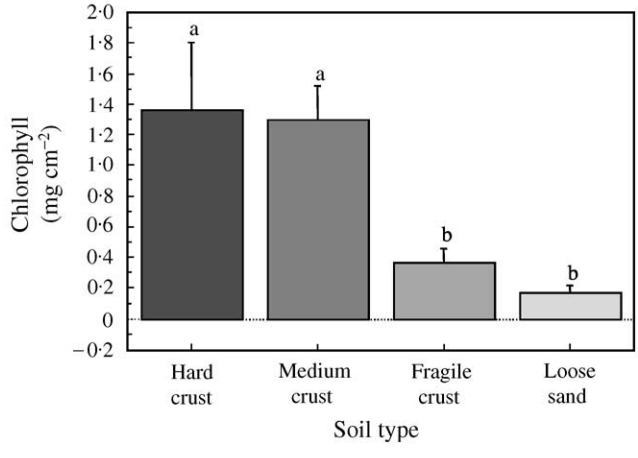


Figure 3. Chlorophyll content of the three crust types in comparison to loose sand. Mean ±SE, values with different letters are significantly different ($p<0{\cdot}006$).

($p<0{\cdot}05$). The crust compaction also showed a similar pattern to that of the protein content, with significant differences between all four soil surfaces and a decrease from hard crust to loose sand ($p<0{\cdot}0001$, Fig. 5).

The distribution of burrows of *S. doriae* among sand surfaces differed from the distribution of random points ($X^2=31{\cdot}2$, df. = 3, $p<0{\cdot}00001$, Table 1). The geckos showed selectivity for temporary crust (fragile crust) and avoided both loose sand and permanent crust (hard crust). The distribution of *Acanthodactylus* burrows was also significantly different from the distribution of random points. These lizards preferred temporary crusts and avoided all other sand surfaces ($X^2=42{\cdot}4$, df. = 3, $p<0{\cdot}00001$, Table 1).

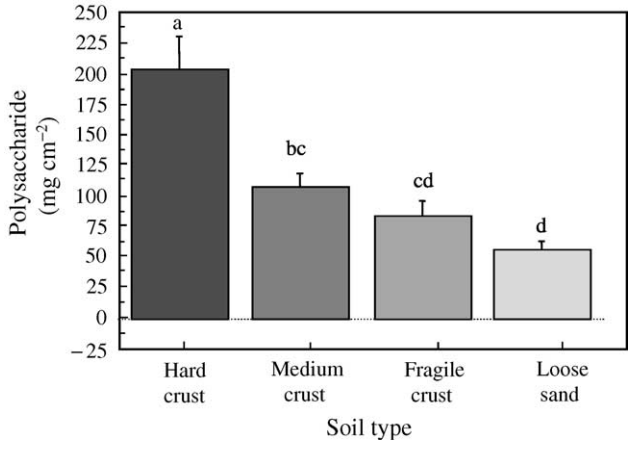


Figure 4. Polysaccharide content of the three crust types in comparison to loose sand. Mean ±SE, values with different letters are significantly different ($p < 0{\cdot}0001$).

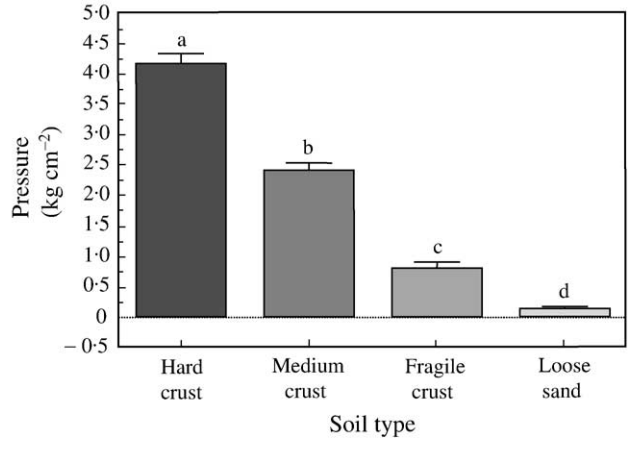


Figure 5. Soil surface resistance of the three crust types in comparison to loose sand. Mean ±SE, values with different letters are significantly different ($p < 0{\cdot}0001$).

