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Physiological and behavioural ecology of the ultra-psammophilous Namib Desert tenebrionid, *Lepidochora argentogrisea*

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The massive dune system of the southern and central Namib Desert supports a varied fauna. Even on the vegetationless dune crests and their slip-faces there lives a variety of endemic invertebrates, tenebrionid beetles in particular, as well as several highly specialized reptiles. This fauna was first described in detail by Koch (1961). Subsequently a series of papers on the climate, geomorphology and the life history of individual species have appeared in the Scientific Papers of the Namib Desert Research Station. Apart, however, from a preliminary study by Kühnelt (1969) and the as yet unpublished data of Edney (1971) and Hamilton (1971), there are no physiological studies dealing with the Tenebrionidae and their mode of adaptation to this specialized desert environment. The present investigation is an attempt to integrate the physiology and behaviour of an ultrapsammophilous tenebrionid species, *Lepidochora argentogrisea*, with the unusual niche occupied by this beetle. We have examined activity patterns, endogenous rhythms, metabolic rate, nutrition, digestion and the water metabolism of this species. In addition, field studies were carried out to examine general behaviour in relation to habitat and prevailing climatic conditions. Most observations were made in the dunes near the Namib Desert Station at Gobabeb, South West Africa.

PROCEDURE

Activity rhythms were studied in the field under natural conditions by means of a field census of the number of active animals above the surface of the sand. In addition, experimental populations of beetles were placed in plastic con-

tainers filled with dune sand. These containers were sunk beneath the surface of the soil outside the weather station compound at the Namib Desert Research Station. The sand level within the container was level with the soil surface outside the container. Thus the surface of the sand within the container was exposed to local environmental conditions modified only by the lip of the container which projected 2 cm above the surface, reducing the effect of wind on the surface. Populations of 5; 10; 20; 40 and 100 beetles were placed in these containers. Each population was replicated twice and the number of active animals on the surface of each container was recorded every hour for 48 hours. Sand temperatures at the surface and at depths of 1; 5 and 10 cm were recorded simultaneously.

Activity patterns in the field were observed by walking along a set course in the field and counting the number of individuals on the surface within a predetermined distance from the course. Observations were made well ahead of the observer's position with binoculars to avoid disturbance effects. Further details of this census procedure are given elsewhere (Hamilton, 1971).

Activity rhythms were also measured by placing freshly captured beetles under constant illumination and temperature ($30^{\circ}\text{C} \pm 0,1^{\circ}\text{C}$) and then recording the oxygen consumption for 30 minutes every hour for 36 hours. Oxygen consumption was measured by placing the beetles in metabolic vials, containing soda lime as a CO_2 absorbant and measuring the inflow of water in a micro-pipette attached to the metabolic vial. The metabolic vials were submerged in a constant temperature bath and were flushed with fresh air after each recording session. All gas volumes were corrected against a thermobarometer and have been reduced to standard temperature and pressure.

Metabolic rate was measured with the same closed system at 10°C intervals ranging from 5 to 35°C .

Nutrition and Digestion were studied by examining the feeding behaviour of these beetles in the field and by microscopic examination of their gut contents in the laboratory. Gut fluid was also examined to determine the presence or absence of protozoa. In addition, an analysis was conducted to establish the extent of the ability of these beetles to digest cellulose. This involved placing ± 200 beetles in a wooden tray filled with sand to a depth of 6 cm and feeding them exclusively on wind-blown dry grass which had been freshly collected from the surface of the dunes where they live. Each morning the beetles were removed from the sand, carefully cleaned to remove sand grains and placed for the duration of daylight in a clean glass bowl in an illuminated photographic dark-room at $\pm 20^{\circ}\text{C}$. Every evening for 12 days the beetles were returned to the sand tray and the faecal material collected. This allowed us to accumulate sufficient faecal material for chemical analysis.

