Population estimates of *Onymacris bicolor* (Coleoptera; Tenebrionidae) in the dunefields of the Skeleton Coast Park, South West Africa / Namibia

by

S.A. Hanrahan
Department of Zoology
University of the Witwatersrand
P.O. WITS
2050
Republic of South Africa

R.I. Yeaton*
Desert Ecological Research Unit
Gobabeb
P.O. Box 953
Walvis Bay
South West Africa / Namibia 9190

*present address
Department of Botany
University of Venda
Private Bag X2220
Sibasa
Republic of Venda

ABSTRACT

Population densities of *Onymacris bicolor* (Haag) (Coleoptera; Tenebrionidae), a locally abundant, endemic species of the Namib Desert, were estimated in four habitat types of the dunefields of the Skeleton Coast Park using the Lincoln Petersen Index and the Jolly Seber method. A population decline was noted between the first estimates in December 1983 and last in January 1985. The preferred habitat changed from Nara plants on the dune slipface initially to the succulent plants found on the floodplain in July 1984 and lastly to the open unvegetated slipface in January 1985. The differences in distribution appear to be related to changes in the vegetation following flooding. The changes in population density follow the expected pattern resulting from reduced reproduction of the species as it enters into a period of dry years.

CONTENTS

1 INTRODUCTION

The Namib dunefields have a rich and diverse beetle fauna of which species of Tenebrionidae are numerically dominant (Koch, 1961; Holm and Scholtz, 1979). While taxonomic and ecophysiological studies have been carried out on these beetles (e.g. Penrith, 1975; Edney, 1971) the structure and dynamics of these insect populations are poorly understood with some observations only now appearing (e.g. Roer, 1975, 1983, 1986; Seely and Louw, 1980). In general, absolute estimates of population size for desert invertebrates are relatively rare (Thomas, 1997; Sheldon and Rogers, 1984).

Onymacris bicolor is one of several hundred flightless psammophilous tenebrionid beetle species found in the Namib Desert. *Onymacris bicolor* is alocally abundant, endemic species that has been described as occurring on white vegetationless coastal barchan dunes of the northern Namib Desert from Torra Bay in South West Africa/Namibia northwards to Porte Alexandre in southern Angola (Penrith, 1975). Northeast of Torra Bay in lightly vegetated transverse dunes (Lancaster, 1980) *O. bicolor* is frequently associated with vegetation, particularly Nara *(Acanthosicyos horrida)* and succulents such as *Sesuvium sesuvioides* and *Zygophyllum simplex.*

Because of their unusual colouration, namely white elytra and black abdomen and thorax, these beetles have been of particular interest because of their fog basking behaviour and thermal biology (e.g. Edney, 1971; Hamilton, 1973), and this interest is likely to continue. Nothing is known of the population density of these beetles or their significance in the food web. Because of the endemic status and limited distribution within the Namib Desert of *O. bicolor,* a preliminary study of these beetles was undertaken using the mark and recapture technique to estimate population density at several points in time over a two year period.

2 MATERIALS AND METHODS

The study site was situated in an area of transverse dunes and floodplain adjacent to the dry Unjab River bed approximately 15 km from the sea (20° 09'S, 13°

14'E) in the Skeleton Coast Park of South West Africa / Namibia. This area is very dry, having a mean annual rainfall of 22-25 mm, but is often cool and foggy with fog occuring from 11-25 days per month. Temperatures measured at the site ranged from 13,5 - 30,8°C during December and 8,5 - 36,2°C during July (data from Weather Burea). Strong south-west winds capable of moving sand (44 m/s) were common (Lancaster, 1980).

Visits to this area were made in December 1983, July 1984, January, July and December 1985. The Unjab River bed is usually dry, but is occasionally subject to flooding. Prior and during the visits to the Unjab the following events occured. The river had flooded in the study site prior to the first visit in December 1983. Rains fell inland and the river flowed again during the following April. There was no significant rainfall prior to the January 1985 trip. It was therefore possible to observe the *O. bicolor* population shortly after two flooding events and a dry period. The river flowed for only one day during October 1985 and there were a few isolated shallow pools of water still present in December of that year. These were not at the study site but were nearer to the sea.

