COMPETITION AND THERMOREGULATORY BEHAVIOR OF THE NAMIB DESERT TENEBRIONID BEETLE GENUS *CARDIOSIS*[1]

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Abstract. Tenebrionid beetles of the genus *Cardiosis* are confined to sand dunes and other sandy substrates of the Namib Desert in South West Africa and Angola. In the northern Namib the breadth of environments occupied by each species is considerably greater than in the southern Namib. This may be due to competition resulting in ecological divergence, since there is sympatry in this genus only in the southern Namib.

All species of the genus *Cardiosis,* including the sympatric *C. fairmairei* and *C. hamiltonuli,* are diurnal. The daily activity rhythm of these species responds to ambient thermal conditions, and fluctuations in ambient conditions result in differing patterns of activity. Substrate and ambient temperatures are the most important microclimatic variables influencing the actual timing of activity. This usually results in a concentration of activity in the least humid hours of the day. On cool days or when winds cool the sand surface, activity may extend through the middle hours of the day. On hot or calm days activity becomes bimodal, with activity limited to intervals when body temperatures can be maintained at levels well above 30°C and substantially below lethal limits. The interval of morning activity is less pronounced than the afternoon activity period and on especially hot days morning activity may be omitted altogether. Unconfined populations of *Cardiosis* extend their activity over considerably greater intervals than confined populations exposed to identical macroclimatic conditions. This is due to the ability of the unconfined population to utilize a broad spectrum of environments, thus locating favorable thermal conditions as they develop in the course of a daily cycle.

The purpose of this paper is to describe thermal and interspecific relationships of tenebrionid beetles within the genus *Cardiosis.* These flightless tenebrionid beetles, which range in size from 2.7 mm (*C. hamiltonuli*) to 7.0 mm (*C. fairmairei*) (Koch 1969), are endemic to the Namib Desert of South West Africa where they are confined to sandy substrates extending from the Orange River in South Africa to the Curoca River in Angola. The highly modified morphological features of this genus, consisting of a subspherical body, sculptured elytra, and elongated tarsi, have been described in detail by Koch (1958, 1969). These peculiarities make this the most highly modified tenebrionid beetle in an already distinctive tenebrionid fauna, suggesting that there may be other correlated and equally distinctive adaptations of habit and habitat.

To date six species of *Cardiosis* have been described from the Namib. The most recent discovery, *Cardiosis hamiltonuli* (Fig. 1), was made in December of 1967 by the author's son (Koch 1969). In the course of behavioral studies of other diurnal Namib Tenebrionidae, I had the opportunity to study five of these species, missing only the southern Namib *C. eremita.* The period of investigation extended from July 1967 through March 1968 and included the territory from the central Namib near Tsondabvlei to the Curoca River in Angola, which is the northern distributional frontier of the genus and the extensive dune systems of the Namib (Fig. 2).

METHODS

This account is based primarily upon direct visual observations. Some of these observations, particularly those of the wary *C. fairmairei,* which often flees when approached by an observer, were facilitated by the use of Leitz 10 by 40 Trinovid binoculars. Escape responses are suppressed when these little beetles cool off in the evening. They may then be followed by the observer on hands and knees and observed as close as the eye can focus.

Environmental temperature measurements were made with a YSI telethermometer, Model 44TD, and fine thermistor probes, YSI stock number 511. These thermistors are plastic-covered. According to the manufacturer they come to within 1% of equilibrium at a new temperature in about one second. This extremely rapid response makes them especially suitable for monitoring environments which change temperature rapidly. The details of the measuring technique and the possible accuracy of the system are discussed in detail elsewhere (Hamilton, *unpublished*). Measurements are considered accurate to closer than 1°C.

The well-equipped weather station at the Namib Desert Research Station at Gobabeb (Fig. 2) provided certain weather data which were useful in interpreting the temporal pattern of activity described here. This weather station is within 2 km of all of the Gobabeb sites described in this paper and in most cases it is within 1 km. The weather station humidity measurements are based upon hygrothermograph measurements corrected with wet/dry bulb humidity

Fig. 1. *Cardiosis hamiltonuli,* photographed in the outdoor observation cylinders described in this paper. The beetle's body is approximately 3.5 mm long. The sand grains are typical of the natural environment of this species, but other *Cardiosis* species are restricted to finer sand substrates.

determinations made three times each day at the Gobabeb weather station.

Vegetationless dunes and gravel plains provide exceptional opportunities for direct observation of insect behavior. Determination of the daily pattern of activity of these insects was made by traversing preselected routes through typical habitats which could be traveled in 30 min or less. All individuals within a specified distance of the line were counted during a walk along the line. Most *Cardiosis* species are relatively conspicuous and few or no individuals active above the sand surface are likely to be missed during such a census. However, the highly mobile *C. fairmairei* becomes more wary as it warms up, and may flee or burrow before the approach of an intruder. The cryptic *C. hamiltonuli* was never seen in the field. Bias in censuses was minimized by the use of binoculars to scan the census line and make counts before advancing.

Observations of the elusive *C. hamiltonuli* were made by capturing individuals in 1-gal cans buried with their tops flush with the surface in the quasi-fluid sand. Specimens captured in these traps were placed in large plastic garbage cans 40 cm wide and 56 cm deep filled to within 5 cm of the top and buried in sand so that the sand line in the container was level with the surrounding sand. Subsurface tem-

peratures in such containers came to equilibrium with undisturbed sands after a few days. When this equilibrium was established, trapped specimens were placed in these containers. The periodicity of activity could be determined by cautiously approaching and observing the captive individuals.

By making regular observations of the contents of a grid of the 1-gal metal can traps, it was also possible to determine the general features of activity periodicity of *C. hamiltonuli* in the field and the extent to which its habitat overlaps that of *C. fairmairei.*

The times in this paper and in two other papers dealing with the activity patterns of Namib Desert Tenebrionidae (Hamilton, *unpublished*) refer to local sun time, not standard time, and can thus be compared directly if allowance is made for seasonal variation in day length.