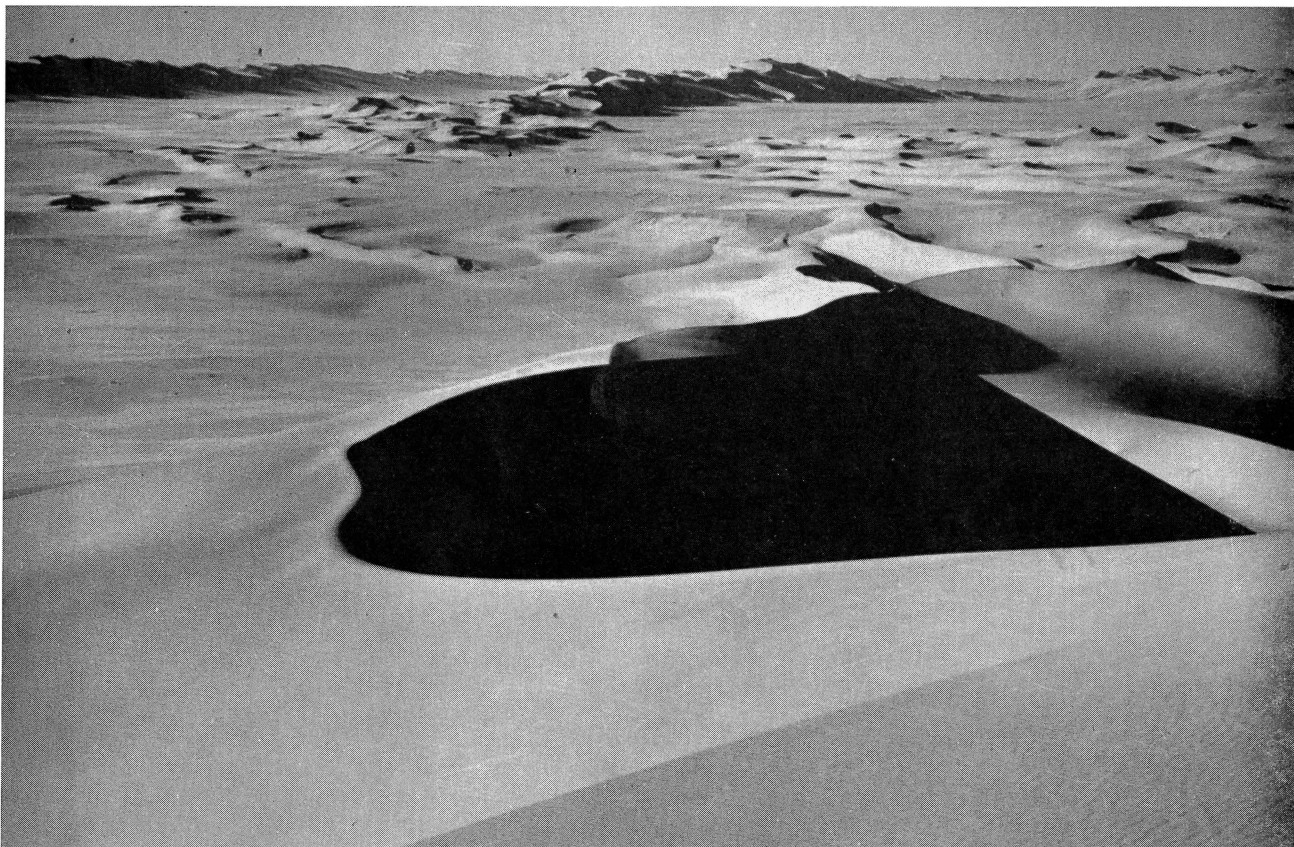


Figure 1. Part of dune system south of Gobabeb. In the foreground the slip-face, preferred habitat of *L. argentorisea*, is in shadow. (Photo: Alice Mertens, University of Stellenbosch).

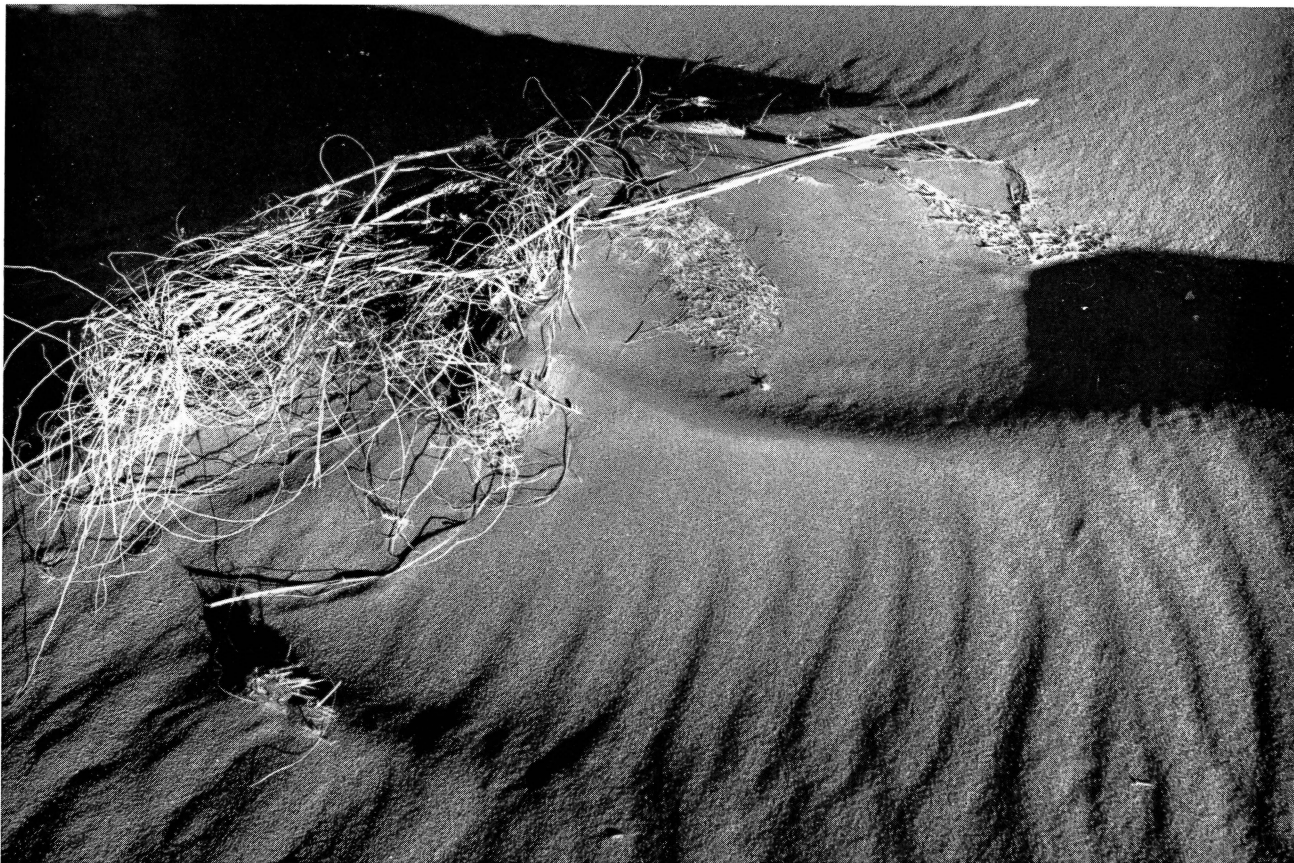


Figure 2. Part of detritus cushion which has collected at the base of a slip-face. (Photo: Alice Mertens, University of Stellenbosch).

