The coexistence of *Onymacris rugatipennis* and *Physadesma globosa* in the Kuiseb River bed, Gobabeb.

PROJECT PROPOSAL: Dr. David Ward.

The large body of zoological theory dealing with the coexistence and competition between species has its origin attributed to Gause (1934), who proposed that no two species could coexist on the same resource. Competition theory has received a great deal of attention from zoologists, stemming largely from the work of Robert MacArthur. MacArthur & Levins (1964) took Gause's (1934) theory and expanded it and placed it in mathematical parlance in what is now known as the theory of limiting similarity. This theory led to numerous studies to examine niche positions and niche breadths of animals in an effort to determine how similar animals could afford to be without suffering interspecific competition. Following on from this, biogeographical theories (MacArthur & Wilson 1967) motivated investigations into community structure with respect to body size and species co-occurrence patterns. The community matrix approach (MacArthur & Levins 1964) has encouraged both direct (via removal experiments) and indirect (via census data) measures of species' interaction coefficients. More recently, theories of foraging behaviour (e.g. optimal foraging theory - Stephens & Krebs 1986) and their implications for community structure (e.g. Holt & Kotler 1987) have stimulated studies of patch use and habitat selection (Price & Waser 1985, Brown 1988). In desert animal communities, these latter theories have been extensively used, particularly in studies of rodent community structure (e.g. Abramsky 1988, Brown & Munger 1985, Kotler

1984; Ward, Abramsky & Rosenzweig in prep.).

I propose here to use a combination of techniques currently used in examination of patch use and habitat selection, along with direct behavioural observation, to determine the factors that permit the coexistence of *Onymacris rugatipennis* and *Physadesma globosa*. These beetles provide a unique opportunity to examine the role of competition and coexistence on community structure for the following reasons:

(a) The two beetle species occur in the same habitat at Gobabeb, and have the same food resource in apparent "defiance" of the predictions of community ecology theory.

(b) The community structure is extremely simple, with few other species present to provide confounding effects on interaction between the species being studied.

(c) Tenebrionid beetles are easy to watch on the substratum, and it is relatively simple to determine the effects of ambient temperature on their behaviour (Seely *et al.* 1988).

(c) The sexual size dimorphism in these two species is pronounced, providing an opportunity to study the effects of inter-sexual competition. This aspect of community ecology has been, thus far, neglected. Males, which are smaller than females, may suffer an ecological dilemma in times of competitive stress because in order to mate and ensure parentage they must remain with the females and suffer the effects of competition with the females for food.

The activity of ectothermic animals, such as tenebrionids, is closely tied to the prevailing ambient conditions. It will, therefore, be necessary to establish the thermal preferences of these species to determine how ambient temperature affects their activity patterns. A considerable amount of attention has been paid to the thermal biology of these animals, largely on account of their diurnal activity patterns and high preferred body temperatures in the extreme environment of the Namib desert (Edney 1971, Hamilton 1971, Louw & Hamilton 1972, Seely _et al._ 1988). However, there has been no attempt to establish the role of temperature preferences of tenebrionid beetles in a community-ecological context. Hamilton's (1975) "maxithermy" hypothesis proposes that the high preferred body temperatures of Namib tenebrionids are selected for to maintain maximum metabolic activity and thus optimize the performance of activities such as foraging. Seely _et al._ 1988 have examined this in detail and found that these beetles do indeed maintain extraordinarily high body temperatures. However, they have, I believe, not examined the crucial ecological part of this hypothesis; namely the correlation between high metabolic activity and food availability. If these beetles are indeed performing in response to an optimization process, they should prefer lower body temperatures when food is in short supply in order to reduce energy use. In the experimental protocol that follows I detail the procedure for establishing the changes in temperature preference with increased starvation. Once this is established in the laboratory, this may be used in conjunction with the activity data in the field to establish the effects of intra- and inter-specific competition on temperature preferences and its effect on the temporal pattern of activity of the beetles.

Experimental protocol:

The following experimental protocol was set up, with the approval of Dr. Seely, during a three-week stay at Gobabeb in February 1988.