RESULTS

Habitat analyses

The only descriptions of the environmental relationships of the several *Cardiosis* species are those provided by Koch with his descriptions of new species. These abbreviated accounts are accurate but do not include the full range of habitat types encountered in this study. In order to identify adequately
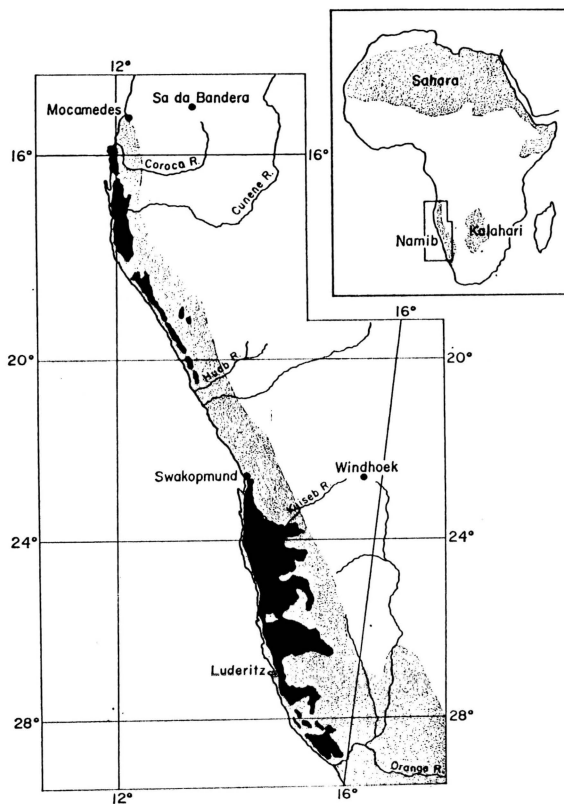
FIG. 2. The Namib Desert of South West Africa. The stippled area receives less than 5 cm average rainfall per year. The inset shows the location of this small desert in Africa. Beetles of the genus *Cardiosis* are largely confined to the vegetationless or sparsely vegetated sand dunes, shown on this map in black. Redrawn from Koch 1962.

the environmental relationships of the species of *Cardiosis,* it is first necessary to describe these environments.

Namib Desert environments may be broadly classified into the littoral bench, the barchan dunes, the sand and gravel plains which lie inland from these dunes (Koch 1962), and the oases. Each of these broad divisions is divided into a number of special physiognomic and biotic features which provide unique habitats for the tenebrionid fauna. One of numerous possible subdivisions of these environments is included in Table 1.

This classification is preliminary and concerned primarily with the Namib Desert and the genus *Cardiosis.* Thus the most complex Namib Desert environments, the riparian forests and sands, are not subdivided at all because they host no *Cardiosis* species. The barchan dunes, which in other deserts or for other purposes might easily be classified as a single environment, are divided here into several subdivisions because of their greater significance to the genus *Cardiosis.*

A full description of the diverse environments referred to in Table 1 would consume many pages without commensurate benefit to the reader. Subsequent reference to specific features of these environments is included only when it is related specifically to the biology of each species. This analysis, made by a single observer, permits consistent interspecific comparisons of habitat preference and occurrence.

The microenvironments of the sand dunes are shown diagrammatically in Fig. 3. The schematic profile representation of the high dunes system includes all habitat types listed in Table 1. In most cases, however, there is less habitat diversity. Only in the high dunes of the southern Namib, as for example in the vicinity of Gobabeb, are all of these habitat types present in a single dune system.

The coastal bench is a flat or gently sloping and generally gravel-covered plain between the Atlantic Ocean and the desert dunes system. The width of this zone ranges from several kilometers to places where the dunes reach the sea and the coastal bench environment is lacking altogether. The environments occupied by *Cardiosis* may be identified as follows:

Gravel-covered sand.—These are flat areas between vegetation-held mounds of sand. The sandy substrate is covered by small (1–3 mm) pebbles. Although this environment is generally devoid of vegetation, grasses may emerge following sporadic rains.

Barren sand.—This is an environment similar to the gravel-covered sand, but lacks gravel.

Vegetated sand.—This environment is also like the two preceding environments, but is persistently covered by perennial grasses and certain characteristic forbs.

Sand mound vegetation.—These are stable mounds of sand held in place by the gannabush (*Salsola* sp.) in the central Namib, which is the only region where I have observed a *Cardiosis* species occupying this habitat.

The oases of the Namib are diverse in vegetative and physical structure. These environments are unpenetrated by the *Cardiosis* with the exception of *C. carpi,* which inhabits sand mound vegetation in the dry river bottoms and their fringes in the central Namib. In the northern and southern Namib river bottom environments, which may be physically and biologically similar to those of the central Namib, no *Cardiosis* species were found. This central Namib environment is structurally similar to the vegetated sand mound environment of the coastal bench. However, the river bottom sand mounds extend several kilometers inland, beyond the first high dunes systems, and are therefore in considerably warmer localities and include a different complex of plant species.

TABLE 1. Namib Desert environments and the occurrence of five of the six known tenebrionids of the genus *Cardiosis*. Plus (+) indicates a favored environment; +M, a marginal environment; NP, that the environment is not present or has not been found in that part of the Namib where the species occurs; and dash (—) that the environment occurs but no *Cardiosis* species are known to occur in that environment. Abbreviations: *C.m., Cardiosis moufleti; C.c., C. carpi; C.t., C. triangulifera; C.f., C. fairmairei;* and *C.h., C. hamiltonuli; C., Cardiosis* (all species). Species are arranged in their order of occurrence from north to south

Environment	C.m.	C.c.	C.t.	C.f.	C.h.	C.
Coastal bench						
Littoral	—	—	—	—	—	—
Gravel plains	—	—	NP	NP	NP	—
Gravel-covered sand	—	+	NP	—	—	+
Barren sand	—	+	—	—	—	+
Vegetated sand	—	+	—	NP	NP	+
Sand mound vegetation	+	+	+M	NP	NP	+
Sand dunes						
Barchan dune slipfaces	+	—	+	+	—	+
Barchan dune crests	+	—	+	+	—	+
Stable vegetationless sand dunes	+	—	+	+M	+	+
Stable vegetated dune sands	+	NP	NP	—	—	+
Intradune valleys	+	—	+M	+M	—	+
Sand mound vegetation	+	—	—	—	—	+
Interdune valleys	NP	—	NP	—	+M	+
Oases						
Sand mound vegetation	NP	+	—	—	—	+
Woodland and brush	—	—	—	—	—	—
Vegetated sand	—	—	—	—	—	—
Riparian forests and sands	—	—	—	—	—	—
Inland plains						
Several environments	—	—	—	—	—	—
Number of environments occupied by *Cardiosis* species	7.0	5.0	4.0	3.0	1.5	12.0
Mean number of environments occupied in each portion of the Namib Desert	6.0		4.0		2.2	
% available environments occupied	70.0%	45.5%	44.4%	30.0%	15.0%	
% available environments occupied per desert	60.0%		44.4%		22.5%	
Desert	Northern Namib		Swakopmund Dunes		Southern Namib	

ACTIVITY PATTERNS

All known *Cardiosis* species are diurnal. A major purpose of this study was to determine the extent to which environmental variables, particularly heat, influence the activity cycles of these species. Analyses of other diurnal Namib, Sahara, and Kalahari Desert tenebrionids (Hamilton, *unpublished*) suggest that body temperatures and the environmental conditions which produce them may have a critical influence upon the temporal, spatial, and behavioral responses of various tenebrionids to their desert environments.

