MADOQUA, VOL. 15, NO. 3, 1987 (217—228)

Reproductive behaviour of the Giant Cricket *Brachytrupes membranaceus* (Drury) in the Namib

by

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ABSTRACT

The reproductive behaviour of the giant cricket *Brachytrupes membranaceus* (Drury) was investigated at Gobabeb in the Namib Desert. Reproduction takes place from January to March. During this period the male never leaves its hole; it digs a 'singing chamber' at the burrow entrance, where it produces an ear-piercing song to attract females. After mating, the male seals the female in an isolated branch at the end of the burrow; and then calls other females.

CONTENTS

1 INTRODUCTION

The giant cricket *Brachytrupes membranaceus* (Drury) (Fig. 1) is widespread in Africa, south of the Sahara (Chopard, 1968; McE. Kevan, 1962; Roy, 1971), and has been recorded from the Hoggar (Chopard, 1941) to South Africa (Smit, 1964).

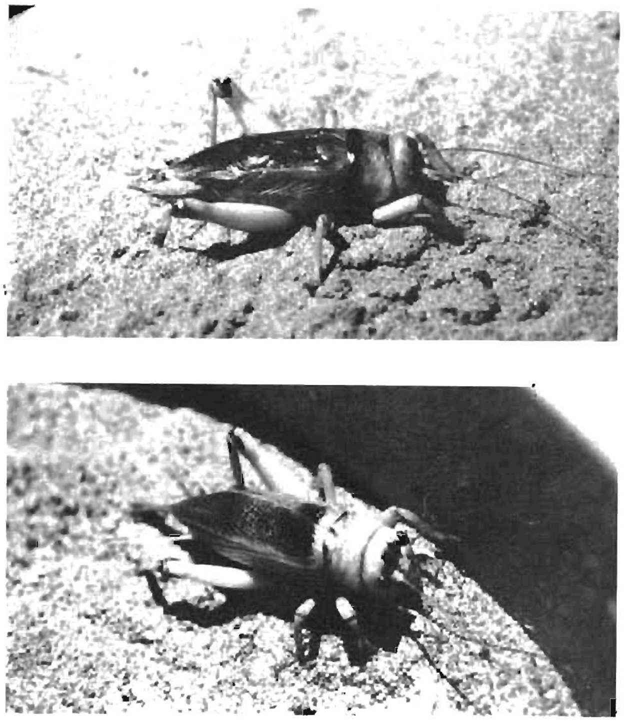

FIGURE 1: Specimens of *Brachytrupes membranaceus* (Drury). Notice the different structure of the tegmina in male (above) and in female (below).

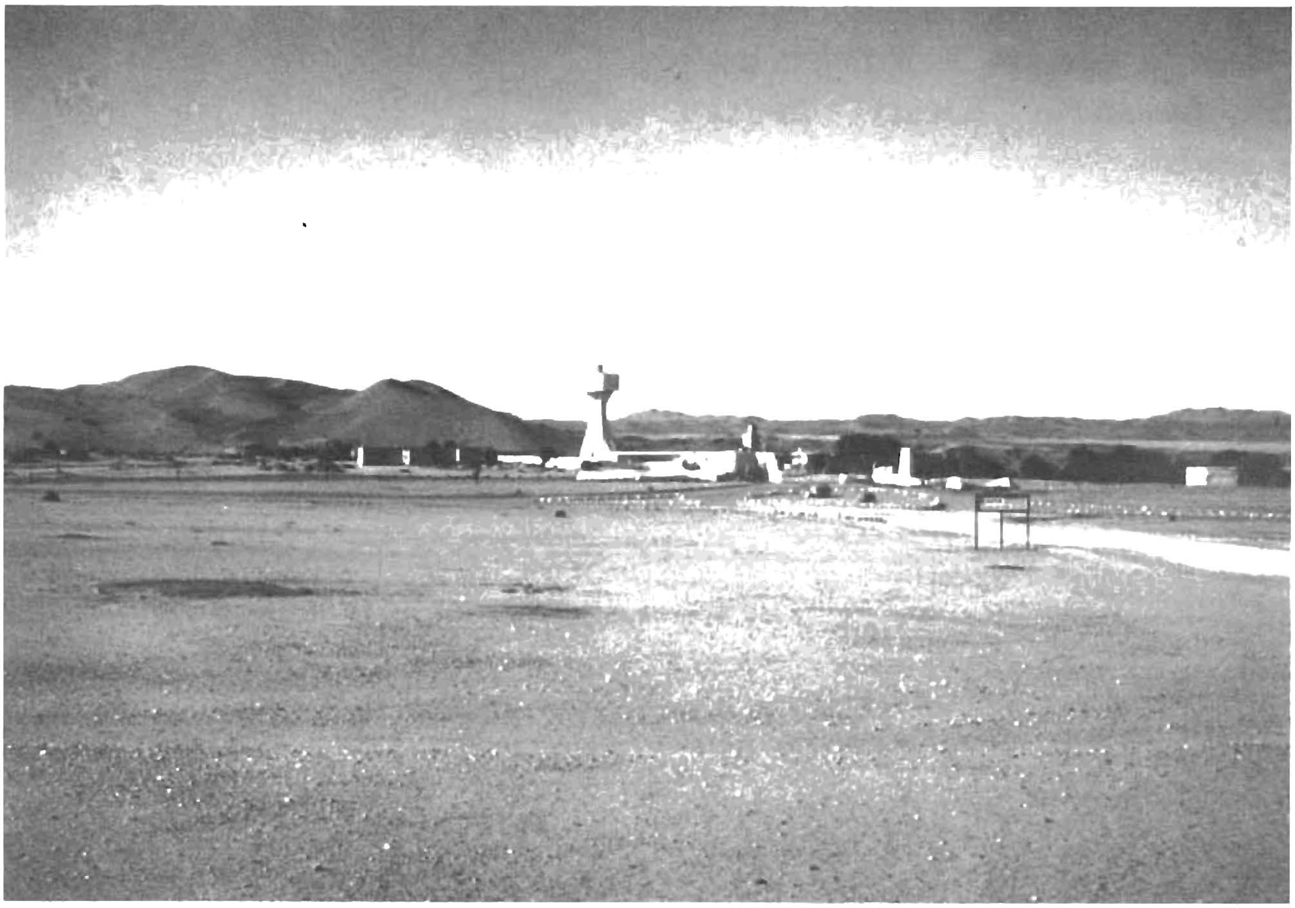

FIGURE 2: View of Namib Research Institute (Gobabeb).