The detritus was also sampled and, together with the faecal material, analysed for nitrogen and cellulose content (A.O.A.C. methods) and gross energy using an adiabatic bomb calorimeter.

Water economy of the beetles was investigated by exposing them to various humidities, examining the effect of dehydration upon the osmolality of the haemolymph, and studying the uptake of water through the cuticle. In the first experiment the rate of weight loss was measured at 0% r.h., 76% r.h., and 97% r.h. over a period of 13 days. The Beetles exposed to 0% r.h. were then exposed to 97% r.h. for 24 hours to determine their possible ability to absorb moisture from an unsaturated atmosphere.

The various humidities were established by placing the beetles in small desiccators containing a saturated solution of $Pb(NO_3)_2$ (97% r.h.), a saturated solution of NaCl (74% r.h.) and silica gel (0% r.h.). This experiment was conducted at room temperature which varied between 19°C and 25°C. The rate of weight loss of *Lepidochora* was compared with a diurnal tenebrionid, *Ornymacris laeviceps*, by including equal numbers of the latter species in the experiment. There were 18 replications for each species at each relative humidity level.

The effect of dehydration on the osmolality of the haemolymph was examined by withholding water and succulent food from *L. argentogrisea* for two months and then placing them in a 0% r.h. atmosphere for five days prior to sampling the haemolymph with micro-capillary tubes. These samples were then compared with those taken from beetles which had received similar treatment, but which had been fully hydrated 24 hours prior to sampling by spraying them on the dorsal surface with fine droplets of water. Osmolality was determined against standard solutions using the method of Gross (1954).

The behaviour of distilled water droplets on the ventral and dorsal surfaces of the elytra was studied under a stereoscopic dissecting microscope in an attempt to determine the capacity of the cuticle to absorb water. This was compared with the rate of disappearance of similar droplets placed on an inert ceramic surface. Beetles also were placed on a micro-balance and their change in weight recorded over several hours after the application of 5 microlitre drops of water to either the dorsal or ventral elytra.

RESULTS AND DISCUSSION

Habitat

The special habitat of *L. argentogrisea* is the loose wind-blown sand on the lee side of the parallel dunes. These soft lee slopes, or slip-faces, are formed by wind driven sand which precipitates on the lee slope of the central Namib dunes. This soft sand (Fig. 1) is easily penetrated by the many species of burrowing beetles, spiders, and lizards.

At the base of these slip-faces there is usually a calm, wind-free hiatus where wind blown detritus, mostly fine dry grass stems and seeds, accumulates. The exact origin of this detritus has not yet been established. It is, however, suspected that the strong easterly berg winds are responsible for carrying it into the dune system where it accumulates frequently in the form of cushions (Fig. 2). This detritus constitutes most of the diet of *L. argentogrisea*.

L. argentogrisea is probably the dominant animal species in the slip-face environment. It is preyed upon by the white lady spider (*Leuchorchestris* sp.) and the nocturnal lizard *Palmatogecko rangei*. When *L. argentogrisea* are captured they feign death through reflex immobility or akinesis. This reflex is so well developed that it is very difficult to distinguish between live and dead individuals. Surface temperatures on the slip-faces vary from maxima above 60°C to just above 0°C and are significantly influenced by the convective cooling action of surface winds. On the other hand, the temperature of the sand below the surface becomes increasingly more uniform with depth and is compatible with animal life for longer intervals (Fig. 3).

Annual rainfall in the study area is negligible and for the purpose of this investigation can be ignored. However, the cold Benguela ocean current along the Atlantic coast produces fogs which regularly extend inland to and beyond Gobabeb. Schulze (1969) has summarized the climate of Gobabeb over a five year period. Fog occurs during every month of the year, and is most frequent in September and October. Fog frequently condenses in the form of droplets upon the dunes, and upon detritus. The osmolality of these condensed fog drops can be as low as 28 mOsm and therefore ideal for usage by the dune fauna (Louw and Holm, 1971).

From the foregoing, therefore, it would be expected that *L. argentogrisea* might exhibit interesting morphological, behavioural and physiological adaptations to this unusual habitat. The morphological peculiarities of this insect have been described in detail by Koch (1962) and the following discussion will attempt to explain at least some of the latter adaptations.

