ON THE BIOLOGY AND TEMPERATURE ACCOMMODATION OF *LEPIDOCHORA ARGENTOGRISEA* KOCH (COL. TENEBRIONIDAE)

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(With 1 table and 5 figures)

During a stay at the Namib Desert Research Station at Gobabeb, South West Africa, it was noticed that *Lepidochora argentogrisea* appeared in great numbers every evening. It seemed to be worthwhile to investigate the conditions for this activity.

Lepidochora argentogrisea, a Tenebrionid beetle endemic in the sand dunes of the Namib Desert, has very distinct periods of activity like many other inhabitants of the dunes, though these periods are extremely short. The first beetles emerge from the sand when their main habitat, the lee-side of the dunes, is side-lit by the last rays of the sun. In Gobabeb this occurs usually before 5 p.m.; the time varies a little depending on the aspect of the dune.

The observations were made during the very hot March of 1964. Variations possibly occur during the course of the year.

The main activity period of the beetles seems to be between 17.30 hr. (5.30 p.m.) and 19.30 hr. (7.30 p.m.), beginning with full shade on the lee-side of the dune. The activity period was extended until the late evening hours in some open air cages exposed to the sun until sunset. It seems therefore that the activity rhythm is dependent on light and temperature. This will be discussed later.

The highest surface temperature measured when the first beetles emerged was 37,5° C, the lowest at the end of the main activity period 19,5° C.

The activity of *Lepidochora* follows a certain scheme. First of all a few beetles emerge from the sand, becoming more numerous as time goes on. They run around, dive 1 to 2 cm into the sand only to emerge again soon. They feed on vegetable and animal matter. Sometimes a small piece of detritus is grasped with the mouth-parts and the beetle retreats backwards very fast. Food offered in the cages (oatmeal and chopped dandelions) was found very quickly.

After roving about irregularly for a while hundreds of beetles gather in certain areas of the dunes ("ball-rooms" = *Tanzplätze*) and romp very rapidly around a small amount of detritus. The "dancing" has a pronounced social character. Mating behaviour could not be observed. Dr. Koch said that mating had been observed on the dunes in March and April of other years. It was probably due to the extraordinary heat in 1964 that I could not see any mating behaviour in March. Beetles which were brought to Europe mated and laid eggs from May to September, so that eggs and young larvae were always available.

Lepidochora stridulates very softly when caught. It would be interesting to know whether they also stridulate when they dance or on other occasions.

Evidently the beetles quickly detect very slight vibrations of the ground, for instance when the observer approaches incautiously. The beetles recognize movements from surprisingly far away and very often dug in in response.

At the end of the activity period the beetles dig into the sand, usually deep enough not to be disturbed by any superficial digging immediately afterwards. Only very few beetles can be found in