FIGURE 3: Part of the area of the N.R.I. where this research has been carried out.

It is well known, particularly in agricultural areas where it is considered a pest (Bunzli and Buttiker, 1955, 1956; Robertson, 1967). In some areas, like Angola, it is part of the nourishment and folk-lore of the natives (Chopard, 1961). It is one of the most notable African field crickets (Rentz, 1968) because of its piercing call, which can be heard at a great distance. Most common in sandy areas, it excavates holes in which it stays during the day (Smit, op. cit.)

Buttiker and Bunzli (1959) described in detail, the biology of *B. membranaceus* in Zimbabwe. In December and January the neo-adults remain inactive beneath the soil surface, and at the end of the wet season they reproduce. Having only one generation a year, the adults die between February and April, that is, at the end of their reproductive season. The post-embryonic development takes place between March and October, and ends in November at the beginning of the rainy season.

Little work has been carried out dealing with the reproductive biology of *B. membranaceus.* We therefore examined the reproductive behaviour of the population living in the Namib Desert (SWA) near the Research Institute at Gobabeb (Figs. 2 and 3).

2 MATERIALS AND METHODS

The gardens of the Namib Research Institute were used as a study area from the end of January to the end of March 1983. Holes of male *B. membranaceus* were located after the first stridulations were heard. Gas lamps were used thereafter to facilitate nocturnal observation. Stridulation was recorded using a tape-recorder Superscope CD-330 with a unidirectional microphone Pioneer DM-31. Meteorological data were obtained from the First Order weather station at Gobabeb while comparative temperature measurements in four habitat types were obtained by using a digital thermometer, Salmoiraghi mod. 201. Temperature, humidity and wind speed 10 cm above the surface and temperature on the soil surface and at a depth of 10 cm were recorded near the burrow. Instrumentation included an hygrometer, Harma Instrument H18064, and an anemometer, Casella G5196.

Laboratoy observations were carried out using glass terraria filled with sand and covered with black paper on four sides.

3 LOCALITY AND STRUCTURE OF HOLES

The 16 burrows discovered were each occupied by a male and were located near or under vegetation.

Individual males of *B. membranaceus* remained in their holes during the entire reproductive period. Each burrow consisted of a tunnel (Fig. 4) 80-100 cm long, 2.5-3.0 cm in diameter and 50-70 cm deep. They did not run rectilinearly, and their cross sectional dimensions were nearly constant. The burrow cavities were separated from the outside by a sandy layer. The tunnels sloped gradually downward with an initial inclination of 35° - 45°. Deeper down the burrow was almost horizontal.

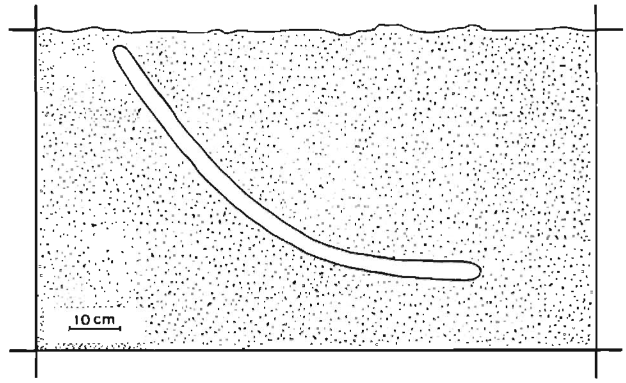

FIGURE 4: Schematic picture of male hole in the reproductive period.

In our field investigations we did not find the females' holes, but in the laboratory we found these no different from those of the males, both in their structure and manner of excavation.

4 BURROWING

The excavation of the hole, observed in the insectary, was carried out with the forelegs, head and mandibles. The very mobile head was used to shape the tunnel. The loosened soil was carried backwards by the mandibles with the forelegs placed close to the head. The 2nd and 3rd pairs of legs supported the body while the mandibles penetrated the substratum, but occasionally the hind legs, thrusting powerfully backwards, were used to kick the sand away. When the tunnel was large enough to house the entire animal, the cricket backed out and, when clear of the tunnel, turned around and reversed back into the hole.

Shortly thereafter, walking on four legs, the insect reappeared, pushing the sand from the burrow with its head and forelegs used in unison. Finally, with a sweeping action of the head, it removed the excavated sand lying near the tunnel. When the tunnel was deep enough, a little remaining sand was heaped near the entrance of the hole, obscuring the entrance and indicating the presence of a hole.

5 STRIDULATORY BEHAVIOUR OF MALES

At sunset the male opened a passage through the sandy layer that blocked the entrance to the tunnel (Fig.