Activity rhythms

The temperature conditions upon the slip-face would lead one to presume that *L. argentogrisea* should be either nocturnal or exhibit a bimodal diurnal activity pattern in order to escape the extremely high mid-day temperatures on the surface. Our data, obtained from captive beetles placed in large plastic containers dug into the ground and filled with sand would seem to suggest that *L. argentogrisea* is strictly nocturnal (Fig. 4). After sunset activity increases sharply (18.00 hr) and persists at a high level until 24.00. Then activity gradually tapers off towards 06.00 hr when the beetles disappear beneath the surface. These results are not in agreement with those of Kühnelt (1969) who maintains that *L. argentogrisea* are

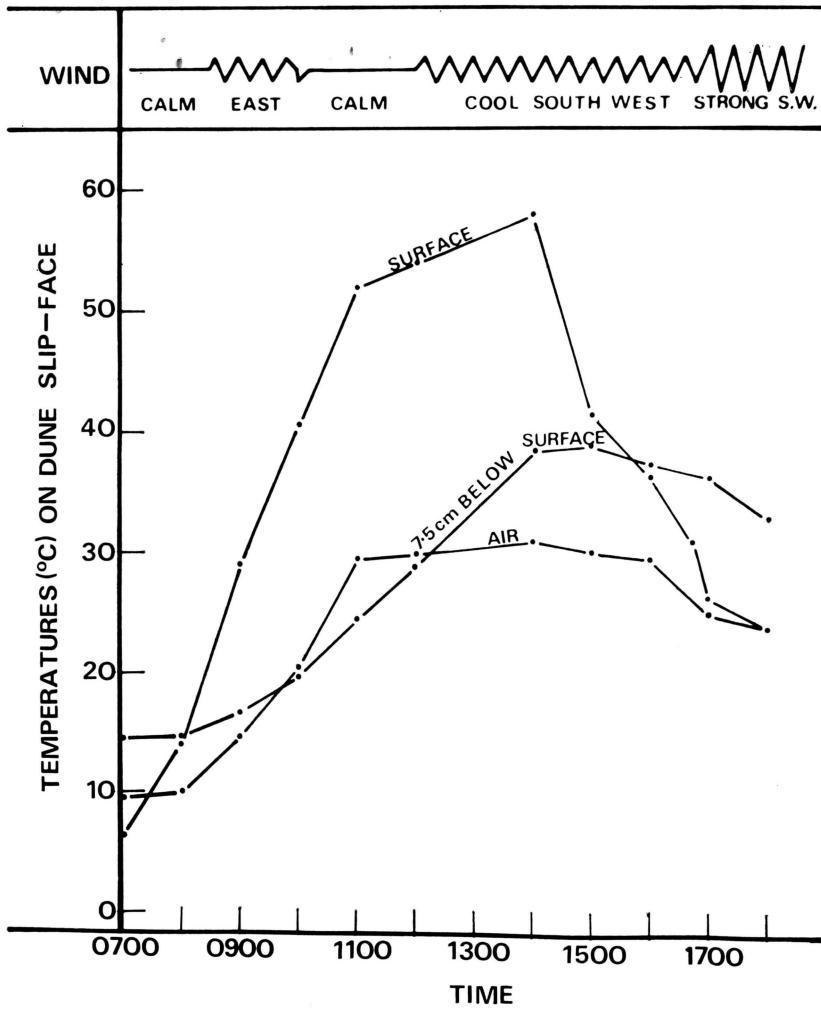


Figure 3. Temperature conditions prevailing upon a slip-face in relation to time of day and wind conditions.

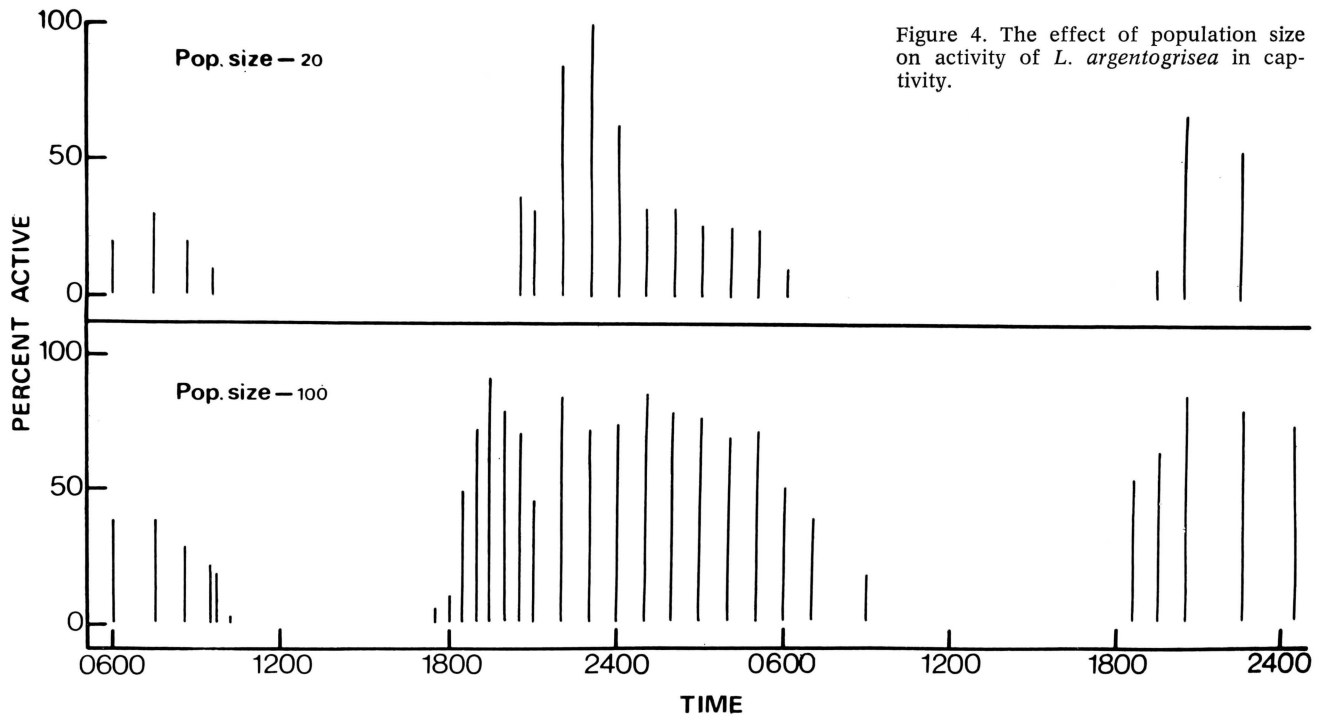


Figure 4. The effect of population size on activity of *L. argentogrisea* in captivity.