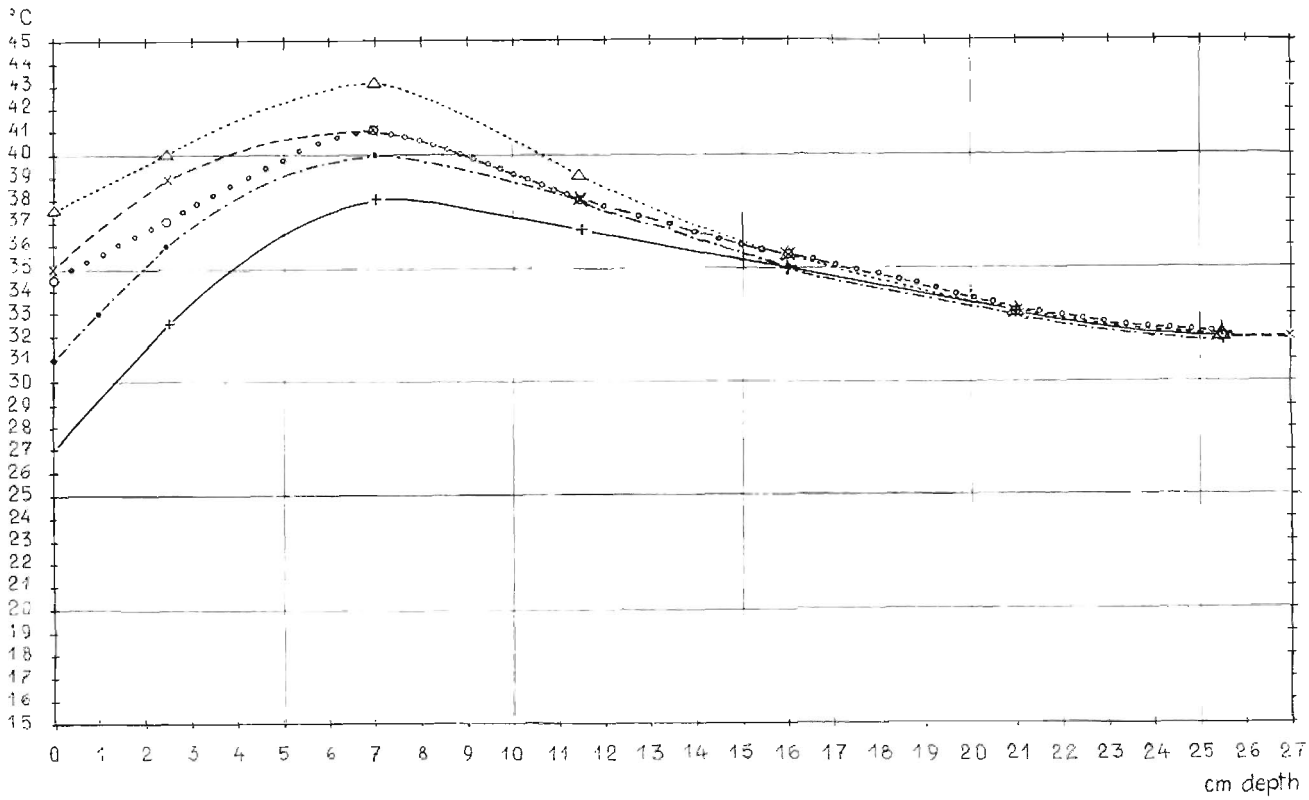
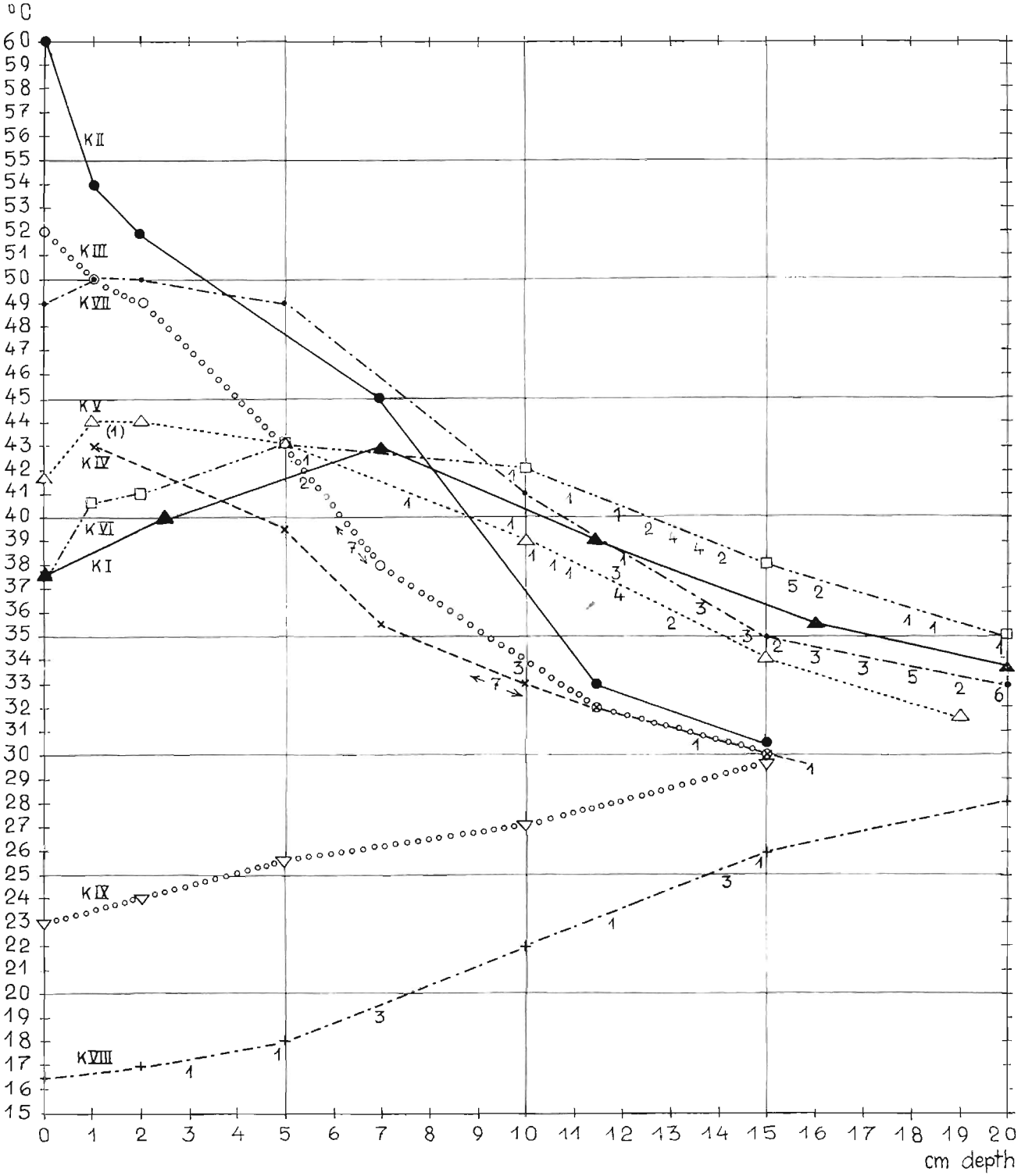