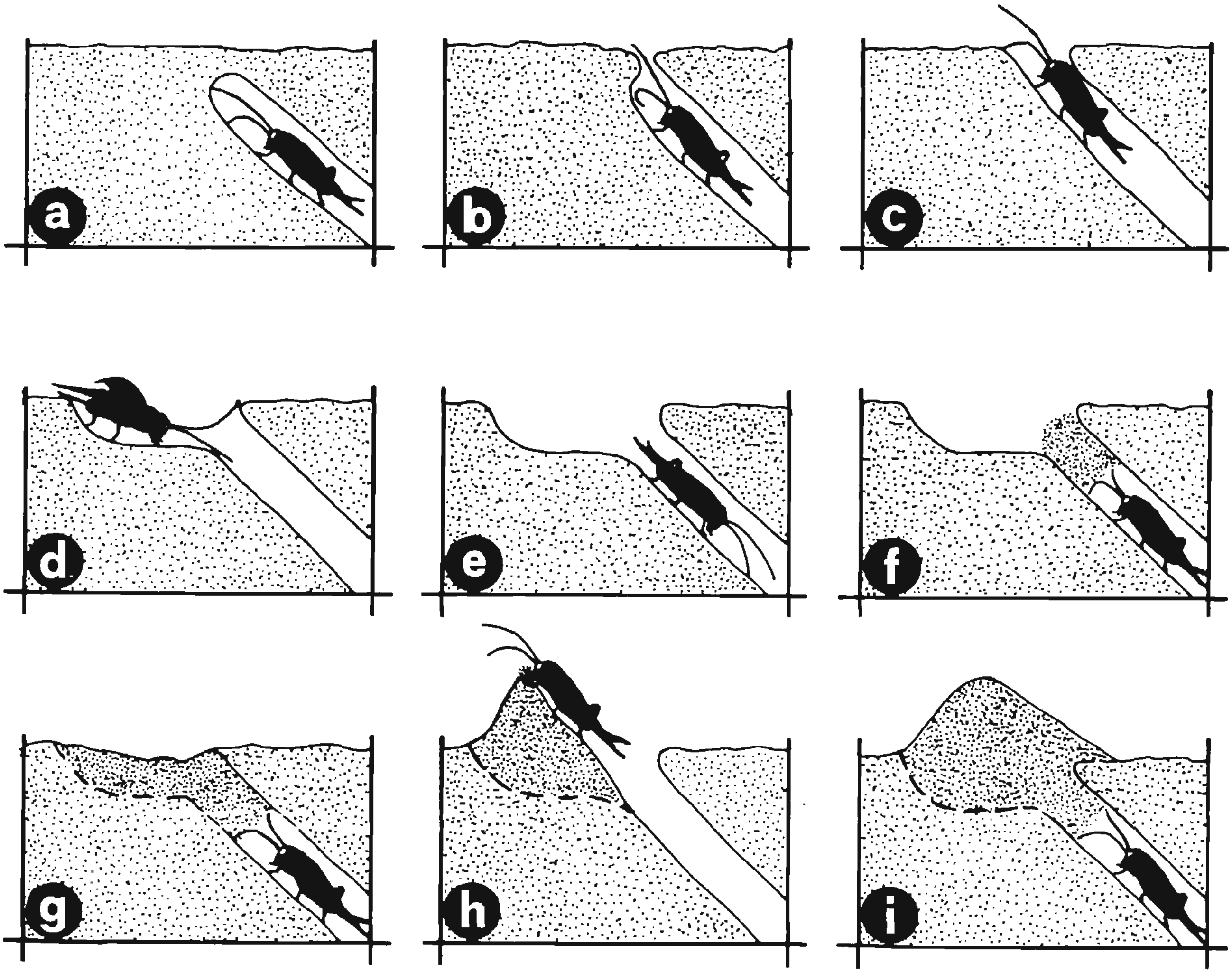

FIGURE 5: Activity phases of the male cricket in the reproductive period. (a) The male reaches the superficial sandy layer; (b) at sunset it makes a breach; (c) it widens the hole entrance; (d) after "open sky chamber" digging, it sings to attract females (e) if frightened, it quickly returns inside the hole for a while; (f) if no females arrive, it closes the hole entrance with a sandy plug and stops its night activity; (g) later on the chamber can be closed with sand: at the following sunset the male repeats the same behavioural sequence from a to d; (h) after a female has been attracted the male bulldozes sand outside, at the end of its night activity; (i) a sandy mound covers the tunnel exit.

5a,b). After a while, it then widened the opening (Fig. 5c) using its mandibles to remove the sand from the hole without emerging from the hole. After an interval, the male appeared and, using its mandibles, excavated a shallow depression (Fig. 6) near the tunnel opening. The male pushed the sand from this excavation into the tunnel as described above, while retreating into the hole. The depression was then smoothed over. On completion this depression had a semi-oval shape (Fig. 7), with horizontal dimensions of 6-8cm by 3-5cm, and a depth of 2-3cm; the longer horizontal axis was aligned with the tunnel entrance. The size and shape of this depression differed depending on the characteristics of the substratum (e.g. soil consistency, presence of rocky components or other objects). The depressions were generally orientated towards W-NW (Fig. 8).

FIGURE 6: "Open sky chamber" in the field.

After completion of the depression, the cricket eventually reversed into the tunnel where it remained for a while, leaving only its antennae visible. Then it came out and, remaining in the depression turned around 180° and, moving backwards a little, began its ear-piercing stridulation (Fig. 5d).

The first stridulating male was recorded at Gobabeb in 1983 on 31 January and in 1984 on 18 January (M.K. Seely pers. comm.). As the reproductive period

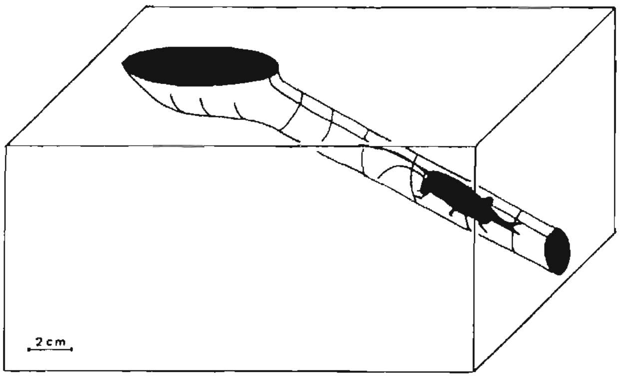

FIGURE 7: Schematic representation of a male hole with the "open sky chamber".

