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Ant assemblages at their dry limits: the northern Atacama Desert, Peru, and the Chott El Djerid, Tunisia

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Ants do not occur in the rocky desert of the Nazca Plain, Peru, except in the vicinity of shrubs in outwash gulleys, where there are two species that have similar activity periods and microhabitats and exhibit interference competition. Only one species of ant was found on the Chott El Djerid, Tunisia, a large, dry salt lake, devoid of vegetation.

Keywords: ants; deserts; assemblages

Introduction

As taxa approach their climatic limits, the question arises whether physical forces override biotic ones in influencing the structure of assemblages. Answering this question is difficult logistically because animals are often scarce and sparsely distributed under marginal conditions. Yet addressing this issue is critical to an understanding of community dynamics.

Heatwole (1989) attacked this problem by studying ant assemblages across the Arctic treeline in Lapland. He found that competition among ants, or between them and other animals, was not apparent towards the tundra end of the gradient but came into play along a gradient of decreasing climatic harshness through birch and aspen to pine forests.

There has been vigorous debate as to the relative importance of biotic *vs.* abiotic factors in structuring invertebrate assemblages in deserts (see Heatwole, 1995) and the suggestion has been made that physical factors exert the primary influence in the harshest deserts, whereas biotic features assume greater importance in milder ones. The present study deals with two ant assemblages under extreme conditions, one in the Atacama Desert of Peru and the other in the Chott El Djerid, Tunisia.

The study areas

The Atacama is a narrow coastal desert of about 360,000 km^2 on the Pacific seaboard

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of Peru and Chile and extending inland into Bolivia (sometimes the northern part is given the separate name of Peruvian Desert). Some localities have mean annual precipitations of less than 2 mm and there are others in which no measurable rain has ever been recorded. Temperatures are mild and show little seasonal variation (annual amplitude 5·7–7·7 °C). March is the hottest month (mean 21·6–24·1 °C) and September the coolest (mean 16·9–19·4 °C) (Rauh, 1985).

There are three substrate types: rocky desert, soil of finer particles and sand dunes. The study site was situated on an extensive, barren rocky plain (Fig. 1), just north of the town of Nazca, Peru (14° 53'S, 74° 54'W). The monotony of this flat, featureless expanse is broken by the famous designs laid out by prehistoric people, and by occasional shallow gulleys (Fig. 1) carrying temporary runoff from the western slopes of the Andes (mainly October to April). The only vegetation in the study area occurred in these gulleys and consisted of sparsely scattered shrubs with a density of 273 live shrubs per ha, with an equal number of dead ones. The substrate was a mixture of rocks and sand (Fig. 1). Thus, there are two distinct habitats separated by a sharp boundary (edge of gulley) rather than a more gradual gradient. These conditions are common over the Nazca Plain, but may be ameliorated at the base of the Andean foothills.

The Chott El Djerid is a dry salt lake in western Tunisia, about 95 km long and 50 km wide (centering on 33° 46'N, 6° 23'E). It is a featureless, flat plain, devoid of vegetation with a thick, cracked surface crust of dry saline soil or salt (Fig. 2), although in places there is subsurface salt water. The Chott was once a source of salt for the trans-Saharan trade.

Materials and methods

The ant assemblage of the Atacama Desert was studied by means of a baited transect. A reel of fishing line with consecutively numbered ribbons tied at 20 m intervals was unwound while walking through the study area. An inverted U-shaped course was followed rather than a straight line so that the end of the transect returned to the vicinity of the starting point. Each ribbon determined the site of a baiting station. At each of the resulting 26 stations a sardine bait was laid on the ground. Eighteen stations fell in an outwash gulley and eight on the barren plain (Fig. 1). In the gulley, a second bait was placed at the base of the shrub nearest to each station, up to a maximum distance of 5 m; at three of the stations no shrubs were within the prescribed limit and consequently only 15 shrubs were baited. Of those, eight were alive and seven were dead. Mean height was 1·3 m (range 0·5–1·8 m) for live shrubs and 0·8 m (range 0·5–1·0 m) for dead ones; mean diameters were 1·8 m (range 1·0–2·5 m) for live shrubs and 1·2 m (1·0–2·0 m) for dead ones.