Container experiments

It soon became apparent that these small beetles respond to short-term changes in micro- and macroclimatic conditions. Since relevant conditions change significantly from day to day and minute to minute, pooled data on daily cycles of activity mask highly predictable activity patterns not only of these *Cardiosis* species but also of other small animals such as the solpugids and lizards living in their environments. Experiments with *C. fairmairei* in containers, as described for *C. hamiltonuli* above, were made at the weather station at the Namib Desert Research Station at Gobabeb, South West Africa. Thus a continuous record of certain meteorological data such as radiation intensity and the standard weather station ambient temperature measurements was available. Soil surface temperatures were also taken in the containers.

Each container was supplied with 40 recently captured *C. fairmairei*. The activity of the population on 3 consecutive days of rather different weather conditions is partially described by Fig. 4. The activity scale is the percentage of the 40 individuals that were on the surface at the time of each hourly observation. There is considerable variation in the pattern of activity on these 3 consecutive days in December
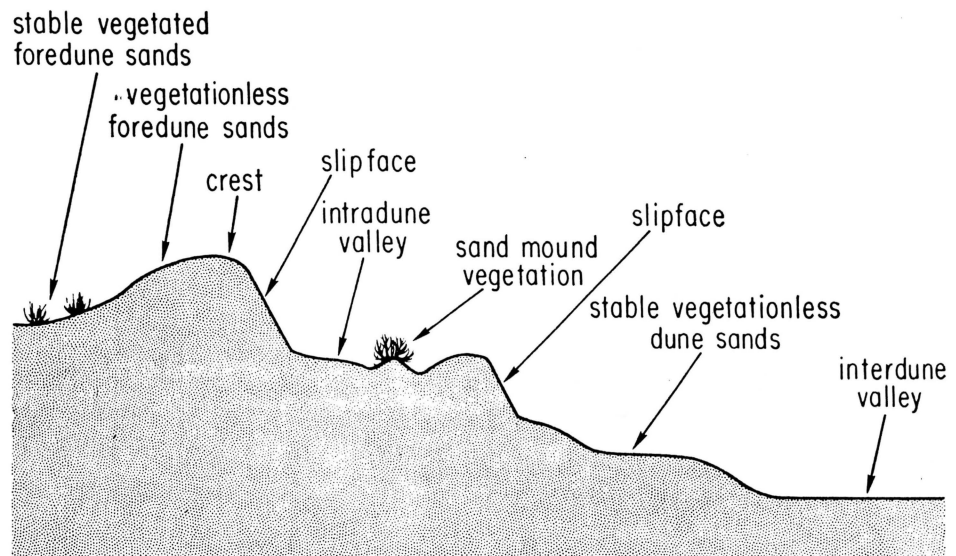
Fig. 3. Schematic representation of sand dune environments occupied by certain species of the tenebrionid beetle genus *Cardiosis*.

1967. On December 9 the activity pattern was bimodal, with a small burst of activity in the morning and heavy activity commencing about 150 min after local noon. The intermittent cloud cover on this date is reflected in the ragged curve for net radiant energy. The following day a persistent, thin, high overcast prevailed through the forenoon and ambient and soil surface temperatures remained relatively low until after local noon. On this date there was an entirely different pattern of activity with no bimodality, and population activity persisted for over 330 continuous min. On the following day the cloud cover was thinly scattered. Radiation levels, ambient temperatures, and especially soil surface temperatures rose sharply in the forenoon and no activity was observed until 180 min after local noon.

On each of these days and on most days on the Namib Desert relative humidity levels are high in the early morning. On some mornings the coastal fog penetrates the entire depth of the vegetationless dunes and heavy dew precipitates. Humidity levels decline throughout the day (Fig. 9) and the peak activity of *Cardiosis* tends to take place in the afternoon when the lowest relative humidities prevail on the Namib (Schultze 1969).

These results show that the surface activity of *C. fairmairei* is facultative and directly related to ambient microclimatic conditions, which are in turn related to macroclimatic conditions. For this reason interspecies comparisons made under field conditions must be interpreted with caution since any such comparison may be simply an indicator of ambient conditions. The sympatric *C. fairmairei* and *C. hamiltonuli* live in distinct and separate environments, and any differences between the activity patterns of the two species could not necessarily be assigned to anything more than differences in the extent of microclimatic variation within the environments of the respective species. To test this possibility, identical test containers were set up in the environment where *C. fairmairei* and *C. hamiltonuli* overlap. A sample result of these experiments is shown in Fig. 5. The relatively small sample size (12 individuals) was due to difficulty in capturing *C. hamiltonuli*. Again, pooled data for several days result in an unreal representation of the actual periodicity of surface activity. If a series of days of differing weather regimens is included the activity interval for both species appears to extend from 0900 to 1800 and to be slightly bimodal, with peak activity in midafternoon.

On all of the 11 days that observations of these experimental populations were made the activity of *C. fairmairei* was greater than that of *C. hamiltonuli* and extended over a shorter interval.

The temperature of the sand surface and the sands at a depth of 5, 10, and 20 cm in the ground next to these containers is shown in Fig. 6. These measurements were made with calibrated thermistors inserted to the appropriate depth on a stick which had been pushed into the sand between the two test containers. A recording mercury thermometer with the bulb just buried in the sand gave a maximum reading of 60.3°C for the day.