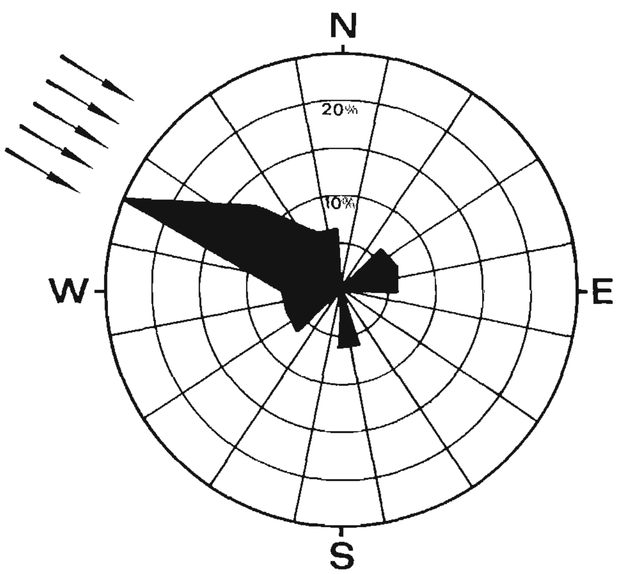

FIGURE 8: Per cent frequency polygon of the orientation of the male chamberhole entrances. The external arrows indicate mean wind direction from January to March: the angular coordinate of the mean vector - calculated by us according to Batschelet (1965) on data from Seely and Stuart (1976) - is 301°.

progressed, the number of stridulating males increased. During February and March, we recorded a maximum of 7 singing males at any one time. Generally the first stridulations were of short duration (e.g. 1.5 minutes) while later in the central phase they lasted for over two hours. During stridulation there were breaks from one second up to 20 minutes, while each sound emitted lasted from a few seconds up to 35 minutes. When disturbed during stridulation the crickets quickly retreated into their holes (Fig. 5e). The last stridulation was recorded on March 14th (M.K. Seely pers. comm.).

The apparent aim of the stridulation was to stimulate females' phonotaxis. If after 1 or 2 hours no females responded, the male returned into the tunnel, closing it with sand, using its head and forelegs, the cricket built a sandy plug at the entrance of the hole (Fig. 5f) which was removed the following sunset, when the behavioural sequence described was repeated. If the chamber was damaged or littered with debris or sand carried by wind (Fig. 5g), it was rebuilt with great accuracy.

Meteorological observations during a period of three days (Fig. 9) showed that the beginning of surface activity — that is, the opening of the hole — coincided approximately with sunset, when the air temperature decreased and tended to be the same as the soil temperature. Stridulation took place only if there was little or no difference between soil and air temperature (Fig. 10). Wind was an important limiting factor in stridulating; the sudden advent of wind, regardless of whether the preliminary behaviour had been concluded, prevented stridulation.

6 BEHAVIOUR OF FEMALES

Observations in the terraria revealed that females opened their shelters at roughly the same time as males and remained inside their holes near the sand surface. They left their holes and guided by the stridulation, flew or walked to the males' hole.

7 MEETING OF SEXES

When a female arrived near the hole of a male the latter stopped singing and, having moved into the tunnel, was followed by the female, where mating took place. After 15-50 minutes the male came out and began stridulating to attract other females.

8 HOLE CLOSING

If singing did not attract a female, the behaviour of the male changed. After the last song, the male stayed inside the hole for up to 45 minutes, after which it reappeared and pushed the sand beyond the edge of the depression using its head and forelegs. Here it stopped and scattered the sand over a great distance, afterwards backing into the tunnel. This activity continued intermittently throughout the night (Fig. 9c). 2

The excavated sand was distributed as an amphitheatre around the entrance of the hole (Fig. 11); the external slope was steeper than the internal. The cricket, climbing the inner slope, carried soil up to the top, and pushed it down (Fig. 5h). At sunrise *B. membranaceus* closed its hole thoroughly (Fig. 12), leaving only a sandy mound 12-13cm high with diameter at the base of 25cm. (Fig. 5i). On one occasion we observed a male which, ceasing its digging at sunrise, closed the entrance of the hole and resumed its normal behaviour the following night. The male came out of new opening near the sandy mound, oriented in a new