active only for a short period after sunset. Our field observations confirm that this beetle is largely nocturnal. Active individuals above the surface have been observed during late afternoon, throughout the night, and during the early hours of the morning. Under calm, wind-free conditions they are extremely sensitive to an approaching observer and therefore quite difficult to observe.

Field observations confirmed the general pattern of activity rhythm observed for captive beetles. However, there was one important difference between the two conditions. The surface of the sand in the containers in which the captive beetles were kept was almost wind free as a result of the projecting lip of the container. No facultative response to wind was observed in the captive beetles. In the field a strong facultative response to both easterly and south-westerly surface winds was noted.

When the beetles emerge during windy conditions they forage actively and frequently grasp small pieces of detritus. On windy afternoons masses of *L. argentogrisea* emerge an hour or more before sunset. On these occasions they are normally on the shaded east-facing lee slopes of the high dunes. However, when easterly winds prevail at this time of day, detritus collects on the sunny west facing slopes and *L. argentogrisea* aggregate there, exposed to full sunlight. This response to wind has been observed at almost all hours of the day and presumably developed to allow the beetles to make maximum use of the detritus which is carried onto the slip-faces by these surface winds. On the other hand the convective cooling effect of the surface winds may lower the surface temperature of the slip-face below a critical threshold, thus allowing the beetles to emerge earlier than usual.

We did not establish critical temperature thresholds in relation to surface activity but our data does indicate that *L. argentogrisea* is forced to burrow beneath the surface when surface temperatures approach 40°C, which is in general agreement with the data of Kühnelt (1969). Kühnelt maintains that the lower temperature limit for surface activity in *L. argentogrisea* is 20°C. Our results did not confirm this as we recorded active beetles above the surface at a temperature of 13.6°C in our captive group, and in the field we have observed *L. argentogrisea* active at surface temperatures as low as 6°C. Actual body temperature measurement of this species and the morphologically similar *L. kahani* and *L. porti* shows levels within 2.5°C of ambient levels during periods of natural surface activity and within less than 1°C of sand surface temperatures. This is in striking contrast with some of the black diurnal Tenebrionidae which may develop body temperatures as much as 16°C higher than ambient air temperatures (Hamilton, 1971B).

Finally, the different population densities studied within the captive group showed that activity rhythms were more clearly demarcated and sustained for longer periods at a high level in the higher population densities of 40 and 100 indi-

viduals per unit area in a container than at lower densities (Fig. 4). This social facilitation of the activity rhythm would lead one to believe that *L. argentogrisea* is gregarious under natural conditions. Field observations confirm this observation. Individual insects are often encountered, but there are places where these beetles frequently mass in hundreds upon the slip-face just after sunset. Under these conditions they forage actively. Social facilitation of activity and a social way of life may enhance the effectiveness of these beetles in detecting predators and in responding to favourable feeding conditions on the surface.

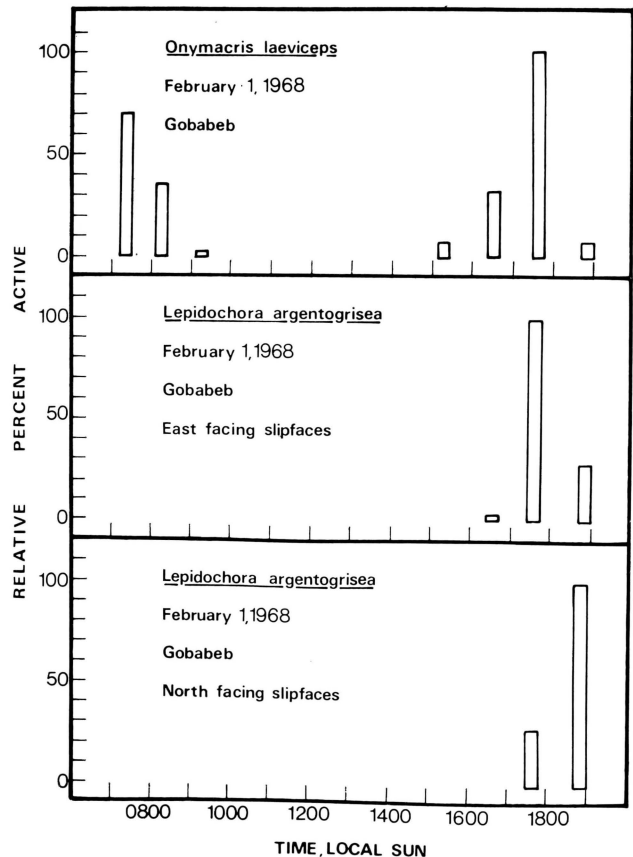


Figure 5. Activity of *L. argentogrisea* on dune slip-faces facing east and north. The observations for the diurnal *Onymacris laeviceps* were made on the same dunes as the *L. argentogrisea* observations.