Census data

On the same date that the data for Fig. 5 were obtained, a census of the free-ranging population of
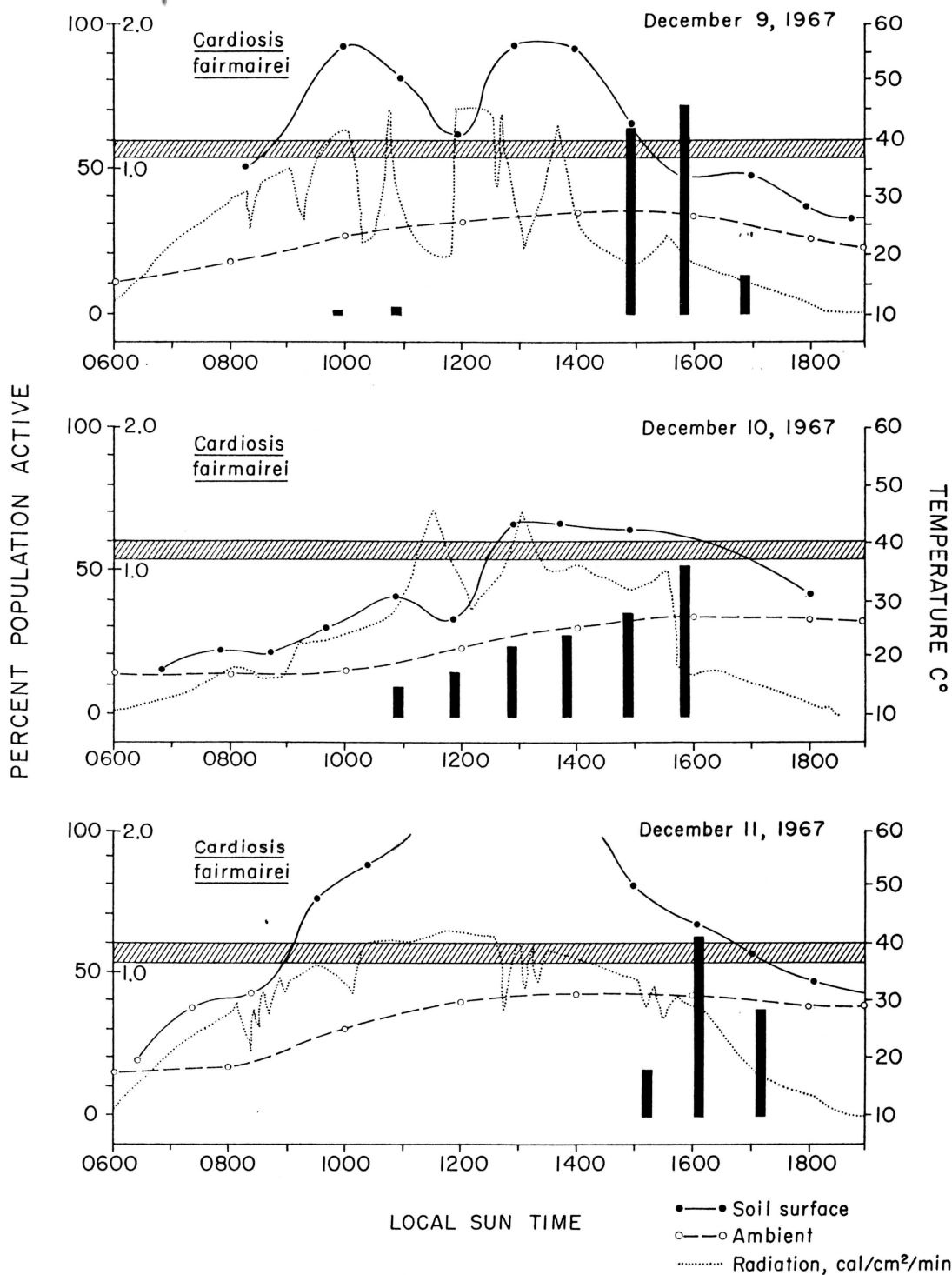
FIG. 4. Activity pattern of a constrained population of 40 *Cardiosis fairmairei* at the weather station at Gobabeb, South West Africa. Activity is shown in percentage on the outside left ordinate, radiations in cal/cm²/min on the inside left ordinate, and ambient and sand surface temperatures on the right ordinate. The cross-barred area is the proposed preferred body temperature of this species according to an hypothesis considered in this paper.
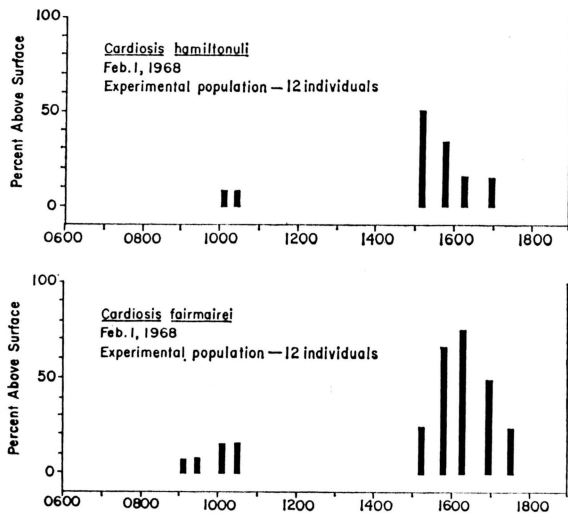
FIG. 5. Activity pattern of constrained populations of 12 *Cardiosis fairmairei* and 12 *C. hamiltonuli* at the same locations where these species live sympatrically.
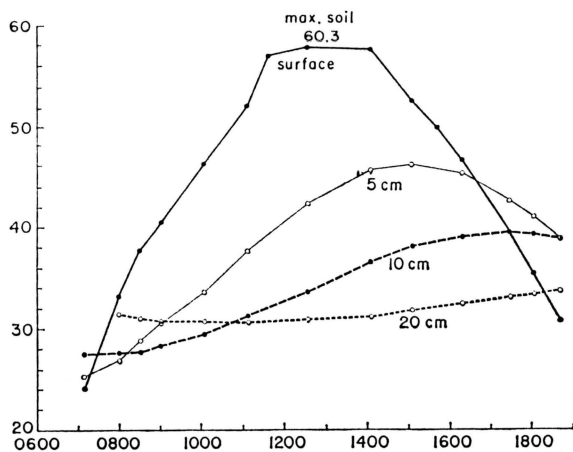

FIG. 6. Soil temperatures on February 1, 1968, at the site of the experiments described in Fig. 4. This is also the natural environment of *Cardiosis hamiltonuli* and under certain conditions that of *C. fairmairei*.

Cardiosis fairmairei was made by walking a 300-m line traversing the diverse habitats shown in Fig. 3. The only habitats where individuals were observed were along a 120-m stretch of the census route that included (i) vegetationless foredune sands, (ii) vegetationless dune crest sands and vegetationless dune slipface sands. This latter environment is here subdivided into (iii) the crest of the dune face within 1 m of the break to the slipface and (iv) the remainder of the slipface. The results of this census (Fig. 7) are based upon the percentage of the greatest number of individuals (47) seen during any of the 11 traverses of the census route on that date.