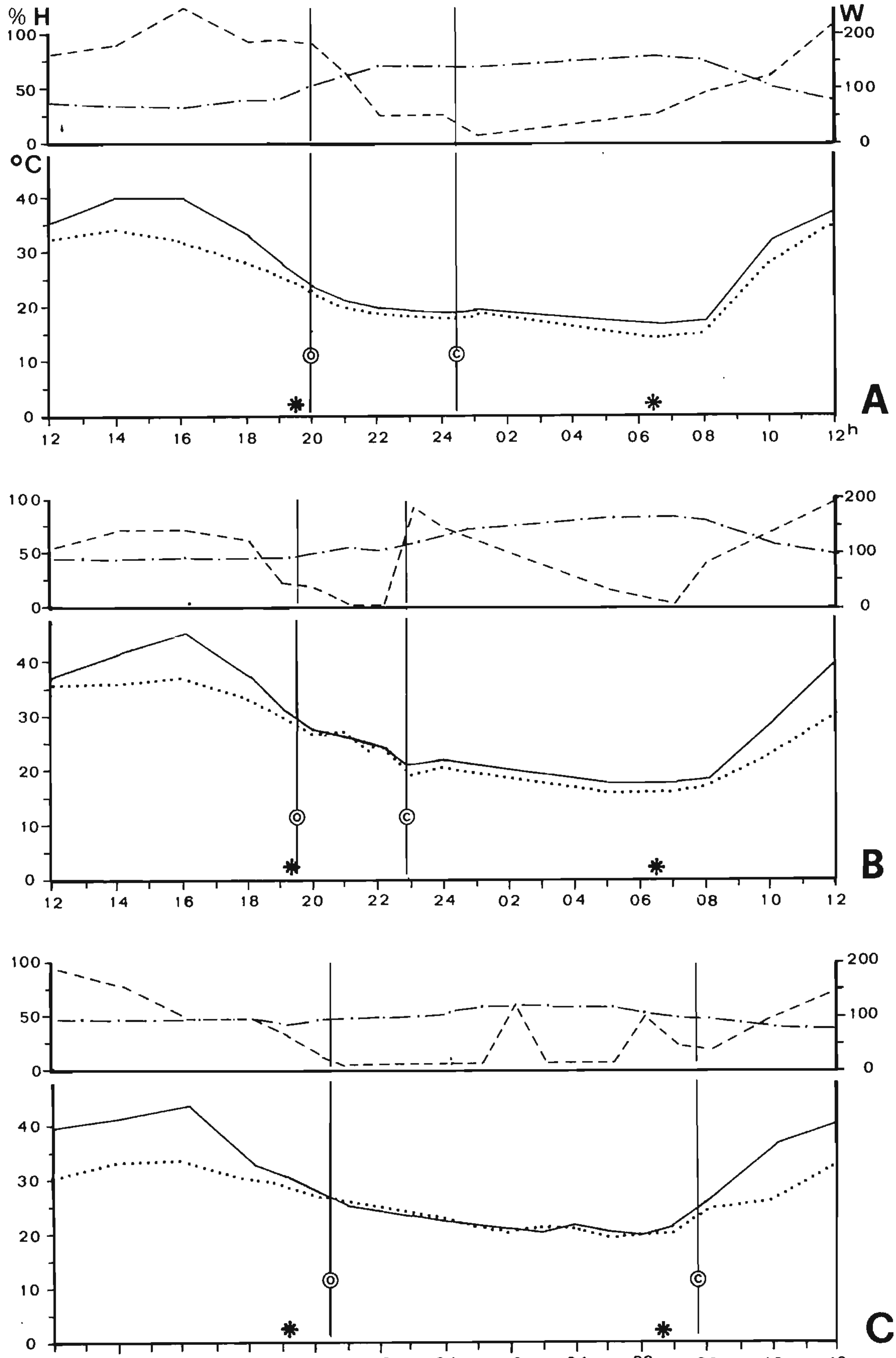

FIGURE 9: Climatic paramters near a male hole recorded on February 16th (A) 17th (B) and 18th (C). Abscissa: hours, SA standard time. Ordinate: % humidity and °C on the left, wind speed in m/min on the right. Dashed line: wind speed; dotted and dashed line: humidity; continuous line; soil surface temperature; dotted line: atmospheric temperature. The inner vertical lines indicate the opening (o) and the closing (c) of the hole. Asterisks indicate sunset and sunrise.