TEMPERATURE PREFERENCES OF *O. rugatipennis* AND *Physadesma globosa* IN AN ARTIFICIAL GRADIENT.

Methods:-

Do experiment on 10 beetles of each sex for each species for the groups of both fed and unfed beetles. Fed beetles are fed *ad libitum* throughout the study period and unfed beetles are not fed at any stage. Unfed and fed beetles must be put into the gradient on the day they are removed from the field to ensure that they have the same temperature preferences as the fed beetles at the start of the experiment. As the unfed beetles become more and more starved they should choose progressively lower temperatures.

Use the circular temperature gradient available at Gobabeb. Ensure that the thermocouples (16 of them) are placed equidistant to one another around the entire gradient box, each taped to an aluminium strip that covers the width of the gradient box at the point that the thermocouple is attached. This ensures that the thermocouple reads the mean temperature across the hot and cold copper pipes (which create the gradient by water passing through them) at that point.

Use the computer-driven thermocouple-reading programme set up by Mr. Francois Malan at Gobabeb to give temperature readings automatically every five minutes.

Weigh all beetles before each experiment and measure their length. Put in one beetle at a time and wait until it settles. Record the temperature shown on the computer at that time for the thermocouple nearest to the beetle. If the beetle is between two thermocouples, record the average temperature.

Repeat this experiment twice a week for four weeks.

FEEDING ECOLOGY OF *P. globosa* AND *O. rugatipennis*.

Methods:

These experiments are based on the experimental protocols of sandtracking (Kotler 1984) and "seedtray experiments" (Brown 1988). These procedures have largely been performed in studies of patch use and habitat selection in desert rodents, but have also been successfully used in studies of ants and lizards (Abramsky & Rosenzweig in prep.). Sandtracking involves using the degree of activity of animals in a particular habitat (determined by the amount of activity in areas where the sand has been smoothed over prior to the experiment) as an indicator of habitat preference. The beetles of the different sexes and species differ in size and pattern of tracks they leave behind, facilitating simultaneous comparison of activities. "Seedtray experiments" involve using trays which contain sand that the beetles usually forage in and including a known amount of the beetles' food (*Acacia* flowers). The amount of food left in the trays subsequent to a feeding bout is known as the giving-up density (GUD). The lower the GUD in a particular micro-habitat, the higher is the animal's preference for the micro-habitat. By comparing changes in activity (using both sandtracking and seedtrays) through the day and under different levels of competition, the micro-habitat "rules" for coexistence can be established.

The details of these experiments are as follows:

1) Fence off 6 areas, each containing at least 2 trees. Each area should contain one `good' tree (where beetles are resident - of Crawford et al. in press) and one `poor' tree where beetles are transient. Choose pairs of trees that show the greatest difference in beetle nos. to include in each fenced-off area.

2) Mark all beetles and place all beetles - of one species only - (at max. natural density) in arenas as follows:- half the arenas with males only and the other half of the arenas with females only. Upon completion of this experiment (see below), put in equal numbers of each sex into all arenas. After these experiments are completed, put equal numbers of beetles of each species into each arena.

3) Clear sandtracking areas (0.5 X 0.5 m) in each arena using a rubber squeegee (hard rubber strip attached to a broom handle commonly used for clearing water away) as follows:- 3 areas in the open (away from canopy), 3 areas close to the tree stem and 3 areas at edge of subcanopy. Clear these areas at the beginning of the day and read tracks every 2 hours. After reading tracks, squeegee sand in preparation for the next reading 2 hours later. Each time tracks are read the number of beetles on the surface, their position (under canopy/in the open and whether they are under the `good' or `bad' tree) and each beetle's number should be recorded. Score each complete pass over the area (from one side to the opposite side) as 1, up to a maximum of 4. If the animal enters from one side and exits on theadjacent side, score a half. The maximum score is set at 4 because more passes over the area than that create an unreadable mess.