The study was conducted in the austral summer. Baits were laid at 1148h of 5 November 1989 and subsequently examined on three occasions: midday, 5 November (1218–1255h), night, 5 November (1815–1930h) and morning, 6 November (0730–0800h). Baits were replenished as they were eaten or dried out. At each observation period, the number and kind of any animal at the bait, or in its vicinity, were recorded, and any interactions noted.

The density of shrubs in the gulley (see above) was calculated using each station as a central point for applying the quarter method (Cottam & Curtis, 1956).

The ant assemblage of the Chott El Djerid was studied purely by searching and collecting by hand during a daylong, lengthwise traverse of the chott on 6 September 1973.

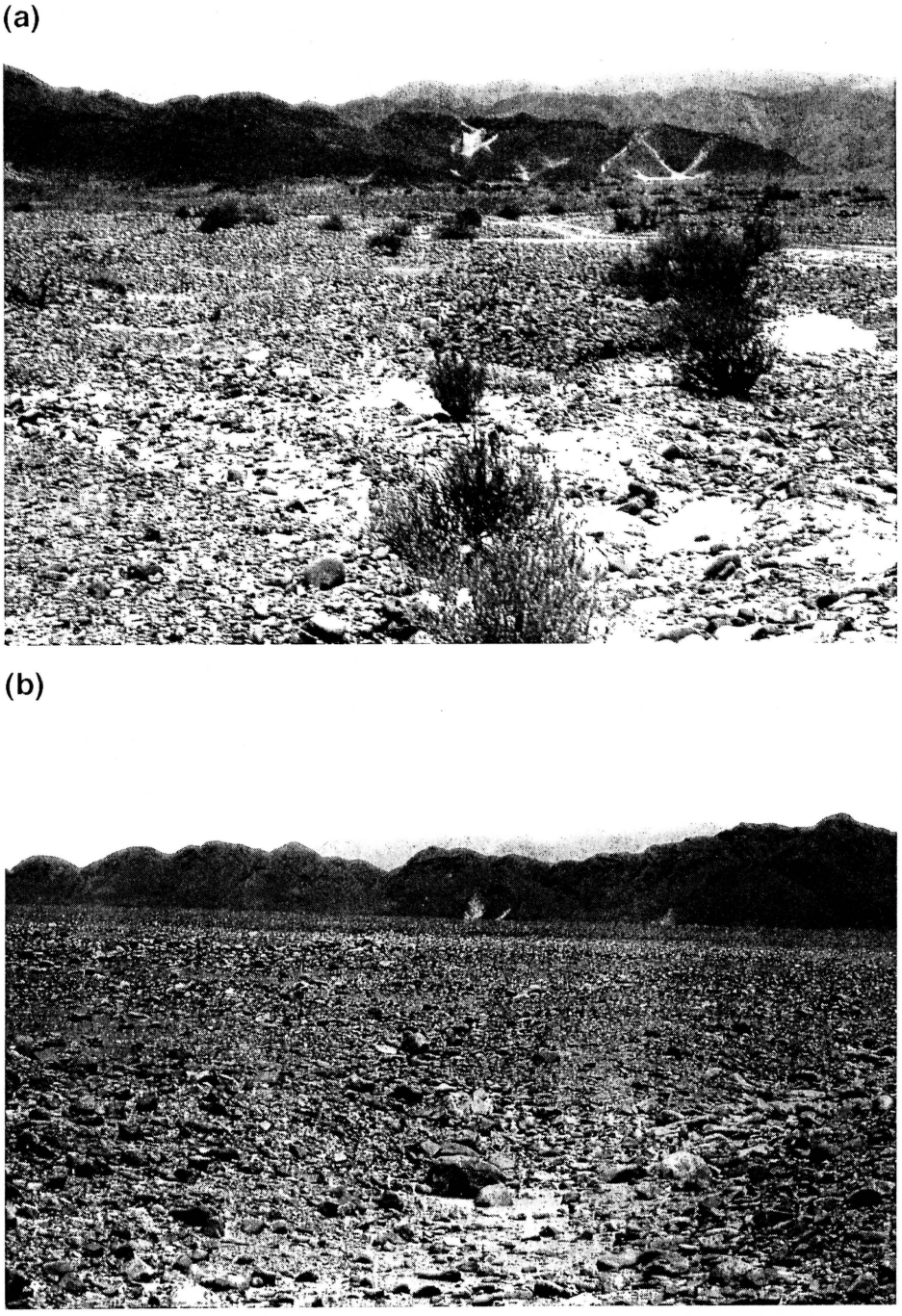

Figure 1. The study site in the Nazca Plain, Peru. (a) outwash gulley, showing shrubs; (b) barren, rocky desert.

Results

Only two species of ants, *Solenopsis gayi* (Spinola) and *Dorymyrmex chilensis* Forel, were found on the Nazca Plain. A third species was observed in the town of Nazca, associated with human dwellings and watered gardens, and was probably an introduced tramp, possibly *Paratrechina*. *Solenopsis gayi* is one of the most common