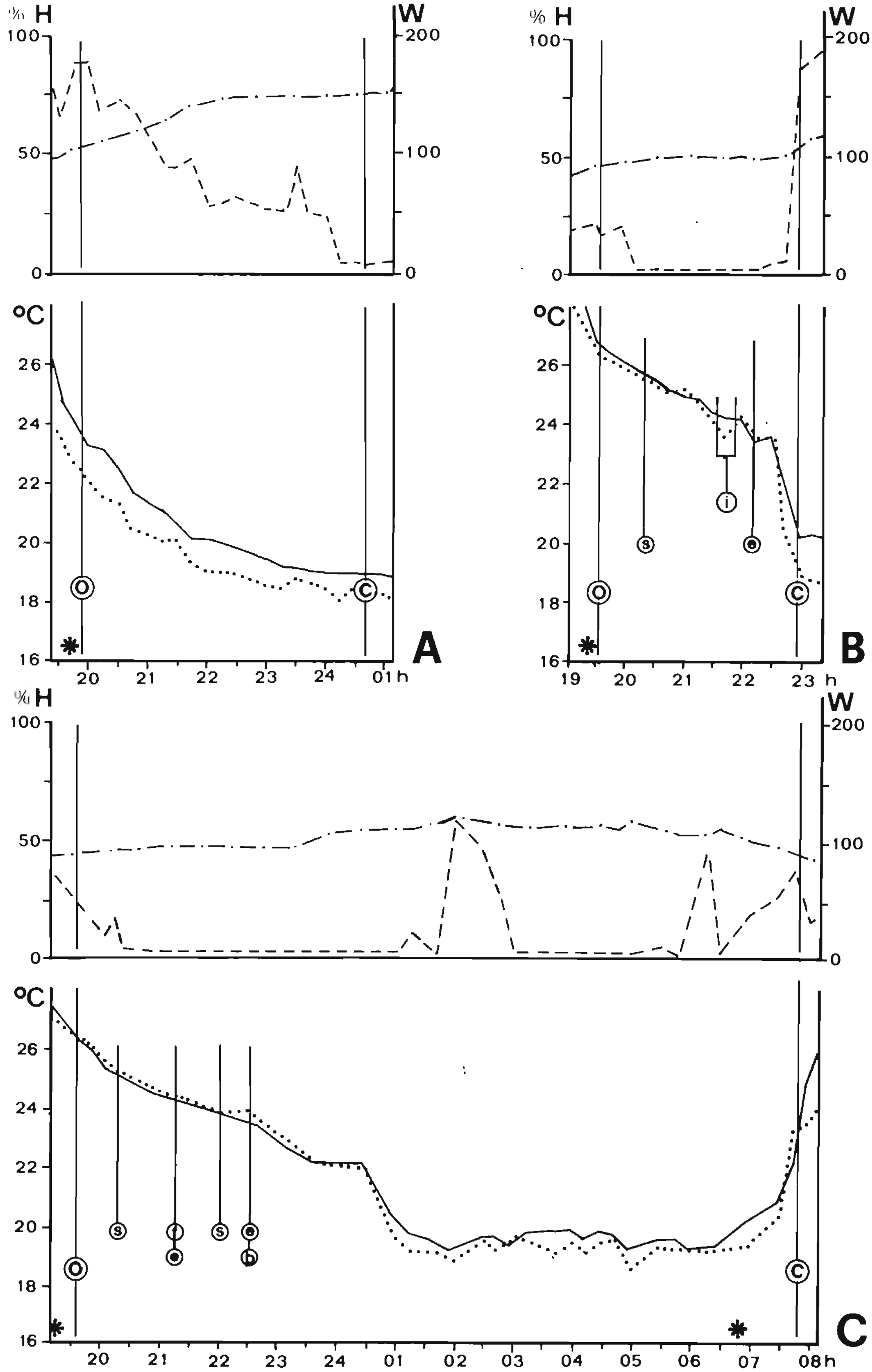

FIGURE 10: Influence of climatic conditions on external activity of one cricket (details of Fig. 9, with recordings every 15 minutes). In the first day (A) it does not sing, in the second (B) it sings and in the last one (C) it sings, it receives one female and then bulldozes sand outside the hole, closing it with a sandy mound. Letters inside circles: opening (o) and closing (c) of the hole; starting (s) and ending (e) of stridulation activity; interruption of singing (i); female arrival (f); beginning of sand conveyance outside the hole (b). Asterisks as in Fig. 9.

FIGURE 11: Sand bulldozed outside the hole and heaped up as an amphitheatre aligned with the major axis of the chamber.

FIGURE 12: Sandy mound after hole closing with a plug at the entrance.

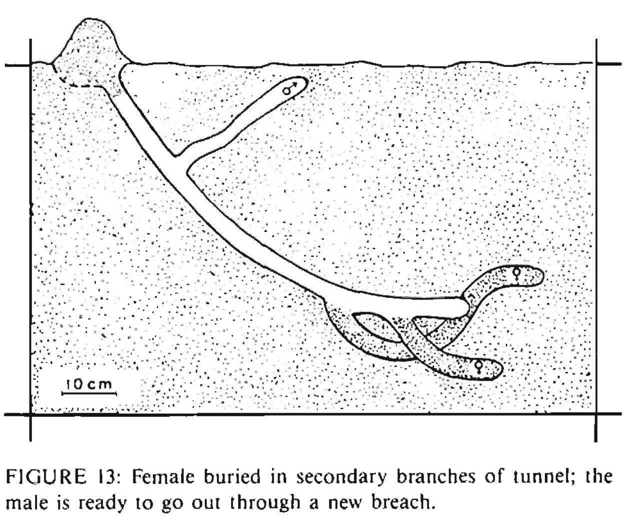

FIGURE 13: Female buried in secondary branches of tunnel; the male is ready to go out through a new breach.

direction (Fig. 14), proceeding once again to perform the behavioural sequence described.

The females remaining in the males' holes were sealed in secondary tunnels without a direct connection to the main tunnel (Fig. 13).

9 DISCUSSION

There are several interesting aspects in the behavioural biology of *Brachytrupes membranaceus.* The choice of a protected place where the cricket digs its hole represents a particularly important adaptation that enables them to survive under harsh conditions. The positioning of the holes suggest that they are not arbitrarily placed but occur where there are less marked thermal gradients, especially during the heat of the day (Fig. 15) and where there is moisture near vegetation, and also 2.

Polygamy as a reproductive strategy may be correlated with the characterists of the environment where the male lives. Wilson (1975) explains the relationship between hostile environment and multiple mating: if the male's location is rich in resources and also offers protection against both predators and inclement weather, the female, joining other females in the rich territory of a polygamous male, will increase its evolutionary fitness more than if it were the only partner of a monogamous male in a poor territory. This case of polygamy may be included in the Orians-Verner model (Orians, 1969).

The male closes the hole completely and shuts each female in a sand-filled branch of the main tunnel thus preventing easy location. We have seen *Gerbillurus paeba* (Smith) and *G. vallinus* (Thomas), two predatory rodents living in the Namib Desert (Holm and Scholtz, 1979), digging into the burrows. The presence of the male in the tunnel may reduce the probability of female predation: so fertilized eggs and species survival are enhanced.

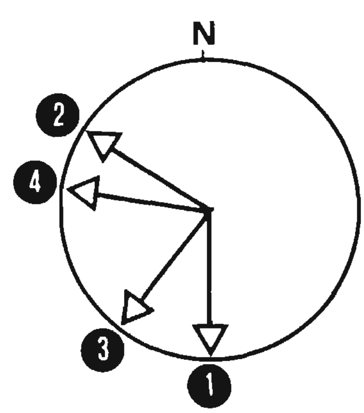

FIGURE 14: Different hole entrance of orientations made by the same cricket.