Discussion

Microphytic soil crusts are formed in the sands of the 'Arava Valley in spite of the aridity of this region. Furthermore, we found within the same sandy soil different stages of succession of the soil crusts. Although microphytic crusts are composed of diverse organisms, the crusts in our study site were dominated by the filamentous cyanobacteria, *Microcoleus* sp. This cyanobacteria is known to form surface soil aggregates by mechanical binding, adhesion to the excreted mucilaginous polysaccharides and attachment of soil particles to sites along the cyanobacterial cell walls (Belnap & Gardner, 1993; Danin, 1996).

Table 1. *The percentages of distribution of burrows of Stenodactylus doriae (*n = *50) (*X^2 = *31·2, df.* = *3,* p < *0·00001) and Acanthodactylus spp. (*n = *50) (*X^2=*42·4, df.*= *3,* p < *0·00001) among the different soil crust successional age, in comparison to soil crust types availability (*n = *68 random points) near Hazeva (northern 'Arava Valley), Israel*

Crust successional stage	Land cover	*Stenodactylus doriae*	*Acanthodactylus* spp.
Loose sand	31	6	0
Fragile crust	43	80	94
Medium crust	13	12	4
Hard crust	13	2	2

Protein content in the crusts reflects the biomass of soil microorganisms in general, that may include, in addition to cyanobacteria, also bacteria, fungi and other organisms. Nevertheless, the fact that all four parameters we measured decreased in magnitude from the well developed, hard crusts to the loose sand supports the assumption that our measurements mostly reflect crust organisms (West, 1990; Johansen, 1993). Polysaccharides may have been derived not only from microphytes, but also from soil aggregates of bacteria in the upper 10 cm of the soil profile (Roberson *et al.,* 1995; Paul & Clark, 1996). However, we believe that they reflect the age of the crusts in our site. In our samples, the polysaccharides are likely to have been produced predominantly by microphytes, because we found loose sand below the thin crust layer, indicating low aggregation by bacteria (Roberson *et al.,* 1995). Bacteria need the available water for their activity, and the low rainfall in this region may be responsible for the lack of developed bacteria aggregates.

The hard crust contains twice the amount of polysaccharides compared to the medium crust. This indicates that the two crust types differ in age, and that the hard crust had a chance to accumulate polysaccharides over a longer period (West, 1990; Neuman *et al.,* 1996). This thick layer of crust (about 9 mm) is produced when sand particles and dust deposits adhere to the polysaccharides. This causes the cyanobacteria to grow upward while thickening the polysaccharide layer (Danin, 1996). The actual layer of live and active cyanobacteria does not exceed the normal thickness in this region (1–2 mm), but the thick polysaccharide layer provides the resistance to digging. The lack of difference in chlorophyll content between the two harder crusts (hard and medium crust) is an indicator of equal microphytic activity (Belnap & Harper, 1990; Lange *et al.,* 1992; Johansen, 1993; Lange *et al.,* 1998) in spite of the different age of these crusts. In these two crusts the cyanobacterial cover is 100%, but because their successional age is different, the amounts of polysaccharides that each accumulated are different. The fact that polysaccharide content did not differ between loose sand and fragile crust may indicate the relatively young age of the first stage of the succession. At the sites we were also able to determine the time needed to form fragile crusts on loose sand since we knew the age of man-made disturbances in the field site (A. Reichmann pers. comm.). The time for creation of fragile crusts ranged between 1 and 2 years.

Lizards preferred to dig and burrow in fragile crust and therefore the distributions of burrows of these species are affected by soil surface characteristics. The geckos avoided two of the four surfaces in the field site and the burrows in the fragile crust were more abundant than expected. Similarly, *Acanthodactylus* lizards also showed strong preference for the fragile crusts. Two of the available soil types seem to be unsuitable for both the geckos and the diurnal lizards: the most developed crusts and

the loose sand. Soil crusts may play an important role in determining burrow location, because the lizards need soil surface stability to provide support for the entrance of the burrows. Crustless loose sand dune is not suitable for burrows of these species. Observations of lizards attempting to dig new burrows in loose sand demonstrated that the lizards often had to stop and move to alternative sites due to the repeated collapse of the roof. In one of these cases, a gecko attempted unsuccessfully to dig burrows in eight different locations, all of which were in loose sand (Bouskila unpubl. data). These observations explain the avoidance of loose sand by the lizards. However, the lizards also avoid the hard crust, which is probably too hard for them to break in order to start their burrow. The geckos used the medium crust in a similar proportion to its occurrence in the field site, thus indicating that it is suitable for digging burrows. Nevertheless, medium crust is not strongly preferred, unlike the fragile crust, where the majority of burrows were dug, in frequencies that were about twice the occurrence of this soil type in the study site (Table 1).