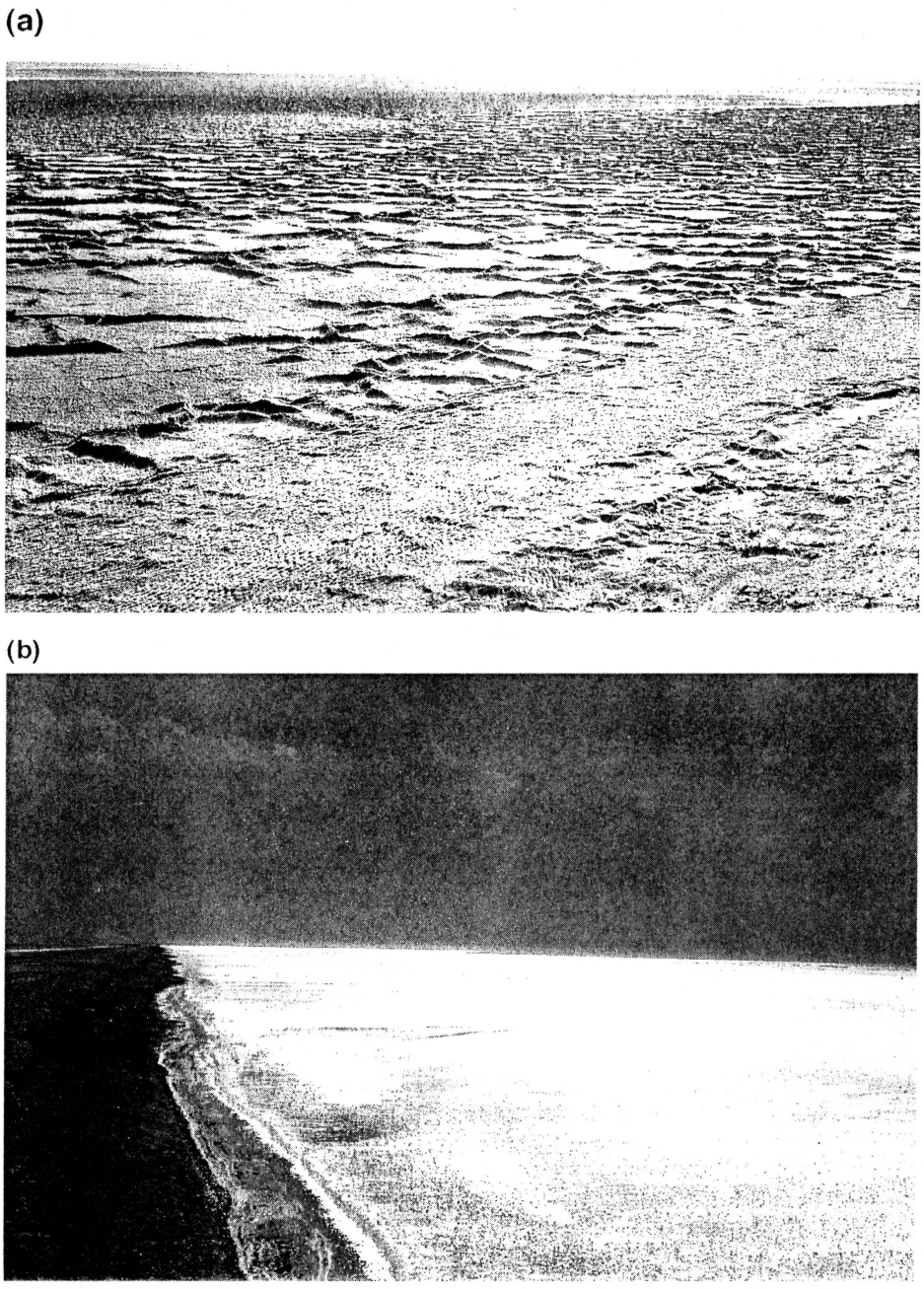

Figure 2 (a) and **(b)**. *Continued.*

(c)

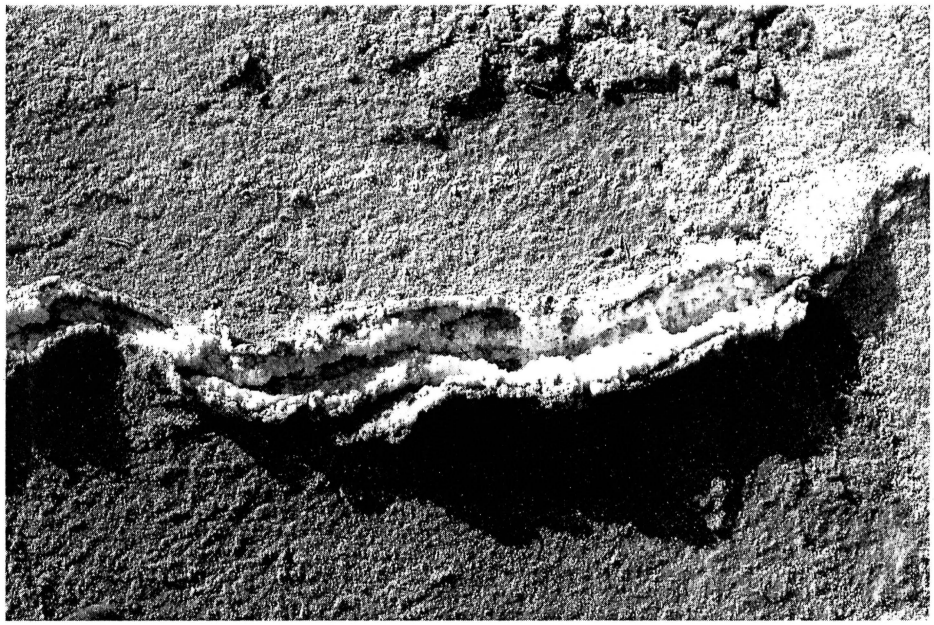

Figure 2. The Chott El Djerid, Tunisia. (a) general panorama of the chott; (b) a heavy incrustation of salt on the chott; (c) a crevice in the salt where crickets hide.

ants in Chile, but especially characteristic of the Espinal Region, and had earlier been collected from coastal Chile near the Peruvian border, about 650 km south of the Nazca Plain; *D. chilensis* has been previously recorded from central Chile (Snelling & Hunt, 1975).