Figure 1: Small barchan-dune, 29th March, 1964, decrease of sand temperature on the slipface of leeward side, in the evening.

X — — — X: 1700 hr., still some sunshine;
△ . . . △: 1727 hr., site with more sunshine, for comparison;
O o o o O: 1745 hr., shades begin to fall;
● —.—.—. ●: 1810 hr.;
\+ ——— +: 1857 hr.

Figure 2: Curves of sand temperatures at different times of the day, on the observation sites. The numbers indicate the number of *Lepidochora* found at the respective depth.

K I:	29th March, 1727 hr., small barchan-dune (from fig. 1, for comparison);
K II to K VIII:	Observation sites near Gobabeb Research Station, all horizontal, only K II is inclined;
K II:	31st March, 1445 hr., overcast until 1100 hr., then full sunshine. Observation site facing sunrise (for comparison).
K III:	31st March, 1500 hr., as K II but horizontal.
K IV:	31st March, 1545 hr., slightly cooler.
K V:	3rd April, 1715 hr.,
K VI:	3rd April, 1800 hr., very hot day.
K VII:	5th April, 1530 hr., very hot, later cloudy.
K VIII:	1st April, 2000 hr.
K IX:	3rd April, 1930 hr.



this way. It is very likely that the beetles withdraw immediately into deeper layers of sand, as practically no beetles could be found during daytime digging either.

Fig. 1 shows the temperature decrease; the table in addition shows light and wind conditions in connection with the activity of *Lepidochora*. The observations were made at one "ball-room", which usually was well frequented. Simultaneously to these observations the beetles visible on about 25 m^2 of the dune were counted. (It is neither possible nor important to give absolutely exact numbers in this case). The decrease of the surface temperature of the sand is not the same everywhere, it varies depending on inclination, altitude and aspect of the lee-side of the dune, as shown by the two curves of 17.00 hr. (5 p.m.) and 17.27 hr. (5.27 p.m.) respectively. The first beetles do not emerge before the surface temperature falls to 41°C or lower (see Fig. 1). Their number increases with decreasing temperature. Later experiments show that sand-layers of a temperature of 41° to 42°C form a barrier for *Lepidochora*. Through this layer the beetles do not emerge, though they dive through it in case of emergency.

In order to observe the temperature conditions and the depth distribution of the beetles some experiments were set up. Some containers filled with sand were dug into the sand and gravel next to the laboratory of the Research Station and some *Lepidochora* added. The conditions were not exactly the same as in the wide-open, wind-piled, loose dune, but the temperature conditions of the sand in the containers and at the dune were much the same (see Fig. 2, curves K, I and K, VI). The surface temperatures in the containers decreased very fast after sunset (Fig. 2 curve K,V, 17.15 hr. [5.15 p.m.] and curve K,IX, 19.30 hr. [7.30 p.m.]). To verify the depth distribution of *Lepidochora* the sand was cautiously removed in shallow layers. The beetles found were always calm so that it seems very unlikely that the beetles had moved while being uncovered. The temperature of each layer was measured. All observations were repeated several times on days with different air temperatures and at different times of the day. The necessary intervals between the experiments were provided for each container (Fig. 2).