The extensive facultative responses which partly determine the activity pattern of *L. argentogrisea* means that comparisons of its activity with that of other species must be made for specific dates and specific wind and temperature conditions. When such comparisons are made the sequence of activity is that *L. argentogrisea* often appears while the strictly diurnal species living in the same environment; *Onymacris laeviceps*, *O. plana*, and *Cardiosis fairmairei*, are still active and the strictly nocturnal *Lepidochoira porti*, *L. kahani*, *Vernayella* sp., etc., have not yet emerged. An example of the relative pattern of activity of *L. argentogrisea* and *Onymacris laeviceps* is shown in Fig. 5. Note that the pattern of activity is different for *L. argentogri-*

sea on dunes which face in different directions. This shift is due to a change in direction of the wind. The beetles on the east facing dunes have not moved to the north facing dunes. Instead, many of them have dug beneath the surface and new individuals have emerged from their underground retreats on the north facing slopes.

Endogenous metabolic rhythm

The mean oxygen consumption of 10 *L. argentogrisea*, measured at hourly intervals under constant temperature and illumination over 36 hours is illustrated in Fig. 6. These results are in fair agreement with the activity rhythm data, i.e., there is a sharp increase in metabolism at approximately 18.00 hr which is sustained until midnight and then tapers off towards morning.

It would appear, therefore, that the nocturnal activity rhythm and the usual time of emergence of these beetles in particular is governed by an endogenous rhythm. However, as previously discussed, there is a facultative response to wind superimposed upon this endogenous rhythm, and Kühnelt's data (1969) suggest that extreme or unusual thermal conditions may also affect the pattern of surface activity.

Nutrition and digestion

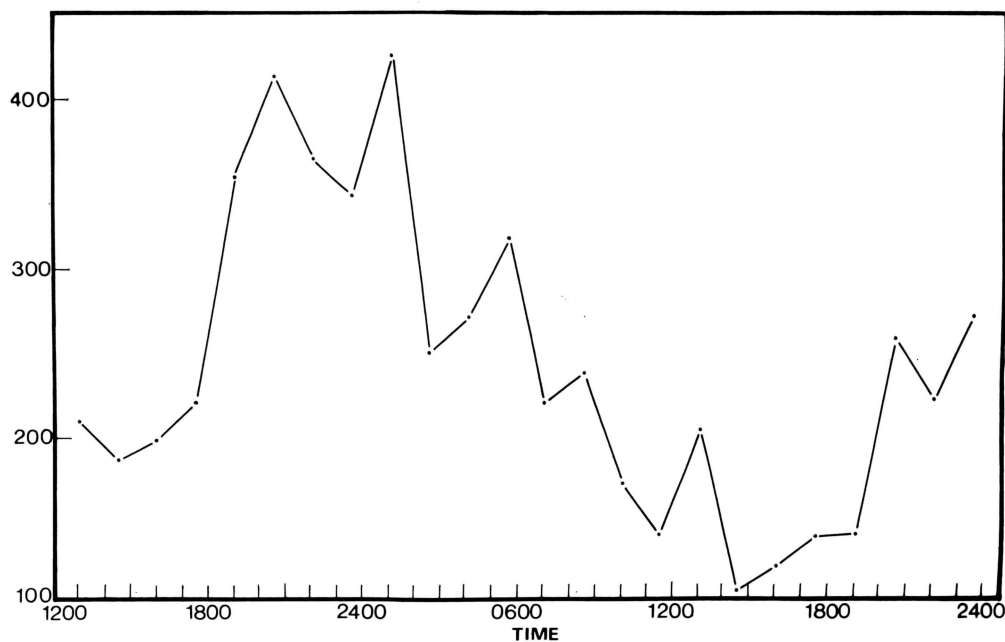
From examination of the gut contents and field observations of feeding behaviour it became clear that wind-blown organic detritus is the major constituent in the diet of *L. argentogrisea*. This detritus consisted largely of dry, fine grass stems with occasional grass seeds and a chemical analysis of this material appears in Table 1. In captivity the beetles accept a wide variety of plant material and feed

vigorously upon animal material. On rare occasions carrion, is present in the dune slip-face and tenebrionids (*Onymacris diosis fairmairei*) feed upon the opportunity arising.

In view of the high cellulose content of the diet of *L. argentogrisea* it was necessary to measure the amount of cellulose digested to measure the amount of cellulose in the weight of faecal material. Exact digestion was not calculated but the cellulose content between the faecal matter and the detritus (41.2%) are capable of effective digestion. Protozoa were found in the faecal matter and it would appear that the digestion is the result of microorganisms and enzymes.

Table 1. Chemical and calorific values of wind-blown detritus which is the major constituent of the diet of *L. argentogrisea*. The values are expressed on a dry weight basis.

Item
Dry matter (%)
Nitrogen (%)
Cellulose (%)
Energy (cal/g)



The results of the digestion trial also show a marked difference in the caloric content between the detritus and the faecal material, which indicates that a reasonably large amount of metabolizable energy is released from the detritus during digestion.

The nitrogen content of the detritus (0,89%) represents a crude protein content of 5,6%. This is presumably supplemented by the occasional feeding on carrion. The high nitrogen content of the faecal material is due in part to the addition of nitrogenous compounds of urinary origin to the undigested residues in the gut.