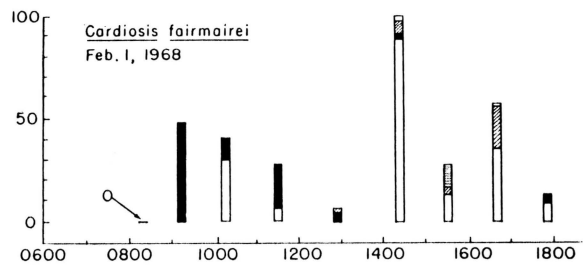These censuses show that activity of the population in the natural environment extended over a pe-

FIG. 7. Temporal pattern of activity of *Cardiosis fairmairei* on the high Namib Desert dunes above Gobabeb, South West Africa. The habitats, described in the text, are (i) the dune slipfaces (cross barred), (ii) tops of the slipfaces (slant barred), (iii) the vegetationless dune crests (solid bars), and (iv) the vegetationless foredune sands (open bars). For details, see text.

riod of about 515 min, while in the constrained environment activity of the same species was limited to approximately 220 min. There are significant shifts in physical location of activity during the day in the unconfined natural population (Fig. 7). Although these changes could be due to the emergence of individuals in different locations at different times of day, direct observations revealed individuals shifting from one environment to another. The distances involved here are not great, even for small animals, since their locomotion may be quite rapid, and it is possible for them to travel over 10 m in a minute, thus traversing all of the environments described above.

In addition to the visual observations reported above, a can-trap analysis (see METHODS) was made to determine as precisely as possible the relative distribution of *C. fairmairei* and *C. hamiltonuli*. Other species of diurnal desert tenebrionids can be effectively analyzed by visual observations but, as explained above, *C. hamiltonuli* was not susceptible to this analysis. Therefore a grid of 40 can traps was laid out on January 21, 1968, and the catch of these traps was determined daily. The location of these traps, which were spaced at 25-m intervals, is shown in Fig. 8. On January 26, 1968, 10 additional traps were added (H7, J7, N7, P7, Q7, L9, J11, I12, T13, and T14), and the entire grid was maintained through February 2, 1968. Collected wind-blown sand in these traps had to be removed and sieved several times a day because of its high rate of accumulation. When a trap fills with sand to the lip, it is possible for the captured inhabitants to escape and no new captures occur. Traps L5, N5, P5, Q5, N7, P7, Q7, N12, O12, P12, Q12, R12, S12, T12, T13, and T14 flooded with sand on one or more occasions.

The captured specimens of *Cardiosis hamiltonuli* were all collected (and constitute a part of the type series—see Koch 1969), while other animals, including all *Cardiosis fairmairei,* were released following capture.
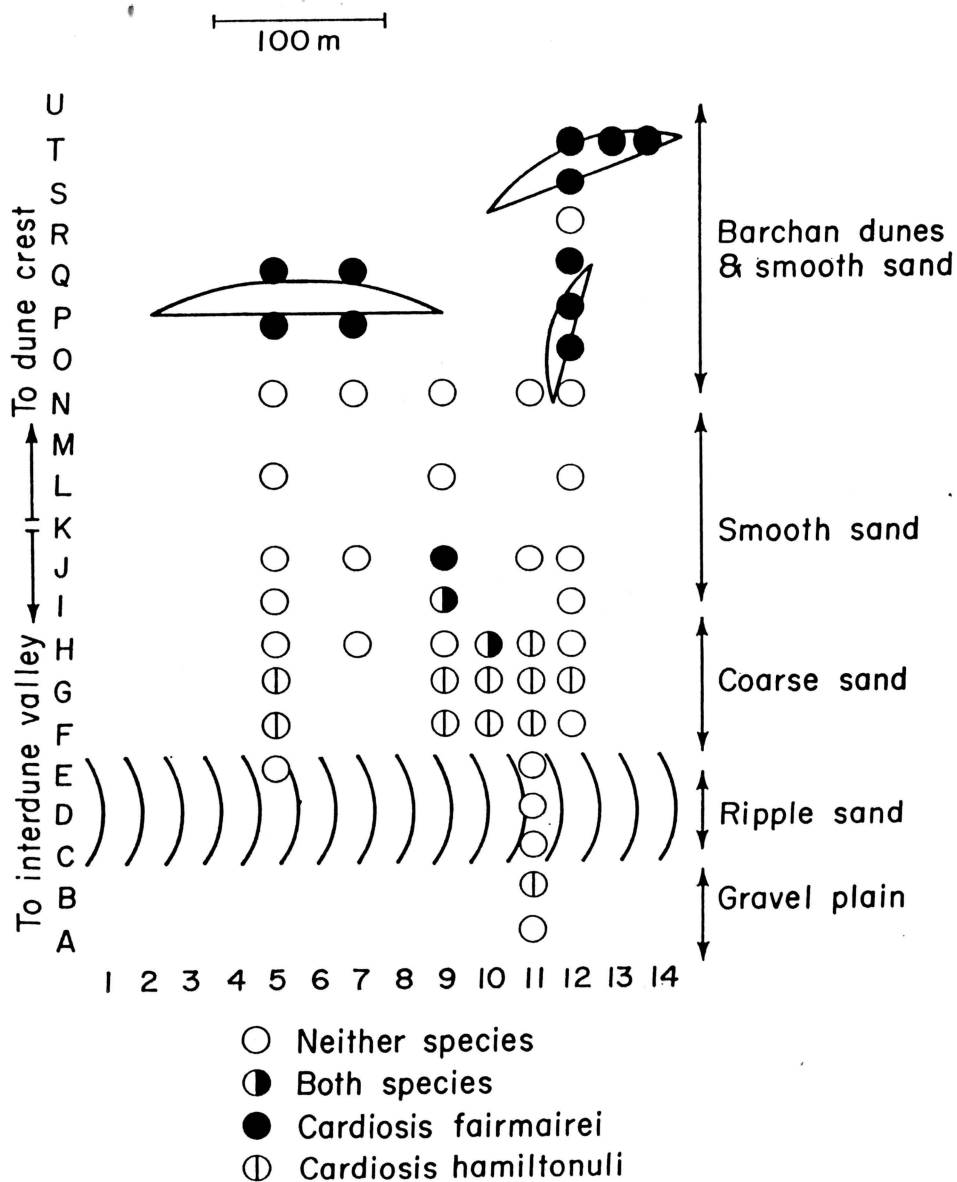
FIG. 8. Can-pit-trap analysis of the distribution of *Cardiosis fairmairei* and *C. hamiltonuli*. Each of the 50 circles represents a trap. The grid interval is 25 m. For details, see text.

The environments within the grid extended from the interdune valley plain to and somewhat above the lower dune slipfaces (Fig. 3). The grid did not include the massive slipfaces of the dune crest where the majority of the individuals of *C. fairmairei* were seen during visual censuses (e.g., Fig. 7). The location of captures shown on Fig. 8 does not indicate the number of individuals per species captured, only their presence or absence. Thus the somewhat irregular attention given to the traps does not detract from the specific interpretations presented here. The only conclusion concerning the temporal pattern of activity of *C. hamiltonuli* that can be made is that it

is strictly diurnal. Each trap was examined in the early evening and at dawn. No individuals were captured during the nocturnal interval.