Curve K, III: — March 31st, 15.00 hr., fair, cloudy until 11 o'clock, therefore very sharp decrease of the temperature with depth. Most *Lepidochora* found at a depth of 5½ to 10 cm.

Curve K, III: — March 31st, 15.00h, fair cloudy cooler than curve K, III, second container. Most beetles found at a depth of less than 11.5 cm.

Curve K, V: — April 3rd, 17.15 hr. In spite of the late hour the shallow sand layers down to 5 cm were warmer than those of curves K, III and K, IV, but cooler than those of K, VI. Most of the beetles in both containers found at a depth of 10 to 13 cm (the numbers of the beetles found are marked next to the respective temperature curve).

Curve K, VI: — April 4th, 18.00 hr. Extremely hot day, so that the deeper sand layers became very hot. Most beetles were found deeper than 12 cm below surface, in spite of the fact that the surface sand-layers had already cooled and the activity period at the dune had started. The beetles which were probably ready to emerge were found close to the upper temperature limits.

Curve K. VII:— April 5th, 15.30 hr., very hot day, passing clouds prevented overheating of the surface. Most animals found between 13 and 21 cm depth.

Curve K, VIII: — April 1st, 08.00 hr. The upper sand-layers still showed the effect of the cool night. The beetles were very unevenly distributed, but most of them deeper than 7 cm.

Curve K, IX: — April 3rd, 19.30 hr. The beetles run on the surface in all containers.

The above observations show that *Lepidochora argentogrisea* digs more or less into the sand during the night, but it is the heat of the day which induces the beetle to dig deeper. Beetles were very rarely found in sand layers warmer than 42° C, most stayed where the sand temperature was below 40° C. In the open dune the beetles probably dig deeper than the limit of 21 cm to which they could and did go in the container.

Some *Lepidochora* were sent to Vienna, where they were kept in a large cage with sand heated by an infra-red radiator. For experiments the beetles were transferred into a deep container filled with medium fine sand. This experimental cage was put into a larger sand-filled vessel in order to get a better vertical temperature stratification in the experimental cage. Occasionally this was heated obliquely from above by a strong infra-red radiator. The depth distribution of the beetles was established by removing the sand layers cautiously. These experiments, though under very unnatural conditions, corroborate the observations made during experiments in their natural habitat.

The experiments on temperature and depth distribution showed the following results (Fig. 3):

Curve 1: — June 24th, 17.15 hr. The *Lepidochora* were put into the container at 18.30 hr. and the heat switched on. The animals withdrew to a considerable depth after the heating of the superficial layers.

Curve 2: — June 25th, 20.30 hr. The container with the beetles had been heated all day. The animals stay rather deep down, but most of them next to the temperature limit of 42°C, evidently ready to