Metabolic rate

The data obtained from measurements of the metabolic rate of *L. argentogrisea*, in terms of oxygen consumption per gram live weight, fell within the expected range (Prosser and Brown, 1965). In view, however, of the profound effect of temperature and the circadian rhythm upon the metabolic rate and the variable environmental temperatures to which the beetles are exposed, it is not possible to calculate a standard metabolic rate for these insects. Nevertheless, if the data contained in Fig. 6 are examined, it will be seen that, if a value of 300 microlitres per gram live weight per hour is taken as the standard metabolic rate, it is an over-estimation of the actual metabolic rate at normal fluctuating environmental temperatures over a 24 hour period. Using this value, and the fact that the mean weight of freshly captured *L. argentogrisea* was 83,1 mg (N = 108), gives an oxygen consumption of 597,6 microlitres per insect per day. Then, assuming a caloric equivalent of 1 litre of oxygen to 5011 calories, we obtain a mean daily caloric requirement of 2,99 calories for each individual beetle.

Although the design of the digestion trial did not allow an exact calculation of digestive coefficients, the data in Table 1 allows us to conclude that at least 884 calories (3827-2943) of metabolizable energy and probably considerably more is available to the beetles in each gram of detritus. This means that the consumption of 3,39 mg of dry detritus would satisfy the daily caloric requirements of a beetle weighing 83,1 mg. Under natural conditions the detritus would probably contain 10% moisture thus increasing the daily feed intake to 3,7 mg of detritus, or about 4,5% of the total body weight. Bearing in mind that we have purposely over-estimated the metabolic rate and under-estimated the metabolizable energy content of the detritus, it appears as if *L. argentogrisea* can satisfy its energy requirements by feeding upon the dune detritus.

Water economy

Edney (1967) has reviewed water balance in desert arthropods and concludes that a large variety of physiological and structural adaptations occur within this group. He has also suggested that, rather than generalize, each species should be

viewed as a whole organism with a specific collection of adaptations that must be consistent within themselves and related to the specific mode of life of that organism.

Table 2. Net loss in body weight of *O. laeviceps* and *L. argentogrisea* at various humidities over a period of 13 days.

	N	0% r.h.		76% r.h.		97% r.h.	
		<i>O.l.</i>	<i>L.a.</i>	<i>O.l.</i>	<i>L.a.</i>	<i>O.l.</i>	<i>L.a.</i>
Mean body weight on day 1 (mg)	18	433,7	81,2	399,6	91,9	411,1	84,6
Mean body weight on day 13 (mg)	18	354,0	63,8	367,4	81,9	392,2	77,0
Net Loss (mg)	18	79,7	17,4	32,2	10,0	18,9	7,6
Weight Loss (%)	18	18,4	21,4	8,1	10,9	4,6	9,0

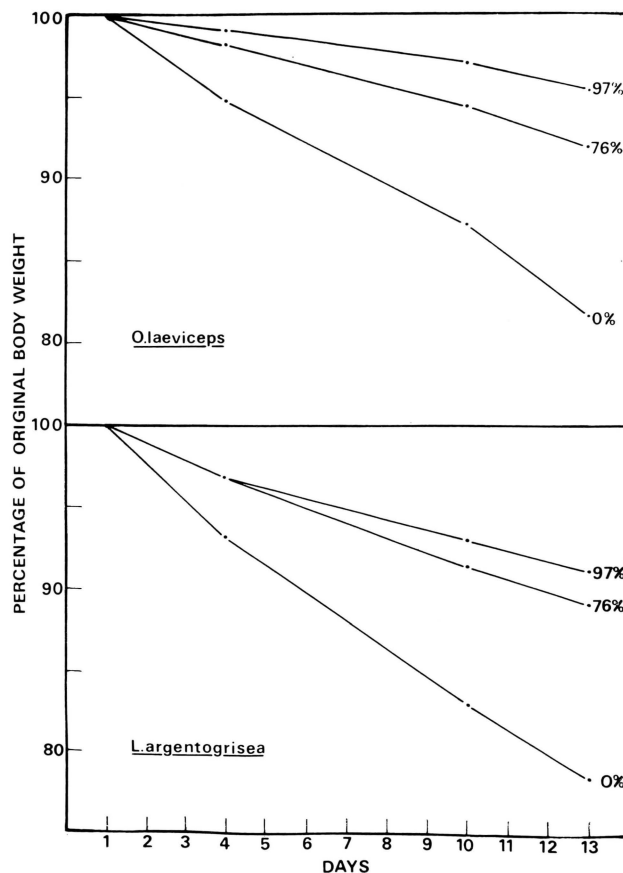


Figure 7. Rate of weight loss in *O. laeviceps* and *L. argentogrisea* at various levels of relative humidity (0%, 76% and 97%).