The capture of specimens of *C. fairmairei* at locations I9, J9, and H10 was a surprise. This species had not been seen in this environment during visual censuses. The surface in this location slopes gently upward toward the dune crest and is covered by freshly blown, fine, smooth sand. Persistent observations subsequently revealed these beetles scattered through this environment during occasions of warm winds with shifting sands. This reduces visibility and the environment is warm. *Cardiosis fairmairei* moves

rapidly under such conditions and these beetles are more alert and responsive to disturbance than when they are cooler.

The results of this survey confirm Koch's (1969) conclusion that *C. fairmairei* and *C. hamiltonuli* are geographically sympatric and ecologically differentiated. However, there is a slight spatial overlap, a fact confirmed by the capture of individuals of both species in the same trap. There is thus the possibility for interspecific competition and hybridization.

DISCUSSION

Activity patterns

Why does the activity of *Cardiosis fairmairei* in captivity differ so greatly from that of the natural, free-ranging population (Fig. 5 and 7)? One answer to this question can be supplied by a hypothesis relating the activity pattern of the ground-dwelling Zophosinae to preferred body temperature levels. Elsewhere (Hamilton, *unpublished*) I present evidence that most of the diurnal Namib Tenebrionidae can be classified as maxitherms, i.e., animals which attempt to maintain body temperatures between 37.5° and 40°C for as long an interval as possible during the daily cycle. This hypothesis suggests that these body temperatures are near the upper intervals for a great variety of animals belonging to diverse phyletic groups.

This hypothesis provides adequate explanations of the activity patterns reported in this paper. No other hypothesis known to me provides as complete a series of explanations of the specific phenomena observed. To make the transition from hypothesis to observation it is necessary to identify the assumptions and their factual basis.

1) It is assumed that most *Cardiosis* activity, including its feeding behavior, takes place on the surface. This conclusion is supported by the fact that individuals have repeatedly been observed speeding about on the surface and eating various bits of wind-blown debris. By comparison, individuals can be recovered below the point where they are seen burrowing into sand even after several hours of submergence. Thus no lateral substrate movements are implicated.

2) It is assumed that the body temperature of as great as and generally greater than ambient temperatures. This conclusion is more problematical but *Cardiosis* is near surface sand temperatures and is comparative evidence for a related and morphologically similar zophosine tenebrionid, *Gyrosis moralesi*, (Hamilton, *unpublished*) supports this conclusion. In the case of considerably larger tenebrionid beetles, where thousands of direct body temperatures were made, this generalization almost invariably held (Hamilton, *unpublished*). However, even an insect as small as *Cardiosis* is able to protect it-

self from the extreme heat of surface sand. This is true even in the barren sand environments occupied by *C. fairmairei* and *C. triangulifera*. For example, using its legs and tarsi as supports, *C. fairmairei* may raise up like a miniature water tower when sand temperatures exceed 45°C. This behavior may raise the center of mass of the body only 2 or 3 mm above the sand surface, but this is already a significant amount relative to (i) ambient temperature, which has an extremely sharp vertical thermal gradient when the surface temperature is much higher than ambient temperatures at 1 m, and (ii) wind speed, which increases rapidly above the surface, reducing body surface temperatures.

Thus the conclusions presented here depend heavily upon comparisons with other species where actual body temperature data are available (Hamilton, *unpublished*) and upon comparisons of the body and lethal temperatures of diverse animal species (Hamilton, *in press*).

The variation of day-to-day activity patterns of enclosed *Cardiosis* (Fig. 4) is probably a result of responses to ambient conditions of temperature and factors affecting it. Thus, on December 9 there was trivial surface activity before local noon, and those individuals which surfaced soon reburied themselves deep in the sand. The major burst of activity developed in the afternoon at approximately the time when the surface temperature cooled to the suggested preferred body temperature level, which is the cross-barred area from 37.5° to 40°C on Fig. 4. During the peak period of activity on December 9, both surface and air temperatures had fallen below the proposed preferred level. However, it is still possible for these beetles to maintain body temperatures as high as 40°C by burrowing a short distance into the sand, where temperatures of 40°C and above are readily accessible (Fig. 6). Burrowing and emergence behavior was often noted.

Examination of the subsoil temperatures at the experimental site where the data for Fig. 5 were gathered (Fig. 6) shows one reason why activity periods tend to be more pronounced in the afternoon than in the morning. In the morning soil surface temperatures are near 40°C, the proposed preferred level, for only a brief interval. Subsoil temperatures are well below preferred temperature levels, and favorable conditions, i.e., those which will sustain a body temperature between 37.5° and 40°C, are fleeting. The desert cools more slowly in the afternoon than it heats in the morning. This is true not only of ambient temperatures at all levels above the surface (Fig. 4 and 7) but also within the soil (Fig. 6). Below the surface, the interval when optimum thermal conditions are available is extensive and may extend well beyond the time when the combination of ambient temperatures, solar ra-
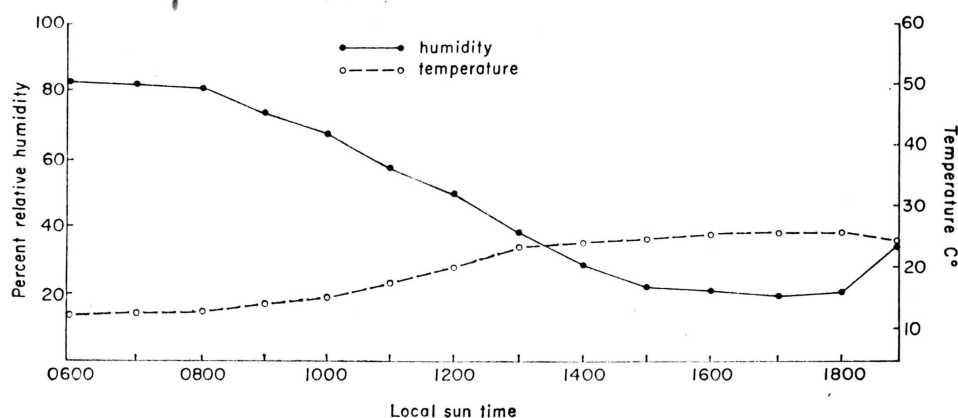
FIG. 9. Ambient temperature and humidity, standard meteorological recording conditions, February 1, 1968, Gobabeb, South West Africa.

diation, and surface temperatures is able to sustain body temperature as high as 37.5°C. The frequently observed sorties to and from the sand suggest that at least *C. fairmairei* is taking advantage of this situation. Thus, activity is concentrated at times which provide a thermal optimum in spite of the inevitable water-loss problems in this desert environment due to high temperatures and low humidity (Fig. 7).