A permanent study site was choosen and used on each occasion (Fig. 1). Four main habitats were incorporated into the collecting area, namely: a dune slipface, a small area of the adjacent Unjab River floodplain sparsely covered by succulents, a large male Nara plant at the dune base on the floodplain and a small female Nara on the dune slip face (Fig. 1). Each collecting habitat was measured and the surface area was calculated. The dune slipface was 2040,5 m^2; the large male Nara plant, 624 m^2; the small female Nara on dune, 22,5 m^2 and the river floodplain, 782 m^2. The total surface area was calculated to be 3446,5 m^2. Although the boundaries of the site were clearly demarcated by either the limits of the vegetation or the physical features of the dune it must be stressed that the beetle population is an open one.

Collections of beetles were made by hand twice daily for 3 days during December 1983, July 1984 and January 1985. Only three collections were made during July 1985 and December 1985. The morning collections were made between 10h30 and 11h30 and the afternoon collections between 15h30 and 16h30. These time periods coincided with periods of maximum surface activity. Once collected, the beetles were counted and marked on the dorsal surface of the elytra with typist's correcting fluid or poster paint (Fig. 2). At each collection the beetles were marked with a different colour. It was therefore possible to establish when and how often each beetle had been captured during a particular visit. Marking with poster paint is not permanent although marked individuals were found up to 2 months later. The marking technique was reliable for the few days of each visit. In January 1985 each beetle was also sexed and individually numbered so

FIGURE 1: The collecting site, adjacent to the dry Unjab River course.

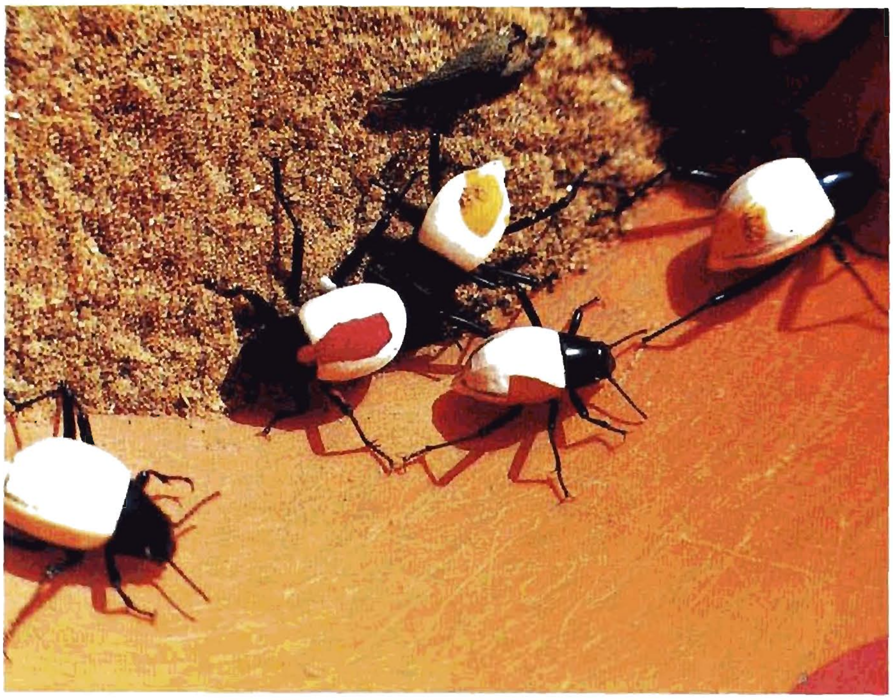

FIGURE 2: *Onymacris bicolor* marked with paint.

FIGURE 3: A young *Sesuvium sesuviodes* plant in flower.

that movement of each individual between habitats could be monitored. The marked beetles were immediately returned to the habitats in which they were captured. On the last day of each collecting period an exhaustive search was made for marked beetles in the vicinity of the study site to establish distances that beetles had migrated from the site.

Population size was estimated by the Lincoln Petersen Index (Petersen, 1896; Lincoln, 1930) and the Jolly Seber method (Jolly, 1965). Our estimates of population size come from numbers predicted by the models and are not based upon the longevity of individuals.

The notation used in this paper is a simplified version of that used by Jolly (1965) and is listed here for convenience.

i = sampling event

N_i = estimate of total number in the population when the ith sample is captured

M_i = estimate of total number of marked animals in the population at sampling event i.

a = M_i/N_i

$\varnothing_i$ = estimate of probability that an animal alive at moment of release of the ith sample will survive till the $i+1$ sample is captured.

B_i = estimate of number of new animals joining the population between the i and i+1 sample and alive at the 2nd sampling time.