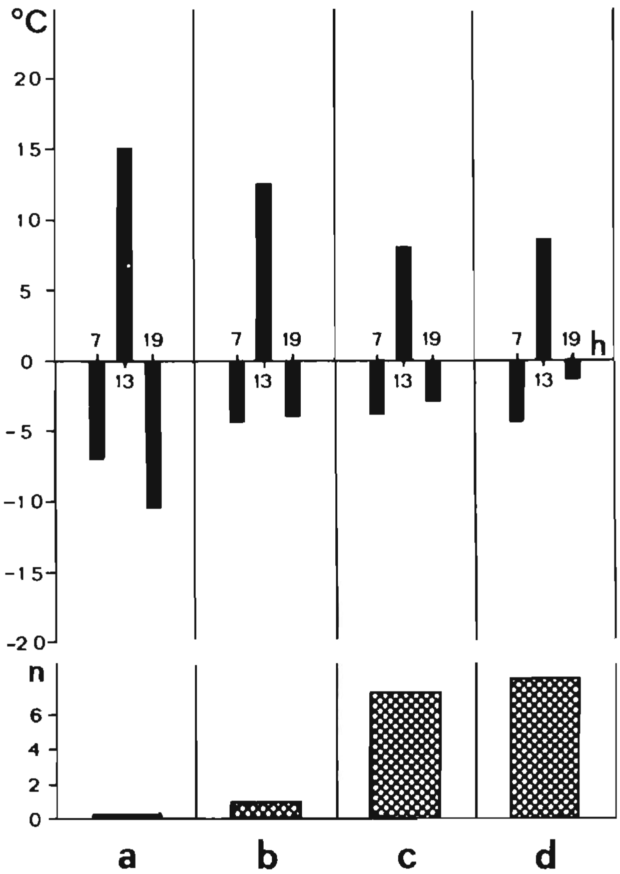

FIGURE 15: Temperature differences (postive or negative) between the soil on the surface and at 10 cm recorded on March 5th at 7h, 13h and 19h in four locations: (a) gravel plain; (b) sandy plain; (c) grass-covered soil; (d) under trees. Below the number (n) of male holes in the four environments.

The male never leaves its hole during the reproductive period; again in fact, individuals observed during eight consecutive days never left their holes seeking food. It also has been observed in *Brachytrupes megacephalus* (Lef.) (Caltabiano, Costa and Petralia, 1982) that reproductive and feeding periods are completely separate.

In *B. membranaceus* the locomotory patterns are particularly complex and specialized. This cricket is able to walk either on four or six legs, and to move either forwards or backwards. Different types of locomotion are involved in burrowing and in carrying sand. Furthermore, it is worth mentioning the important role of the mandibles both in excavation and removal of sand. *B. megacephalus* (Caltabiano, Costa and Petralia, op. cit). and *B. achatinus* Stoll. (Gosh, 1912), related sand dwelling crickets, also utilize their mandibles in digging.

The construction by the male cricket of an "open sky chamber" which has the function of directing and amplifying the sound emission is remarkable. It consists of a substratum modification for acoustic purposes that very few insects only those such as *Gryllotalpa vineae* B.-C. (Bennet-Clark, 1970) and *B. megacephalus* (Caltabiano, Costa and Petralia, op. cit.,) are able to build. The difference in orientation of the successive singing chambers, may have adaptive value; the meaning of this behaviour may be that of acoustic projection in another direction to increase the probability of attracting other females. In the short-tailed cricket *Anurogryllus celerinictus* the preponderance of north-facing entrance tunnels has a thermoregulatory function (Bell, 1979). In *B. membranaceus* a direct relation between the chamber-hole entrances and the direction of winds at Gobbeb (Seely and Stuart, 1976) has been pointed out (Fig. 8). The correspondence between the hole entrances and the direction from which the wind at Gobabeb blows is also suggested from their distributions in the four quadrants (Fig. 16). The chambers may act as "wind cones" able to track wind shifts. Even in birds there are examples of nest entrances oriented according to the wind direction (Ricklefs, 1976).

B. membranaceus is able to select the best climatic conditions for singing. Singing occurs when and as long as the atmospheric temperature is low enough to provide good sound-wave refraction on the ground: these conditions are essential (Michelsen and Noche, 1974) to obtain the maximum sound propagation and the best acoustic recall. The stridulation takes place when the wind falls (Fig. 10) and it ends in the night when temperature values decrease to daily absolute minimum.

We could not verify where mating took place. In *B. megacephalus* (Caltabiano, Costa and Petralia, op.

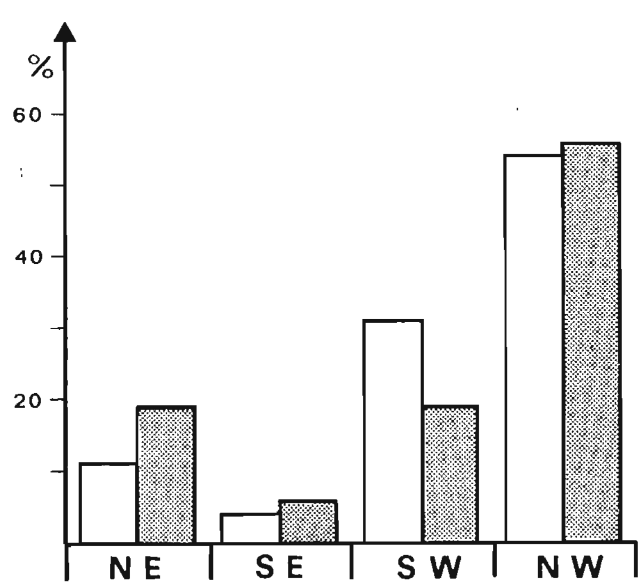

FIGURE 16: Histogram of wind directions (light columns) and chamber-hole entrance orientation (dark columns) in the four quadrants.