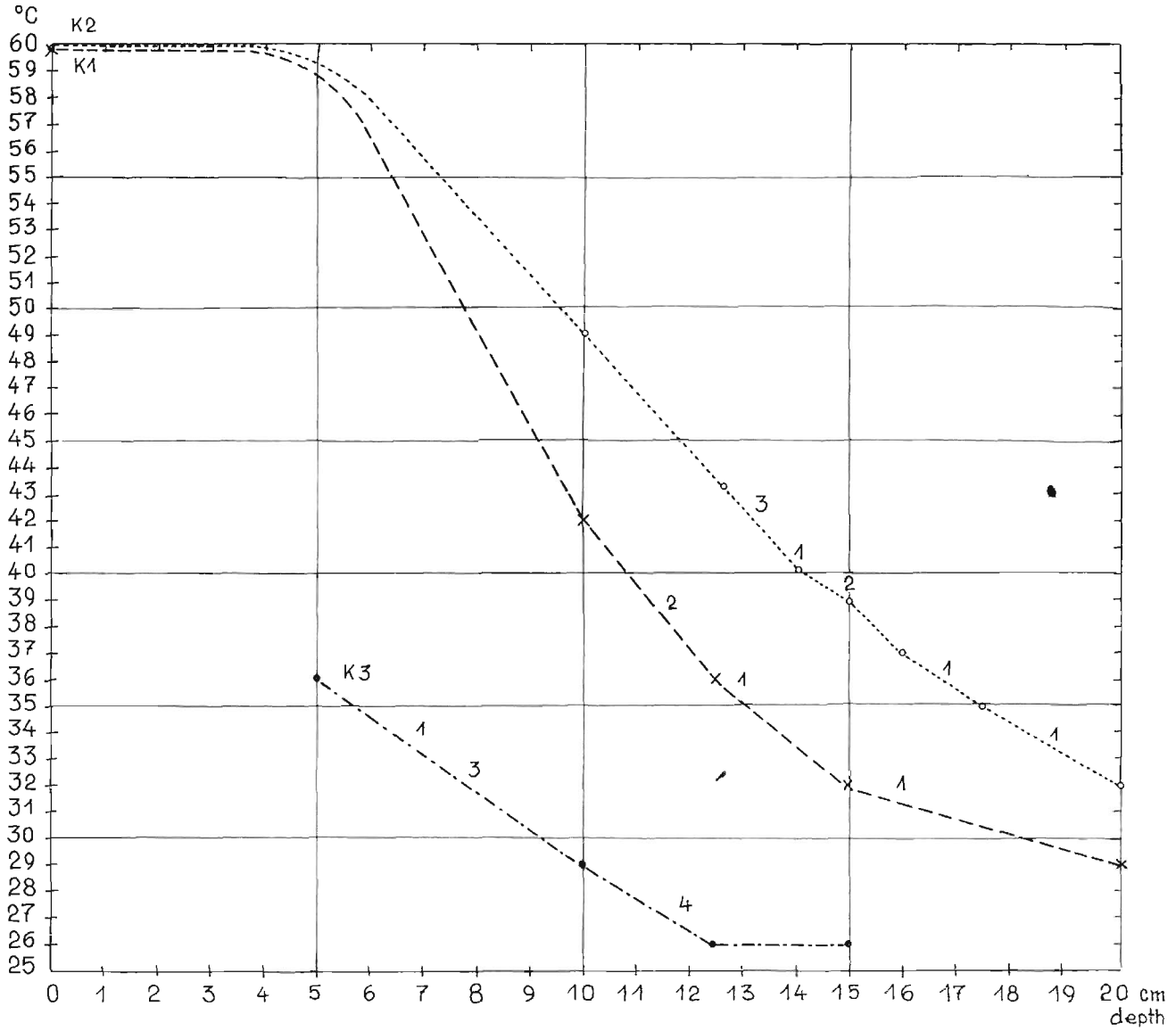


Figure 3: Curves of sand temperature at different times of the day in experimental containers with artificial heating.
K 1: 24th June, 1715 hr., strongly heated since 1230 hr.
K 2: 25th June, 2030 hr., strongly heated all day long.
K 3: 26th June, 1115 hr.. strongly heated for 1½ hours.

emerge if the temperature decreases further (compare June 25th, 21.15 hr. and Fig. 2, curve K, VI).

Curve 3: — June 26th, 11.15 hr.. After 1½ hours of heating the beetles were more or less distributed at random in sand layers of medium depth (compare Fig. 2, curve K, VIII).

It can be assumed that the beetles emerge due to an internal circadian rhythm; the exact moment, however, is determined by other factors. This seems to be corroborated by the following experiments.

June 24th, 17.30 hr. Ten beetles already highly active were transferred from the cage to the empty experimental container and cautiously covered with 20 cm of sand at a temperature of 30° C. (In the field the beetles are frequently covered with sand when a dune ridge slides, so this happens normally and does not disturb the animals very much). 1½ hours later seven beetles had already emerged.

June 25th, 21.15 hr. Eight *Lepidochora* were hindered from emerging by heating the container all day long. After being dug up they were covered with 10 cm of lukewarm sand; ½ hour later five had emerged and were running on the surface, the other three followed a little later. At 23.00 hr. all beetles sat quietly on the surface (caged beetles do