SD(N) = standard deviation of N_i
SD(∅) = standard deviation of $\varnothing_i$
SD(B) = standard deviation of B_i

3 RESULTS AND DISCUSSION

3.1 Changes in vegetation and habitat

The dune changed seasonally and depended on the prevailing wind direction. In December and January collecting periods the dune area was a slipface whereas in July it formed a dune slope on the windward side of the dune. The succulents, mainly *Sesuvium* (Fig. 3), which originally provided about 10% ground cover in the flood plain region chosen provided about 20% cover in July and 30% cover in January 1985. However, by this time, although the plants had increased greatly in diameter, the central portions of many were dead or dying. By December 1985 substantial hummocks of sand had accumulated around the succulents, most of which were dead. The Nara had grown considerably over the two years but was in very poor condition by January 1985 as young shoots, flowers and fruits were heavily infested with aphids and enclosed in black crusts of aphid material. This condition persisted and was observed again in December 1985. A pool of water was found about 2km from the collecting site in December 1985. Numerous Nara and *Sesuvium* seedlings were present in the drying mud flats surrounding the pool, illustrating the initial phases of development of the type of vegetation present at the collecting site.

3.2 Population size

The results of the mark and recapture experiments are given in Table 1. An estimation of the population size as calculated by the Lincoln Petersen Index has been included so that the data collected in July and December 1985 could also be compared although the number of samples was small. The results obtained from December 1983 — January 1985 have further been analysed using the Jolly Seber method. The latter method is preferred because it takes the number of collecting events into the estimation of population size and provides a more conservative estimate. Estimates of population size, catchability, probablility of survival, additions to the population, and variances for these estimates appear in Table 2. The most important assumption made in this preliminary study of *O. bicolor* was that the samples collected on the sand surface were representative of the total beetle population

TABLE 1: Numbers of *O. bicolor* marked and recaptured from 1983 – 1985. Estimates of population size using the Lincoln Petersen Index are included.

Sampling event no.	Total no. of beetles captured & released	No. beetles recaptured from event no.						Population estimate
		0	1	2	3	4	5	
December 1983								
0	136							
1	222	53						570
2	198	25	97					500
3	198	7	31	95				564
4	200	6	23	45	78			587
5	193	7	10	10	29	85		696
July 1984								
0	175							
1	124	64						339
2	43	3	16					532
3	178	16	60	12				542
4	79	5	4	5	38			530
5	85	0	4	0	29	36		463
January 1985								
0	69							
1	53	30						120
2	45	8	11					216
3	50	8	3	19				195
4	33	2	0	2	20			188
5	21	0	1	1	4	5		279
6	21	0	0	0	1	7	9	193
July 1985								
0	3							
1	6	1						18
2	42	4	3					36
December 1985								
0	7							
1	8	2						28
2	4	1						24

TABLE 2: Results of the population analysis carried out using the Jolly Seber method.

i	ai	Mi	Ni	∅i	Bi	SD(N)	SD∅	SD(B)
December 1983								
1				0.8640			0.0508	
2	0.2387	115.0	481.9	0.8199	− 13.3	48.2	0.0382	30.4
3	0.6100	232.9	381.8	1.0357	82.9	19.3	0.0612	23.9
4	0.6717	319.9	476.2	0.7372	22.3	31.8	0.0603	17.1
5	0.7600	283.8	373.4			24.8		
6	0.7306							
July 1984								
1				0.5682			0.0459	
2	0.5161	99.4	192.6	1.5312	257.5	13.5	0.2852	107.0
3	0.4419	244.1	552.5	0.5066	− 5.1	138.8	0.1000	27.9
4	0.4944	135.8	274.7	0.5510	37.7	23.7	0.0703	16.3
5	0.6582	124.4	189.0		22.8			
6	0.8118							
January 1985								
1				1.3565			0.2597	
2	0.5556	93.6	168.5	0.4085	44.4	37.9	0.1001	19.4
3	0.4222	47.6	112.8	0.5704	5.6	22.5	0.0949	9.6
4	0.6000	42.0	70.0	0.6976	10.6	7.7	0.1384	6.0
5	0.7273	43.3	59.5	0.5678	22.9	10.9	0.1680	11.4
6	0.5238	29.7	56.6			16.1		
7	0.8095							

present. Probability of capture estimates (Table 2) indicate that this was a reasonable assumtion.