In the northern Namib the center of geographic distribution of *Cardiosis moufleti* and *C. carpi* is in the more moderate coastwise environments characterized by unique white adesmine and zophosine beetles (Hamilton, *unpublished*). In these environments surface temperatures are less extreme and the slope of the daily surface temperature curve is less than that in the warmer interior regions occupied by *C. fairmairei* and *C. hamiltonuli*. Both *C. moufleti* and *C. carpi* regularly practice what appears to be a form of thermoregulation never observed in the more intensively studied *C. fairmairei*. This is shallow burrowing into the surface layer of sand so that the body is partly covered by the warm (measured temperatures ranged from 36.2° to 41.0°C in the case of *C. moufleti* near Porto Alexandre, Angola) afternoon sand. The winds are steadier and more persistent in these coastwise environments, and the sun-warmed sand may slowly drift to cover these sand-basking beetles.

On November 18, 1967, at 1425, I observed an individual *C. carpi* burrow into the shallow sand on the sunward slope of a gannabush (*Salsola* sp.) sand mound near the mouth of the Unjab River. At this time there was a brisk wind and the air temperature was 23°C. A thermistor probe inserted into the sand beside this beetle measured 41.8°C. The beetle emerged 22½ min later, traveled about a few minutes, then dug deep into the sand of the gannabush mound to spend the night. This is one of the few

situations where it is possible to share sensory empathy with an insect; when shallow burrowing behavior prevails, thermal conditions are ideal for barefoot travel on the desert or for lying naked in the warm sand.

On December 10, 1968, an entirely different activity pattern prevailed (Fig. 4). Soil surface temperatures barely exceeded the proposed tolerance levels and solar radiation was weaker. Activity began late in the morning and continued to increase throughout the day, reaching a maximum in the late afternoon when ambient and soil surface temperatures were near their peak for that date. On this date midday weather conditions were low enough to be compatible with activity, contrasting with the previous day. On the following day, December 11, there were higher surface and air temperatures than on either of the two previous dates and there was little cloud cover to break the full force of solar radiation. During most of the day there was little activity, and no active individuals were noted in the forenoon. Activity commenced in the midafternoon when "ambient" temperatures were near their maxima. Actually, soil surface temperatures and ambient air temperatures in the *Cardiosis* environment were plummeting at this time (Fig. 3) 3 mm above the sand surface. On all three dates the level of surface activity reached 50% when the sand surface temperature dropped to about 42°C. On the basis of comparisons with other maxithermic tenebrionid beetles (Hamilton, *unpublished*), it seems probable that body temperatures were at approximately 38°C at this time and began to decline from this level later in the day. All of the diurnal Namib Desert Zophosinae investigated by me seem to be maxitherms, and the thermoregulatory behavior and activity patterns of the *Cardiosis* species I studied suggest that the members of this genus are no exception.

The results of these observations of activity during

consecutive days of variable thermal conditions allow an explanation of the discrepancy between the responses of *C. fairmairei* (and *C. hamiltonuli*) under natural but confined conditions (Fig. 5) and under completely natural conditions (Fig. 7) on the same date. In the enclosures the cafeteria of available environments is less diverse and the potential for behavioral thermoregulation is more limited. Thus constrained *Cardiosis* have little opportunity to seek favorable thermal environments. They can (i) move into the shade of the rim of the enclosure, (ii) rise up on their legs to escape the full effect of the sand surface, or (iii) burrow into the sand to reach more favorable thermal conditions. By comparison, in nature they are able to (i) move from one environment to another, (ii) traverse substrates of different temperatures, (iii) range into and out of the lee slope of the dune according to prevailing wind conditions, and (iv) expose themselves to the sun or shade of the dune crests. Sand surface temperatures may range from excessively warm to well below preferred levels. In addition, all the responses available to the constrained population are also available to the free-ranging individuals. The more intensive action of the free-ranging population early in the morning is probably due to the fact that most individuals burrow into the east-facing slipface sands which are oriented toward the early morning sun. This environment warms more rapidly than the flat surface sands within the enclosures.

Depression of activity in the natural population at midday on February 1, 1968, suggests that even with the thermoregulatory options described above, conditions at midday may exceed the thermal tolerance of *C. fairmairei* for prolonged intervals. On other cooler or windier days peak activity occurs at or near midday.

Thus, the following observations are compatible with the central hypothesis that the daily cycle of *Cardiosis* is largely facultative and is a response to ambient conditions which permit maximum tolerable body temperatures to be sustained for a maximum interval:

1) The pattern of activity may be significantly different in individuals exposed to different thermal conditions at the same locality on the same date.

2) Maximum activity levels are reached in constrained and natural populations when thermal conditions are compatible with the maintenance of body temperatures near 40°C.

3) Individuals dig into the sand when surface temperatures exceed the conditions stated in (1), above.

4) Individuals do not appear or remain on the surface when ambient conditions are such that significantly lower (less than 35°C) body temperatures would result.

5) Comparison with other diurnal Namib Desert tenebrionid beetles (Hamilton, *unpublished*) suggests that the body temperature of these beetles during periods of peak activity is near 40°C.

6) The activity patterns are not correlated with humidity, suggesting that some factor, here identified as an optimum body temperature, is more important to these desert insects than minimizing water loss.

Morphological adaptations

In his discussion of the systematic position of *Cardiosis hamiltonuli*, Koch (1969) recognized three intrageneric groupings: (i) *C. moufleti* and *C. carpi*, (ii) *C. fairmairei*, *C. triangulifera*, and *C. eremita*, and (iii) *C. hamiltonuli*. He set aside *C. hamiltonuli* as unique because of several distinctive morphological characteristics which he related to a possible evolutionary shift from the diurnal Zophosina (a tribe of the Zophosinae) to the nocturnal Dactylocalcarina. The relevant characteristics are (i) depigmentation and weak sclerotization of the cuticle, (ii) reduction in eye size, (iii) weakly developed supra-orbital structures, and (iv) spinose armatures on the legs and other body parts. In addition to these characteristics, *C. hamiltonuli* has a number of unique anatomical characteristics which are found in all other *Cardiosis* species as well as all of several hundred species of zophosine beetles belonging to 10 genera. Thus, any consideration of *C. hamiltonuli* as a primitive form must be put aside and its unique characteristics must be considered in terms of positive adaptations.