Usually, with diligent searching, some life can be found even in extreme habitats. However, this was not the case in the present study and no ants were found at any of the baited stations in the open, rocky desert, nor were any ants, or other animals, discovered there by extensive searching and turning of rocks.

By contrast, ants did occur in the gulley. Eleven (61%) of the 18 baits located on the ground away from shrubs were found by at least one species of ant at some time or other during the study. Of the eight baits at the base of live shrubs, six (75%) were discovered by ants, whereas only two (29%) of the seven at the base of dead shrubs were visited. A general search did not reveal any species in addition to those attracted by baits.

In the gulley, the distance from baits in the open to the nearest shrub averaged 2·8 m (range 1–6 m) when the nearest shrub was alive and 5·8 m (2–10 m) when the nearest shrub was dead. Within those limits, distance of baits from shrubs did not seem to influence their accessibility to ants. There was no significant difference between distances of visited and unvisited baits from shrubs (Mann-Whitney U Test, $p = 0{\cdot}43$). Of the three baits beyond the 5 m limit, one was visited (6 m from a live plant) and two were not (8 m and 10 m from dead shrubs).

Both species of ants foraged primarily at night and in the morning. Only one bait was visited at midday (Table 1).

Of the 37 observations of ants at baits, 26 (70%) were of *Dorymyrmex* at the bait alone, 9 (24%) were of *Solenopsis* alone and only two (5%) were of both species at the same bait simultaneously. As determined by Chi-square analysis (see Miller *et al.*, 1994, for application of method), the ants visited baits together significantly less often

Table 1. *Ants occurring at baited transects on the Nazca Plains*

	Solenopsis gayi			*Dorymyrmex chilensis*		
	Morning	Midday	Night	Morning	Midday	Night
Stations in bare desert (n=8)						
Number occupied	0	0	0	0	0	0
Percent occupied	0	0	0	0	0	0
Stations in gulley (n=18)						
In open (n=18)						
Number occupied	4	0	0	8	0	10
Percent occupied	22	0	0	44	0	56
At live shrubs (n=8)						
Number occupied	2	0	3	4	1	3
Percent occupied	25	0	38	50	13	38
At dead shrubs (n=7)						
Number occupied	1	0	0	1	0	1
Percent occupied	14	0	0	14	0	14

than expected on the basis of random association ($p < 0{\cdot}005$). On one of the occasions when they did occur together, small numbers of *Solenopsis* were seen feeding and carrying food away while *Dorymyrmex* was merely foraging in the area, not in contact with the sardine. On the other occasion, a few *Solenopsis* were being attacked by superior numbers of *Dorymyrmex*.

Replacement of one species by the other at baits occurred between observation periods. There were six instances of *Dorymyrmex* being replaced by *Solenopsis* and only once did the reverse occur, therefore, it would appear that *Solenopsis* is the dominant species in encounters; on seven occasions it was found mobilized, completely encircling a bait. This was observed only once in *Dorymyrmex*. Nevertheless, *Dorymyrmex* seems to be numerically dominant and finds more baits than *Solenopsis*. Thus, *Dorymyrmex* appears to be the first to find and exploit a bait, only to be replaced later at many of them by *Solenopsis*.

On the Chott El Djerid, no plants and only two species of animal were found. Large black crickets (unidentified) were observed in cracks of dried salt and under cakes of salt. Ants of the species *Cataglyphis desertorum* Forel foraged, even under the heat of midday, running rapidly over the surface, at locations well out of sight of the edge of the chott or of any vegetation or non-saline soil.