The estimates of population size using the Jolly Seber method indicate that the population was relatively constant throughout each of the short sampling periods. Although population size varied by a factor of three in any sampling period the estimates of the variances of the population size show that these results fall well within the accuracy range suggested for preliminary population studies by Robson and Reiger (1964). In order to obtain an indication of *O. bicolor* numbers per unit area the final estimate of population size from each sampling period was considered. The range was calculated from those figures representing the 95% confidence limits for each estimate, namely, 9.4 to 12.3 beetles per 100 m^2 in December 1983, 4.2 to 6.8 beetles/ 100 m^2 in July 1984 and 0.7 to 2.6 beetles / 100 m^2 in January 1985. There is a very obvious decline in population density over the first thirteen months of the sampling period. This decline continued during 1985. Although the population is relatively small compared to the large numbers of insects captured in non-desert environments the reduction in population was very noticeable. During December 1985 only about two hundred beetles *in toto* were found during several days of intensive searching along 8 km of dunes adjacent to the river bed. In December 1983 this number of beetles could be found in 1 hour of collecting. The decrease in numbers observed in this study appears to be a general observation for the region (S. Braine, pers. comm.). Another beetle species that had been common namely, *Onymacris marginipennis*, was also hard to find. It is unfortunate that there was insufficient time to repeat the number of collecting episodes in July and December 1985. The numbers of animals obtained were small and variable.

Unpredictable rainfall events have dramatic influences on desert environments and are known to trigger substantial increases in plant and animal biomass (e.g. Seely and Louw, 1980). The times chosen for these mark and recapture experiments fortuitously coincided with unusual conditions. It would appear that the population as first sampled had possibly expanded after the flooding of the river and then gradually declined. This phenomenon would be similar to that recorded for beetle species around Gobabeb after the rains in 1976 (Seely and Louw, 1980; Wharton and Seely, 1982). Considerable variation in population densities of six species of tenebrionid from the Mojave Desert have also been reported (Thomas, 1977). The variation in density was not studied in relation to variation in climatic conditions and the densities of the different bettle species studied varied independently of one another (Thomas, 1977).

It is interesting to speculate on the cause of the population decline. Large birds, seldom seen in these regions, had been noted more frequently since the rains (Braine, pers. comm.). During January 1985 we noted Ludwig's bustards *(Neotis ludwigii)* flying from one patch of Nara to the next, pecking at material at each site. An examination of their droppings revealed large amounts of beetle exoskeleton. *O. bicolor, O. marginipennis* and *O. uniquicularis* were recognised. Seely (1985) reported a similar event after the 1976 rains. The droppings of the large lizard *Angolosaurus* were also found to contain *O. bicolor* elytra. In the Namib Desert the quantitative impact of predators on the populations of adult tenebrionids is unknown (Seely, 1985). Crawford (1981) suggests that the decline in any beetle population is unlikely to be a result of heavy predation by migrant and local predators except in unusual circumstances. The Namib Desert offers unusual circumstances where beetles are obvious, exposed and long-lived prey.

3.3 Emigration and immigration

One of the advantages of the Jolly Seber method of analysis is that it allows estimation of the numbers of individuals entering and leaving the study site. Apart from one occasion in July, 1984, when 257 beetles were estimated to have entered the site, most estimates of immigration were small, i.e. under 50, but the estimated variances of these figures were high (Table 2). Conversely when the emigration figures were calculated using the formula $L_i = (l-\emptyset_i)N_i$ it was found that these were higher, ranging from 48,5 to 270. We interpreted this to mean that emigration exceeded immigration. 'Emigration' could represent a number of possibilities: death from ageing or predation, failure to emerge from the sand, and finally true emigration. Only one marked beetle corpse was found on the site during the sampling sessions. No evidence of marked beetles on the site being preyed upon was noted, though the possibility has been discussed. The presence of people near the collecting site may have scared off predators during the sampling periods. Falure to emerge from the sand as well as direct emigration probably account for the figures obtained.

Emigration was not observed at the time of release when beetles burrowed into the sand, but did occur at some point because marked beetles were found when the surroundings were searched on the fourth day in December 1983, July 1984 and January 1985. Most marked beetles recovered away from the experimental site were found near the flood plains at the bases of successive parallel transverse dunes. A decrease in number of beetles was noted with increasing distance from the river bed. These results are similar with those of Roer (1975) who reported large scale movement of *O. plana* in the dune fields parallel to the Kuiseb River bed. No beetles were found across the river. The largest number of those that had moved away from the river bed were found on the same dune up to 1.5 km from the site, indicating that they had moved along the dune. About 7% of the total number of beetles marked were recovered on the fourth day in both December 1983 and June 1984 and 4% in January 1985.