This study indicates that lizards mostly use young crusts to support the entrance of their burrows. These fragile crusts, if left untouched for several years, convert into harder and thicker crusts according to the successional processes mentioned above. When fully developed, the hard crusts are avoided by lizards.

Alternative explanations for the selectivity of the fragile crust were considered. Fragile crusts may be more convenient for locomotion during foraging or may support more prey for the lizards. Both alternatives can be ruled out, at least for *S. doriae*, because in this species, locations of feeding grounds are often far (up to 90 m, mean 21·75 m) (Bogin, 1999) from the burrows, and also because geckos were often found active on the hard crust (Bogin, 1999). In addition, foraging grounds were significantly richer in arthropods than the areas around burrows (Reichmann, 1998).

The results of this study indicate that an extreme level of trampling (either high or low) , may prevent the establishment of shelters essential for the survival of the lizard species that are the most common in the 'Arava sands. This conclusion seems to be consistent with the intermediate disturbance hypothesis (Connell, 1978; Petraitis *et al.,* 1989). The intermediate disturbance hypothesis predicts that the highest species diversity will be at intermediate levels of disturbances. In extreme cases (too harsh/common or too mild/rare disturbances) only few species are predicted to persist. The reason is that under a regime of harsh or common disturbances, only few species can withstand the deteriorated conditions, and under mild or rare disturbances, a few species will dominate the system and prevent the establishment of others (Connell, 1978; Petraitis *et al.,* 1989). Two differences between the intermediate disturbance hypothesis and the situation we described need to be pointed out. In our study, we dealt with three species only, while the hypothesis discusses effects on diversity at the community level. Another difference stems from the mechanisms that apply to our field site. Both excessive disturbances (trampling of soil crusts) and rarity of disturbances deteriorate the physical properties of the habitat for the lizards, while in situations where the intermediate disturbance hypothesis has been applied, the effect of mild or rare disturbances operates through competitive exclusion of species. According to the hypothesis, only common disturbances cause deterioration of the habitat (Connell, 1978).

These results have important implications for land conservation and management, because sandy areas that are over-trampled (by livestock or off-road vehicles) are often converted into crustless sand (Busack & Bury, 1974; Bury & Luckenbach, 1983; Luckenbach & Bury, 1983). Trampling by humans, if exerted repeatedly on an area, may have similar effects: trampling by groups of students in a sandy area in the 'Arava Valley turned large portions of the habitat that were previously covered by fragile crust into moving sand dunes. As a result, *S. doriae* shifted burrow locations and dug burrows in less-preferred habitats, indicating that fragile crust may be a limiting factor when the sand is over-trampled (Bouskila unpubl. data). The opposite process may

also occur in sandy areas from which animals are excluded, where crusts may develop undisturbed by livestock or wildlife. Hard crusts eventually cover undisturbed areas, and the habitat becomes unsuitable for small burrowing vertebrates, such as lizards. Studies that deal with effects of grazing on animals or plant communities (e.g. Loft *et al.,* 1991; Bullock *et al.,* 1994) often point out the negative effects of grazing. Recently, the importance of intermediate levels of grazing to native plant communities has been acknowledged (e.g. Johansen, 1986; Marble & Harper, 1989; Perevolotsky, 1995; Noy Meir, 1998). Trampling destroys soil crusts (Zaady *et al.,* 2001), and thus determines the extent of crust cover, the proportion of old *vs* young crusts, and the availability of sites for lizard burrows. Because the survival of small vertebrates in hot sandy deserts often depends on digging shelters (Haacke, 1975), and because the maturation of soil crusts with time is a general phenomenon (Zaady *et al.,* 1997), our findings are probably relevant also to other organisms and to other areas. Similar effects of crusts and disturbances were described in Australia (Eldridge & Greene, 1994) and in the western Negev dunes (Danin, 1996). In both these sandy areas, reptiles and small mammals constitute a substantial portion of the fauna (Bouskila & Dickman, 2001) and the processes described here are also likely to apply to them. Land conservationists and managers should take these soil parameters into consideration when planning the management of natural habitats and nature reserves where lizards are an important component of the ecosystem.

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