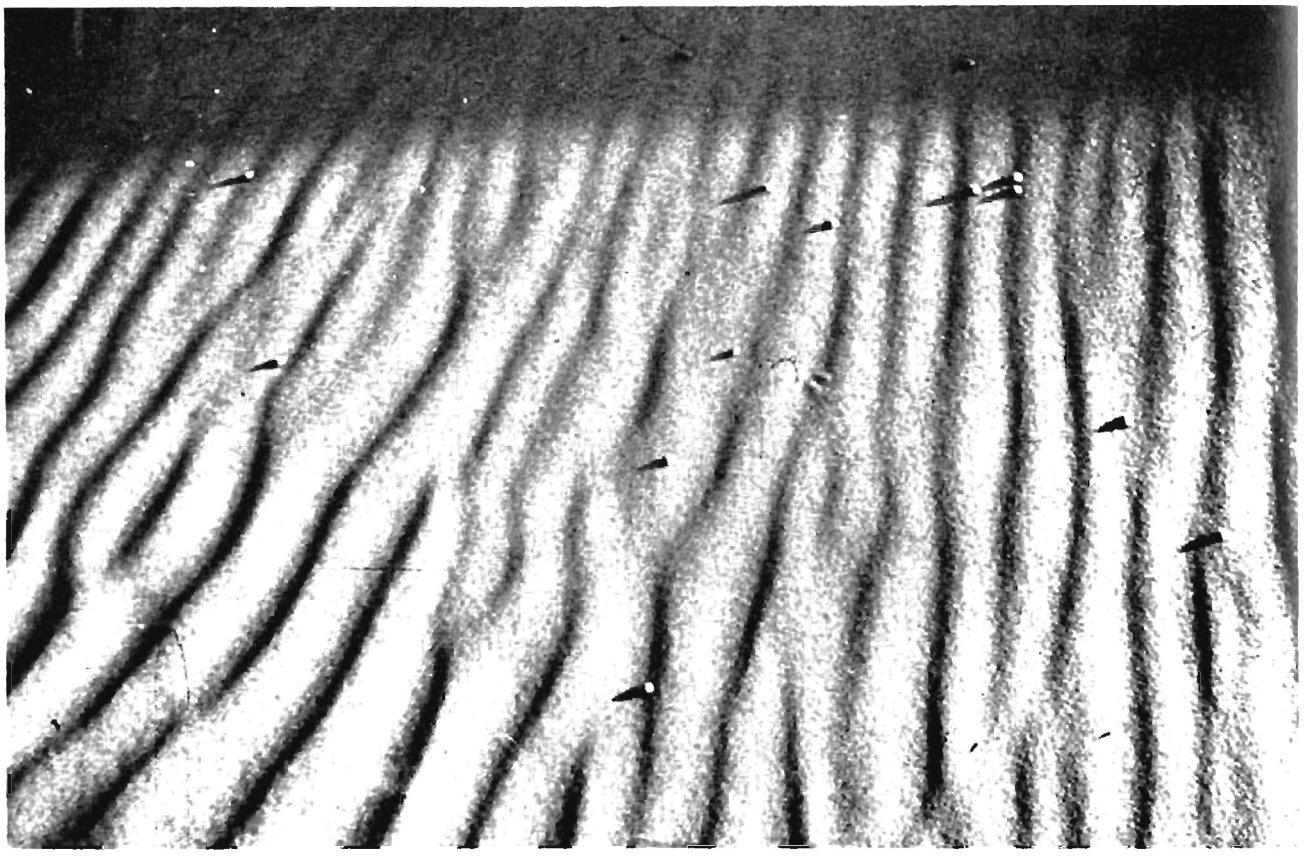


Figure 4: *Lepidochora argentogrisea* romping on the edge of the shadow on a small barchan-dune west of Gobabeb, 29th March, 1964, 17.00 hr.

not dig in as fast and as regularly as in the field). This experiment shows that the activity period can be shifted to late evening hours by external (exogenic) factors. A less important shift has been mentioned when the activity period of the dune-dwelling *Lepidochora* was compared with that of the beetles in the outdoor cages.

Finally some observations were made on beetles which were either dug out or were in the open for one reason or another. They show that *Lepidochora* is highly sensitive to irradiation. Exposed to the sun they dig in immediately. In some experiments the beetles were put on cool sand. The sun radiation was hardly noticeable on the skin of the observer as the sky was overcast. Nevertheless the beetles had dug in after 7 to 10 seconds. In another experiment the infra-red radiator was switched on upon two *Lepidochora* sitting in a cool cage; 10 to 15 seconds the animals started to run around and after 1 to 3 minutes they dug in.