One of the assumptions made in the Jolly Seber model is that migration is permanent. This may well not be true in the present case. If it had been possible to continue the sampling over longer periods of time it may have been found that although individuals migrated from the site in time they returned to it. For example during the December sampling period at the last collecting event 7 beetles appeared that had been marked only during the first capture event. These individuals could either have left the site and returned, or may not have emerged from the sand during the collecting periods for several days. In general the highest rate of recapture occurred in the following session (Table 1).

Marking did not appear to influence the beetles immediate chances of survival as only one individual died after capture. Marks on beetles were not rapidly destroyed. They remained distinct on laboratory maintained individuals for at least six months though loss of paint through abrasion by sand occurred gradually. In the field marked beetles were recovered two months later but no marked individuals were found after the six month intervals.

3.4 Distribution of beetles in the four habitats

The distribution of *O. bicolor* in the four habitats within the collecting site is illustrated in Fig. 4. The beetles were concentrated in different habitats at each visit namely, the male Nara in December 1983, the flood plains in July 1984 and the dune slipface in January 1984. The percentages graphed in Fig. 4 represent averages of the total number of beetles captured during each sampling series. The proportions of the population found in each habitat were consistent throughout each sampling series. On only one occasion in July were more beetles found on the slip face than among the succulents of the floodplain.

Contrary to expectation the numbered beetles (January 1985) did not exhibit random movement between the four different habitats. Of the 55 beetles that were recaptured on one or more occasions 30 were recaptured from the same area.

Unfortunately nothing is known of *O. bicolor* dietary preferences. The marked preference for different habitats noted between December 1983, June 1984 and January 1985 may have reflected a temporary shift in dietary preference. The beetles were seen to eat the

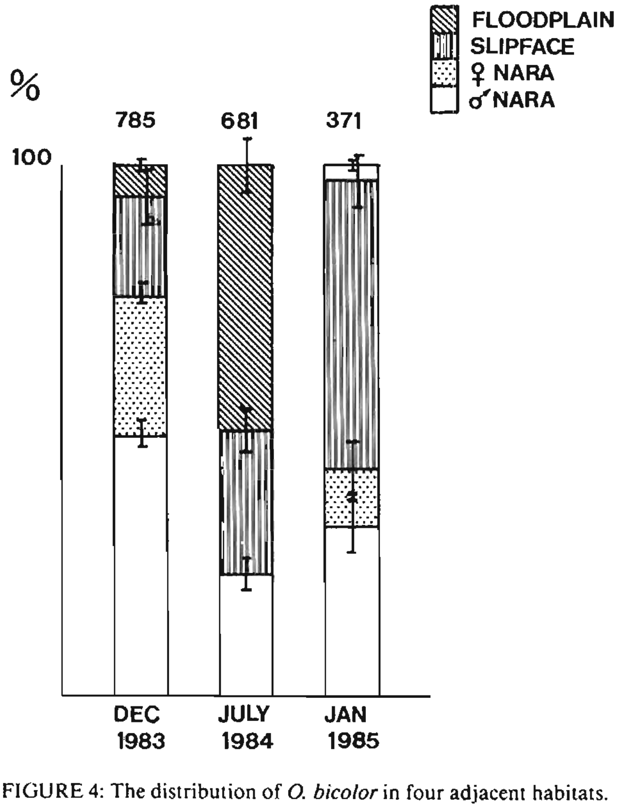

FIGURE 4: The distribution of *O. bicolor* in four adjacent habitats.

fresh young succulent leaves during the July session and were frequently seen chasing after wind blown detritus on the slipface during January. This aspect requiries further study as the choice of habitat could result from many factors other than food choice. For example, the succulents possibly provide a more humid, cool microclimate, whereas the Nara may provide protection from predators.

4 CONCLUSIONS

The population of *O. bicolor* in a localised area is subject to constant immigration and emigration. The larger numbers recorded at first may have resulted from an increase in population density after the flooding of 1983. The decline in population numbers may have partially resulted from predation by other animals such as lizards and migrant birds although progressive desiccation of the environment in the absence of rain or water in the river bed may also be a contributing factor.

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