Discussion

Snelling & Hunt (1975) noted that the ant fauna of the Atacaman region was generally impoverished, and that the northern part of the desert seemed to be devoid of ants altogether, and served as a barrier isolating Chile from northern faunal incursions. This was generally true of the barren Nazca Plain. Only in a specialized habitat, dependent upon runoff of water from distant mountains rather than upon local precipitation, were ants found. Even there, species richness of the ant assemblage was very low, only two species being observed. The temperature of the Atacama Desert is moderate by desert standards, and in view of the adaptation shown by ants of other deserts that allow them to forage during extreme heat (see Heatwole, 1995), it is likely that factors other than thermal ones are limiting the richness of this assemblage. The

most likely possibility is dryness, either through a direct effect on the animals or through limitation of their food supply. Fog occurs in winter in the southern part of the Atacama, but not during any season in the northern part (Rauh, 1985). In a virtually rainless desert, only the gulleys, with their occasional runoff from the distant Andes, contain sufficient moisture to sustain vegetation. Even there, conditions are marginal and approximately half of the shrubs are dead.

The gulleys not only provide more moisture for the ants, but support vegetation that serves either directly as food, or as the base of a food chain leading to ants. *Solenopsis gayi* is omnivorous; in the present study it was observed feeding on a seedpod which had fallen from a shrub, as well as scavenging at sardine baits. Whether *D. chilensis* is omnivorous or not is unknown.

Shrubs also exert a major influence on the distribution and abundance of the invertebrate fauna of other deserts. Franco *et al.* (1979) found that the density of microarthropods in the Mojave Desert was greatest at the base of shrubs and progressively declined with depth in the soil and farther from the shrub. Freckman & Mankau (1977) found desert nematodes to be similarly distributed.

Another factor restricting ants to gulleys may be soil type. Patches of sand in the gulleys may provide a suitable substrate for nesting. The only nest found in the present study was one of *Solenopsis* dug into the sand.

Even in this species-poor assemblage, interference competition is operative, suggested by the negative association of these two species at baits, and directly evidenced by their combat over food when observed together. *Solenopsis* seems to be dominant. The two species are neither temporally segregated, as they have similar activity periods, nor are they separated spatially, both being restricted to the vicinity of live shrubs in runoff gulleys.

The present observations apply to summer however, some deserts show seasonal changes in species richness of ant assemblages, different species being active above-ground at different times of year (Heatwole & Muir, 1991) and the same may apply to the Atacama. Thus, additional species of ants may become active above-ground in the gulley during more benign seasons. It is unlikely that this occurs outside the gulleys in view of the report by Snelling & Hunt (1975) that this part of the Atacama Desert is devoid of ants.

In contrast to the Atacama Desert, the Chott El Djerid is not only dry, but is hot and highly saline. Soil temperatures in arid central Tunisia exceed 40 °C in September and approach 70 °C in summer (Heatwole and Muir, 1979). The sole ant species there, *Cataglyphis desertorum*, belongs to a genus well known for its high temperature tolerance (Délye, 1957; Heatwole & Harrington, 1989) and for its ability to forage at the elevated midday temperatures of hot deserts (see Heatwole, 1995). Its occupancy of a habitat that is not only thermally harsh, but salty, raises interesting physiological questions. In the absence of autochthonous plants, the fauna of the chott must depend, either directly or indirectly, on exogenous food. Dry salinas in Australia provide a similar example (Mitchell, 1973). Insects are attracted to the white surface of the salina at night, which appears much like water, and are trapped on the hygroscopic salt surface and killed when the temperature rises the next morning. Other insects may be blown onto the salinas by offshore winds. Resident ants (*Melophorus* sp.) depend on these allochthonous insects for food. Perhaps the salt surface of the Chott El Djerid acts in the same way. The ants and crickets may depend, or perhaps even compete, for such windblown or other allochthonous food. It is likely that ants and crickets, both commonly omnivorous, also feed on each others' dead bodies.

In summary, species richness of the ant assemblage of the Nazca Plain in summer ranges from two interacting, eurytopic, but not primarily desert-adapted, species in refugia (sparsely vegetated gulleys) to a complete absence of ants in the desert at large. The Chott El Djerid, by contrast, has one species of ant, unusually adapted to desert extremes, especially high heat.

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