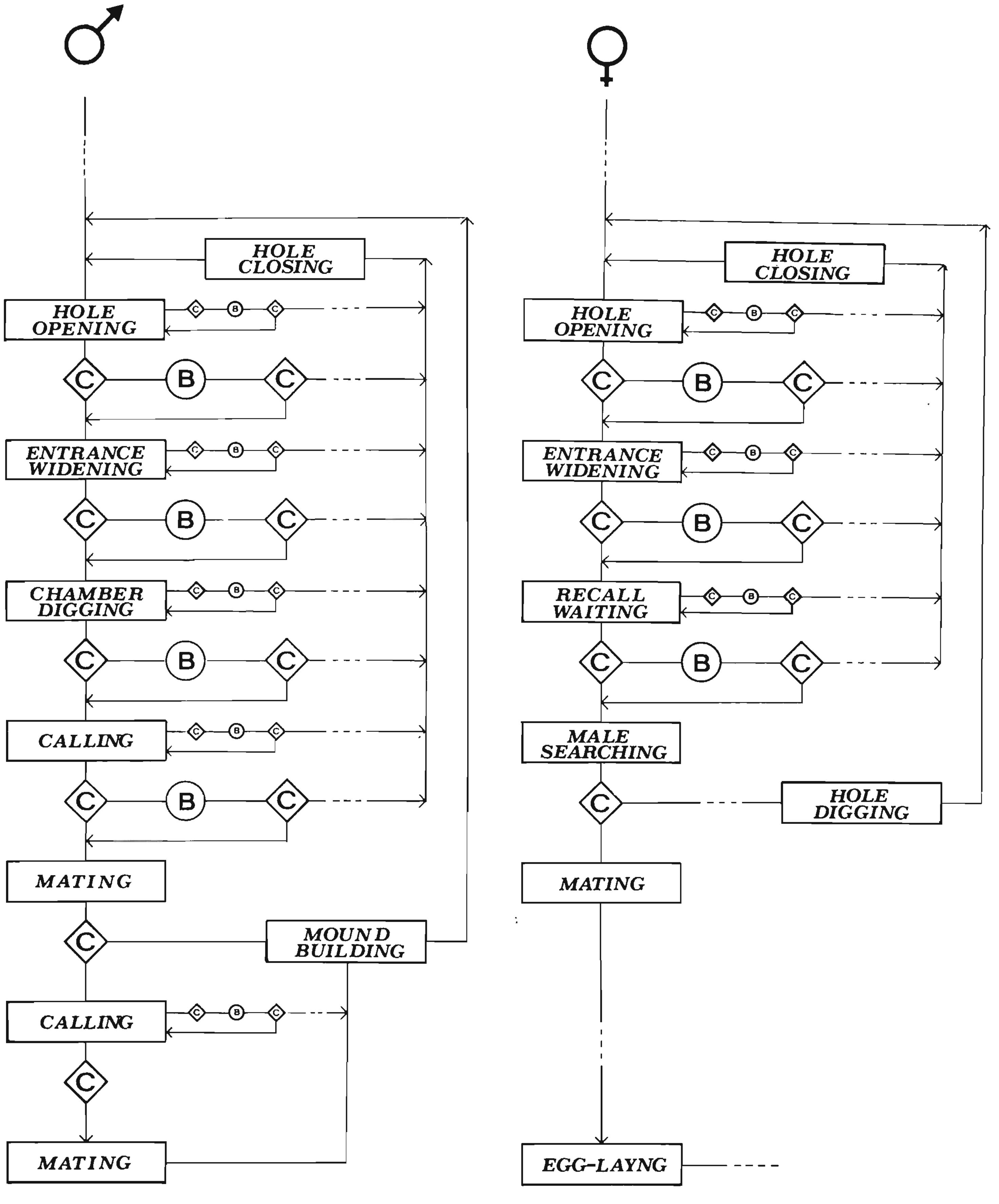

FIGURE 17: Ethogram of *Brachytrupes membranaceus* in the reproductive period. The main behavioural phases are indicated in the rectangles. Rhombs and circles symbolize environmental check (C) and break of activity (B) during each phase (smaller symbols) or between two successive phases (larger symbols).

cit.) the spermatophore removal, which is very rapid, represents the entire mating procedure and takes place immediately after the meeting of the partners. In *B. membranaceus* the situation may be similar.

We have no direct proof of the existence of multiple mating in *B. membranaceus,* but we do not exclude this possibility. The production of several spermatophores in a short time is found in other crickets such as *Gryllus domesticus* L. (Khalifa, 1949) and *Gryllus campestris* L. (Chopard, 1938).

The presence of several females indicates the existence of a type of sociality in *B. membranaceus,* even if limited to the reproductive stage. With *B. megacephalus* the maintenance of the couple for a certain time is suggested by the fact that, at the end of the reproductive period, the dead partners are found in the same hole (Caltabiano, Costa and Petralia, op. cit.)

10 CONCLUSIONS

B. membranaceus shows a high degree of behavioural complexity derived from adaptations to life in an arid environment. The observations made during the reproduction of *B. membranaceus* enabled us to reconstruct ethograms for both sexes (Fig. 17), although some points are as yet, hypothetical. In both cases the various activities related to reproduction followed one another with a continuous series of checks to verify environmental conditions, which allow male calls, mate-meeting and mating.

As indicated in the male ethogram there seems to be a decrease of external awareness after the female entered, and when the hole would be exposed to predators. However, the risk involved is small as the mating takes place rapidly and probably in the inner tunnel.

In the female pattern there was also a critical phase, when she left the hole looking for the male and was then more exposed to predators. Furthermore, we observed in the laboratory, that if the female did not find the male hole, she made a new shelter for herself. We never saw them return to their original holes.

Further research on the life cycle of this species is suggested. A comparative ethological analysis of the genus *Brachytrupes* may be of great interest to verify ethological convergences.

11 ACKNOWLEDGEMENTS

We express thanks to the Italian Research National Council (C.N.R.) for the research assignment, and to the University of Catania (Italy) as well as to the Research Center for Faunistic and Tropical Ecology (Florence, Italy), particularly to its director Prof. Leo Pardi, for their financial support.

We wish to acknowledge the Directorate of Nature Conservation and Recreational Resorts of South West Africa for permission to carry out our research in the Namib Desert and for numerous facilities. Our gratitude is also due to Dr. M.K. Seely, director of the Desert Ecological Research Unit, not only for her scientific advice about the Namib, but also for her help on many occassions. We also thank the DERU staff and the Nature Conservators at Gobabeb for their warm and friendly welcome.

We sincerely thank Prof. Marcello La Greca of the Institute of Animal Biology and Genetics of the University of Catania for the species identification and for his valuable advice and encouragement, and finally the Ethological Research Group of the same Institute, for their constant and essential collaboration from so far away.

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