4) Put 5g of Acacia flowers (beetles' preferred food) in a `seedtray' mixed in well with sand (an approximately even layer 1 cm deep). Seedtrays should be 0.5 X 0.5 m by 1 cm deep. The seedtray should be sunk in the sand so that the lip is flush with the substratum. Place seedtrays as for sandtracking. At the end of each day, the flowers must be sieved out of the sand and weighed. If the amount of food eaten in a single day proves to be insignificant, extend the number of days that the trays are left out. In order to determine how many days are enough, approximately half the food eaten in the most preferred tray should be aimed at. The number of days that trays are lft out must be kept constant throughout all experiments. There must be sufficient flowers to ensure that the beetles will not eat all of it over any one experimental period (i.e. one must always weigh something after the experimental period is up).

5) Leave the beetles in the arenas for about a week before starting each experiment. Then do one day of sandtracking, followed by one day (or several days if very little food is eaten in just one day) of seedtrays - repeat 5X. Thereafter, remove half the animals from each arena and repeat the above. Then, remove half again and repeat. In arenas with both males and females, remove half the females each time, keeping the number of males constant. When experiments are conducted with both species in together (in equal numbers), remove half of the species that is naturally more abundant (P. globosa) each time, keeping the numbers of the other species constant. No seedtray experiments can be done here because you cant tell which species has eaten from the seedtray.