If *L. argentorisea* is viewed in this light, it becomes apparent that it is admirably adapted to survival within its niche and that these adaptations are consistent within themselves. For example, the activity rhythm, circadian rhythm, digestion and metabolism of this organism all consistently favour survival on the slip-face of the dune. Moreover, as will be seen, the water economy of this species, in terms of resistance to desiccation and water gain is equally consistent with survival in its unusual micro-habitat. The resistance of *L. argentorisea* to desiccation was measured by exposing the insects to various humidities and measuring the rate of weight loss; most of which can be assumed to be water loss, over a period of 13 days. The results in terms of net loss are summarized in Table 2 and in terms of percentage of original body weight in Fig. 7. These data clearly show that, even at 0% r.h., the beetles are highly resistant to desiccation. The percentage weight loss recorded for *L. argentorisea* is similar to the value obtained for *Tenebrio molitor* by Walters (1966) under similar conditions. We can conclude therefore that the cuticle of *L. argentorisea* is relatively impermeable to water loss and it was not surprising to find, after the insects had been switched from 0% r.h. to 97% r.h., that they showed no significant gain in weight. It is also of interest to note that at each level of relative humidity the rate of weight loss was slightly higher in the case of *L. argentorisea* when compared with *O. laeviceps*. This may be in part due to greater impermeability of the cuticle in the diurnal *O. laeviceps* but may also be related to the greater surface area per unit of body weight in the case of the smaller *L. argentorisea*. In regard, however, to the latter possibility, Edney (1971), while studying rate of water loss in seven species of Namib tenebrionids, found that there was a significant correlation between weight and water loss expressed as a percentage of original weight on a log/log scale. Finally, it should also be noted that a relative humidity of 0% is most unlikely to be encountered by *L. argentorisea* in its natural habitat, although, when easterly berg winds blow the relative humidity can fall below 5%. This however, is an unusual weather condition and Schulze (1969) has recorded a range in mean monthly relative humidity from 36-60% r.h. at Gobabeb. Moreover, the range in mean monthly relative humidity between 18.00 and 06.00 hr, when *L. argentorisea* are usually active, ranges from 24 to 87%.

Although *L. argentorisea* is clearly resistant to desiccation, they must gain water in some way. Preformed water in the food and water of oxidation are obvious sources. Another possibility is fog water, which frequently condenses on the dunes. In the latter respect, *L. argentorisea* covered with fine drops of condensed water have been observed on the surface of the dunes during heavy fog. This observation confirms observations on another unidentified species of Namib tenebrionid by Jensen (1970). Furthermore, we have observed water droplets clinging to the ventral surface of these in-

sects in the late afternoon (17.00 hr) after an early morning fog.

These field observations indicate that a source of free water is readily available to these beetles. Is this water absorbed? To investigate this possibility we examined the behaviour of small water drops (<0,5 microlitres) on the dorsal surface of the elytra. These droplets appeared to be rapidly absorbed but no gain in weight of the insect was recorded. Two water drops of known volume (5 microlitres) were placed on the dorsal surface of the elytra while the insect was resting on a microbalance. The balance immediately recorded a gain in weight of 10 mg but after a mean time elapse of 58,5 min the water drop had disappeared and the beetle had returned to its original weight. This trial was conducted with similar results on the ventral surface of the elytra. Moreover, when the rate of disappearance of these water drops was compared with equivalent sized drops placed on an inert ceramic surface at the same temperature (23°C), it was found that the drops placed on the insect cuticle evaporated more slowly. This was probably due to a mono-molecular layer of lipid surrounding the water drop after it had come into contact with the cuticle (Beament, 1964).

Table 3. The effect of hydration on the osmolality of the haemolymph of *L. argentorisea*.

Treatment	N	Osmolality of the haemolymph (mOsm)	
		Mean	S.D.
Hydrated	12	339	± 20,3
Dehydrated	12	427	± 15,9

It would seem therefore that water is not absorbed directly through the cuticle of *L. argentorisea*. This, however, cannot be concluded with absolute certainty from these few simple experiments, as water uptake by the cuticle is a complex process and one that varies from one anatomical area to another on the same insect (Beament, 1964). Further critical investigation is clearly required.

The alternative route for uptake of fog water by the beetles is through direct drinking of condensed free water which condenses on the dorsal surface and runs over the margin of the elytra and eventually comes in contact with the mouthparts. To test this possibility, dehydrated beetles were sprayed with fine drops of water. The osmolality of the haemolymph 24 hours later was compared with unsprayed controls. The results showed a highly significant reduction in osmolality of the haemolymph of the sprayed beetles (Table 3). Furthermore, examination of the experimental digestive tract showed the presence of a clear fluid. Other beetles were sprayed with water containing a blue dye, trypan blue, and the dye was subsequently recovered in the digestive tract. It would seem,

therefore, that *L. argentogrisea* makes efficient use of condensed fog water and that the most probable mode of uptake is by drinking.

SUMMARY

The tenebrionid beetle, *Lepidochora argentogrisea*, is entirely dependent upon wind-blown detritus for subsistence in its vegetationless environment. At 30°C, reasonable estimate of the mean temperature of its environment, a beetle of average size requires about 3.7 gm of detritus for daily maintenance. *L. argentogrisea* is able to digest cellulose and most of its diet consists of dry vegetable matter. However, when animal debris is available it becomes the preferred dietary item.

The surface activity of *L. argentogrisea* is facultative, and determined in part by temperature, the activity of other individuals, and surface wind. The inactive phase of the daily cycle, which usually includes all of the middle hours of the day, is spent below the surface. Activity, probably triggered by an endogenous rhythm, is initiated at dusk on windless evenings.

The water economy of *L. argentogrisea* appears to be slightly less efficient than the diurnal *Onymacris laeviceps* which lives in the same vegetationless environment. *L. argentogrisea* appears to be unable to absorb water through its cuticle but probably drinks water that collects on its cuticle during the regular fogs it encounters in its natural environment.

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