The field observations reported here show that *C. hamiltonuli* is strictly diurnal in its activity (e.g., Fig. 4, Fig. 5). The time interval for observations on Fig. 4 and Fig. 5 extends only from 0600 to 1900, but observations were continued on a 24-hr basis on all of the dates indicated in these tables, with negative results for activity at night. Thus the unique morphological characteristics of *C. hamiltonuli* noted by Koch cannot be related to nocturnal tendencies, and alternative interpretations of these characteristics are implicated. Based upon the preceding discussion of the thermoregulatory biology of this species, it seems probable that *C. hamiltonuli* is restricted to an environment that imposes restraints on the potential duration of activity, reducing the need for a highly sclerotized cuticle. *Cardiosis hamiltonuli* also lives in an environment where moister subsands prevail. Thus, while the sympatric *C. fairmairei* spends its inactive intervals in dry shifting sands exposed to strong drying winds, *C. hamiltonuli* lives in a region that supports a limited vegetative growth, notably the distinctive *Monsonia ignorata* (Geraniaceae).

The functional significance of the reduced eye size is not apparent, but it could be related to the fact that *C. hamiltonuli* is highly camouflaged and may depend upon crypsis rather than flight to minimize predation. Further conclusions in this regard will depend to a considerable extent upon direct field observations of the behavior of this species. So far attempts to make such observations have proved unsuccessful.

Habitat utilization

The data concerning habitat preference summarized in Table 1 represent the first detailed comparison of the habitat relationships of any of the remarkably diverse Namib Desert Tenebrionidae. There are two main conclusions to be drawn from these observations. The most secure is that there are differences among the several *Cardiosis* species in their preference for physical environments. This is somewhat surprising when one considers the facts that (i) all members of this genus are highly modified in terms of morphology, suggesting that they are specialized in adaptation to a narrow and specific environment, and (ii) with one exception these are allopatric species inhabiting and restricted to different physical environments adjacent to and therefore accessible to the physical environments occupied by allopatric species. These comparisons are based largely on the physical characteristics of environments and are feasible and relevant in the case of *Cardiosis* because many of the environments are nearly or entirely vegetationless. Therefore a comparison of the environmental preferences of sand-dune-dwelling animals can be more precise than an analysis of vegetated environments. The physical features of sand dune environments are the result of wind and sand, and as a result approximately the same physiognomic environment is replicated in blown-sand environments, desert or otherwise, throughout the world.

Thus, the fact that *C. carpi* and *C. moufleti*, allopatric northern Namib species, barely overlap in their choice of habitats (Table 1) requires explanation. Two categories of explanation are available. One is that features of the physical environment other than those so far considered here are significant to members of this genus. It is not apparent what these hypothetical factors might be. The effect of climatic variables—heat, humidity, and insulation—seem effectively ruled out by the data presented here, which demonstrate that the daily cycle of climate can be utilized in a variety of ways depending upon ambient conditions. Thus, the interior populations of *C. fairmairei* living in a much hotter macroclimate than *C. moufleti* and *C. carpi* are actually active under ambient conditions which approximate those of the species which are living in the mediterranean climate of the coastal bench. If the maxithermy hypothesis

is confirmed, as I conclude it is by the data presented elsewhere (Hamilton, *unpublished* and *in press*), and if *Cardiosis* is a maxitherm, as I feel I have established with the data presented here, then *Cardiosis* can find thermally optimal conditions anywhere that environmental parameters affecting body temperatures reach and exceed a critical threshold level during a day. This critical threshold level is surpassed daily throughout all Namib Desert environments.

A second explanation of the interspecific variation in habitat choice is that it may be attributed to competition with other species of tenebrionids (or other insects or animals) which have not successfully penetrated the specific environments in certain parts of the desert. The matter of extrageneric competition seems plausible, and beetles occupying the *Cardiosis* dune crest niche in the regions where *C. moufleti* occur seem to be present. I favor this hypothesis and it will be the subject of further studies in the Namib Desert.

The second, more tentative, general conclusion to be drawn from the interspecific habitat preference comparisons of Table 1 is that interspecific interactions within the genus *Cardiosis* have resulted in the narrowing of habitat preference in the southern Namib, presumably as a result of interspecific competition. This conclusion must be considered preliminary since there is only one example of sympatry, that of *C. fairmairei* and *C. hamiltonuli*. Where these species come together they barely overlap in space (Fig. 7), but are in direct overlap in terms of periodicity of activity. The breadth of environments penetrated by these sympatric species is narrower than any of the other *Cardiosis* species, suggesting a greater degree of ecological specialization than is the case in the central and northern Namib, where evidence (Koch 1969) suggests that *C. hamiltonuli* is morphologically the most highly specialized member of the genus. Its cryptic habits and color pattern are a further indication of its divergence from the typical *Cardiosis* adaptive zone. Animals restricted to narrow environments are preadapted to the development of specialized morphocrytic adaptations (Hamilton, *in press*). *Cardiosis fairmairei* also shows indications of divergence and specialization. Its center of abundance is on the dune crests, while the distribution of other dune-crest-inhabiting *Cardiosis* species (*C. moufleti* and *C. triangulifera*) scatters across the dune crests to include other environments as well. Thus the evidence for competition and morphological and behavioral divergence in response to it seems reasonably well established in the case of the sympatric *C. fairmairei* and *C. hamiltonuli*.

This conclusion concerning ecological differentiation leads to a potential explanation of the unique Namib Desert Tenebrionidae confined to the vegeta-

tionless regions of sand dunes (Koch 1961, 1962). As far as is known this environment has not been penetrated anywhere in the world by tenebrionid species to the extent that they are restricted to it. The only dunes-dwelling tenebrionids in other deserts—the Madagascar dunes (Koch 1961); the Gobi (Koch, *personal communication*); Sahara (Koch, in Somalia, 1961; Hamilton in Egypt, personal observations); Sonora (personal observations); and Kalahari (personal observations)—extend into adjacent environments. Furthermore these dunes-dwellers in other deserts tend to be more abundant in the adjacent vegetated environments (personal observations in the Sahara, Kalahari, and Sonora Deserts). The data on ecological differentiation of *Cardiosis* provided here suggest that the degree of specialization exemplified by *C. fairmairei,* and also shared by numerous other Namib species belonging to three separate subfamilies (Adesmiini, Eurychorini, Zophosini), may be correlated with and possibly be the result of the extraordinary diversification of the Namib tenebrionid fauna (Koch 1961, 1962). This in no way suffices, however, to explain how the Namib Desert developed its exceptional species diversity in the first place. Consideration of numerous hypotheses dealing with the origins of species diversity is well beyond the purview of this paper.

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