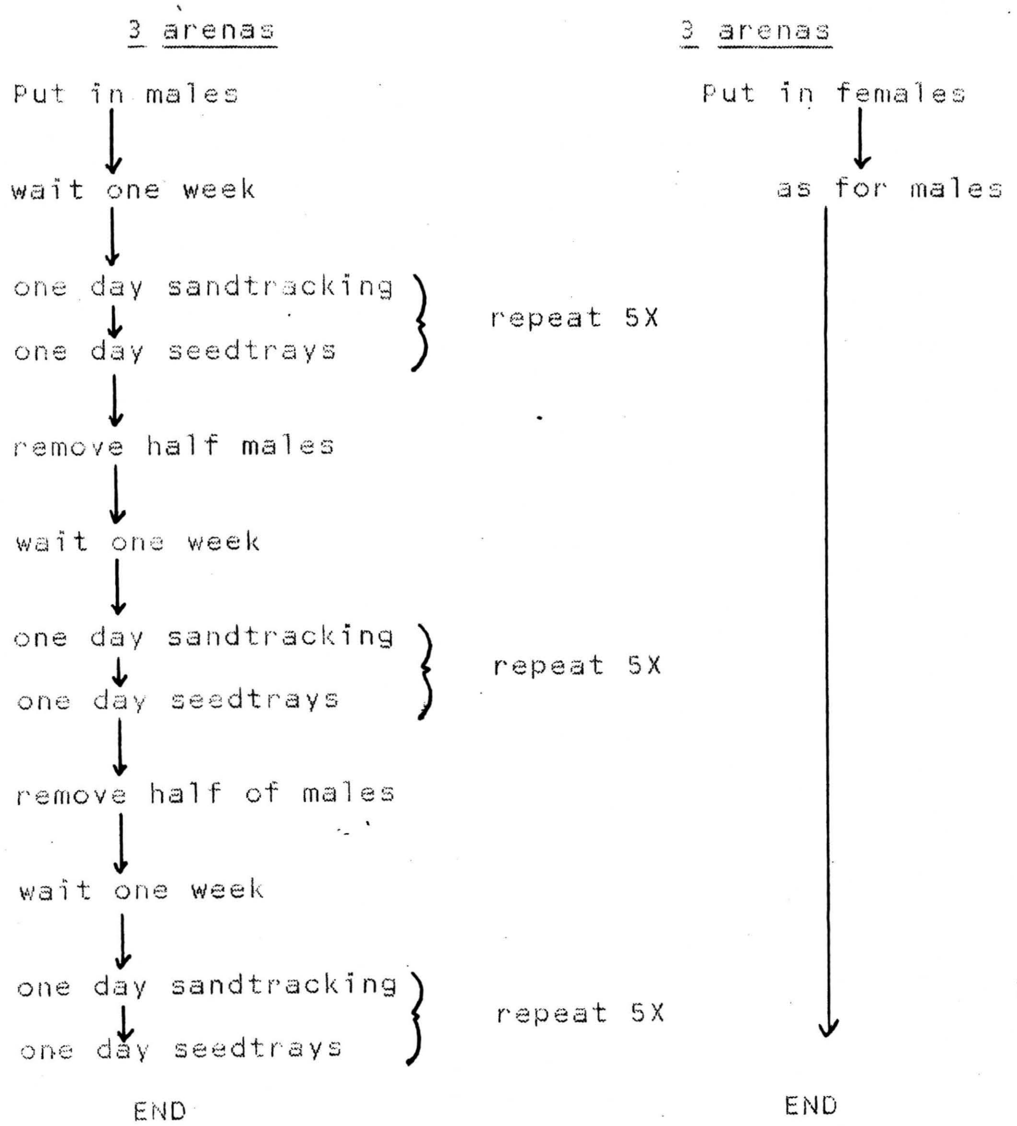
In addition:-

a) Six arenas with half males and half females (for each species), removing half the females each time. Experiments as for single sexes.

b) Six arenas with half P. globosa and half O. rugatipennis, each at maximum natural densities. Do no seedtrays here, only sandtracking. Remove half of the P. globosa each time after ten days of sandtracking, so that you are left with quarter of the original numbers of P. globosa at the end of the experiment.

SUMMARY

P. globosa/O. rugatipennis:-



Interpretation of the Results of the Field experiments:

1) Movements of individuals from one tree to another may occur when competition is strong or food availability low under a tree.

2) High activity in the sandtracking areas indicates preferences for specific areas. These preferences may vary temporally, e.g. beetles may prefer open areas where they can heat up early in the morning and then seek shade later in the day.

3) Low giving-up densities in the seedtrays indicates preferred feeding areas.

4) Competitive effects (intra- and inter-sexual and interspecific) will be shown by changes in preferences for different areas and by changes in levels of activity.

5) High activity (shown by sandtracking) and high giving-up densities in the seedtrays will show that feeding areas may be divorced from areas used for other activities.

These experiments will establish the preferences of these beetles for different parts of each habitat mosaic and the relative importance of intra- and intersexual competition, as well as the importance of interspecific competition on community structure in the Kuiseb riverbed. The results of these experiments of particular interest to the field of community ecology will be the effects of intra- and inter-sexual competition on inter-species relationships because these effects have hitherto been ignored owing to the difficulty in separating these effects from population-wide effects.

REFERENCES

BROWN, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* 22: 37 - 47.

EDNEY, E.B. 1971. The body temperature of tenebrionid beetles in the Namib Desert of southern Africa. *J. Exp. Biology.* 55: 253 - 272.

GAUSE, G.F. 1934. *The struggle for existence.* Williams & Wilkins: Baltimore.

HAMILTON, W.J. 1971. Competition and thermoregulatory behavior of the Namib Desert tenebrionid beetle genus *Cardiosis*. *Ecology* 52: 810 - 822.

HAMILTON, W.J. 1975. Coloration and its thermal consequences for diurnal desert insects. *In* HADLEY, N.F. (ed.), *Environmental physiology of desert organisms.* pp. 67 - 89. Dowden, Hutchinson & Ross: Stroudsburg, Pennsylvania.

HOLT, R.D. & KOTLER, B.P. 1987. Short-term apparent competition. *Am. Nat.* 130: 417 - 430.

KOTLER, B.P. 1984. Predation risk and the structure of desert rodent communities. *Ecology* 65: 689 - 701.

LOUW, G.N. & HAMILTON, W.J. 1972. Physiological and behavioural ecology of the ultrapsammophilous Namib Desert tenebrionid *Lepidochora argentogrisea.* *Madoqua* 1: 87 - 95.

MACARTHUR, R.H. & LEVINS, R. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proc. Nat. Acad. Sci. USA* 51: 1207 - 1210.

MACARTHUR, R.H. & WILSON, E.O. 1967. The theory of island biogeography Princeton Univ. Press: Princeton.

PRICE, M.V. & WASER, N.W. 1985. Microhabitat use by heteromyid rodents effects of artificial seed patches. Ecology 66: 211 - 219.

SEELY, M.K., ROBERTS, C.S. & MITCHELL, D. 1988. High body temperatures of Namib dune tenebrionids - why ? J. Arid Environments 14: 135 - 143.