Speedy reaction to sun or heat rays is of the utmost importance to the beetles. Two which could not dig in under heat radiation became immobilized before the sand surface reached a temperature of 39° C. One of them was heat-paralyzed and recovered in the cold, the other one was already dead.

In this experiment the beetle reached its maximum limit of heat tolerance before the temperature of the sand surface rose to 39° C. This maximum temperature is evidently below 43° C as Fig. 2 (curves K, III, K, V and K, VI) and Fig. 3 (curve 2) show. The one *Lepidochora* found in a sand layer of 44° C (Fig. 3, curve K, V) was very inactive.

If a *Lepidochora* is put on sand of 46° C or more in full sunshine it digs in fast but emerges very fast again, runs a short distance, tries again to dig in and emerges again. (Experiments of this kind must be terminated after a short time or the beetles may be harmed*).

* C. K. BRAIN, 1963 (Observations on the temperature tolerance of lizards in the Central Namib Desert, South West Africa *(Scient. Pap. Namib Desert Research Stn.*, No. 15) reports a similar behaviour in dune-dwelling lizards which used to dig in when overheated; if they were put on too hot sand they tried to dig in but emerged again very soon.

CONCLUSION

The activity of *Lepidochora argentogrisea* Koch follows an endogenous circadian rhythm which is synchronized by the temperature.

SUMMARY

While most Tenebrionid beetles either show diurnal or nocturnal activity, *Lepidochora argentogrisea* is active only shortly after sunset. It has been found that a circadian endogenic rhythm governs the activity of this beetle.

Investigations have been started to find out with which factor the activity rhythm is synchronized. In the field changes of light and temperature run parallel with the activity. Experiments have shown that temperature is the master factor, while light is practically unimportant.

The temperature limits within which *Lepidochora argentogrisea* is active, are 20°—37° C. A sand layer with a temperature of 41° — 42° C prevents the appearance of the beetles on the surface of the dunes shortly after the sun has ceased to warm up the surface. After a certain time most beetles are at the surface whirling around in circles which often enclose plant debris. This activity seems to have a social significance, but mating behaviour has not been observed at the time of the investigation.

When the sand surface cools down to about 20° C the beetles dig into the sand and reappear only the next day around sunset. The depth to which the beetles dig in varies seemingly according to the temperature gradient within the sand. This has been found by using artificial arrangements. In the free dunes the beetles seem to move much easier up and down and from field experience it is suspected that they dig in immediately to the final depth, where they stay until the next sunset.

In case a hot sand layer below the surface prevents the digging in, the beetles soon reappear on the surface and are easily paralyzed by heat under experimental conditions. A prolonged influence of temperatures higher than 42° proved to be dangerous.

ACKNOWLEDGEMENTS

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Figure 5: *Lepidochora argentogrisea* on the edge of the shadow on a small barchan-dune west of Gobabeb, showing from right to left different stages of digging in. The time difference between each of the stages is about 5 seconds. 29th March, 1964.

TABLE: **Light and wind conditions, evening decrease in sand temperatures (°C) at various depths (cm), and main activity of *Lepidochora argentogrisea* on the leeward slipface of a small barchan-dune west of Gobabeb, on 29th March, 1964.**

Sand temperature (°C) at various depths	at hours (S.A.S.T.)									
	1700 still some sunshine	1727 site with more sunshine (for comparison)	1745 shades beginning to fall	1755 surface of slipface in shade	1820 slight wind	1840 slight wind	1850 sunset, sand whirling across surface	1857		Dark
Surface (0.0 cm)	35.0	37.5	34.5	32.0	31.0	29.0		27.0	24.0	24.0
2.5 cm	39.0	40.0	37.0	37.0	36.0			32.5		
7.0 cm	41.0	43.0	41.0	41.0	40.0			38.0		
11.5 cm	38.0	39.0	38.0	38.0	38.0			36.5		
16.0 cm	35.5	35.5	35.5	35.5	35.0			35.0		
21.0 cm	33.0	33.0	33.0	33.0	33.0			33.0		
25.5 cm	32.0	32.0	32.0	32.0	32.0			32.0		
27.0 cm	32.0									
Number of individuals of *Lepidochora*, on about 25 m² of 'Ball-room'	Single specimens moving	'Ball-room' activity starting							Activity confined to 'Ball-room'	
			—20		—24	—40	—48	—67	—48	—59
			—33		—30	—60	—60	—75		
					—40	—44	—70	—76		
					—47					
					—50					