Predation and Environment as Selective Forces In the Namib Desert

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Abstract. Two hypotheses are presented to explain the absence of apparent adaptations to avoid predation in the long-lived adult tenebrionid beetles of the Namib Desert. The intensity of predation on this group has not been established. By examining the consequences of varying levels of predation, however, tentative suggestions are presented concerning the probable impact of predation on the evolution of the conspicuous tenebrionid fauna of the Namib Desert dunes.

Introduction

Within an ecosystem, prey species may evolve physiological, morphological or behavioural adaptations to escape from their predators (e.g., Maiorana, 1976; Ricklefs, 1973). Physiologically, they may escape by increasing their reproductive output, attempting to 'satiate' their predator's hunger, allowing some offspring to produce a future generation (e.g., Lloyd and Dybas, 1966; Janzen, 1971). Morphologically, prey species may develop defensive structures (e.g., Branch and Branch, 1981), or toxins (e.g., Tschinkel, 1975) or crypsis (e.g., Wickler, 1968). Behaviourally, they may actively escape capture (e.g., Roeder, 1962, in Emlen, 1973), or be active when their potential predators are not (e.g., Wallwork, 1982) or live in places inaccessible to their predators (e.g., Branch and Branch, 1981). The above adaptations are not mutually exclusive and are often combined in a single prey species.

These adaptations are to be expected whenever a species is exposed to predation. However, the importance of predation within a desert ecosystem is a matter of some speculation (e.g., Noy-Meir, 1979/80). Its evolutionary role usually has been considered to be small (Buxton, 1923 and other references in Cloudsley-Thompson, 1979), presumably because of the low population densities of prey and of potential predators in the desert ecosystem. However, Crawford (1981), noting that a large number of taxa of desert invertebrates are basically nocturnal, wrote 'it is tempting to conclude that avoidance of predation has been a powerful unifying link in the selection of nocturnality among these species.' Providing his own counter-argument, he stated that there are many nocturnal predators in deserts and that, moreover, diurnal prey species are numerous and may, in fact, be exposed to as much predation as the nocturnal fauna. At least two major questions to consider about the role of predation as a selective mechanism in desert ecosystems are distinguished here. First, 'are there sufficient numbers of predators within deserts to act as selective agents?' and second, 'are the adaptations, such as nocturnality, in desert organisms the result of predation acting as a selective force or the result of selection by other factors?'

In contrast, the importance of the harsh desert environment as a selective force goes almost without question, and numerous studies have documented a variety of morphological, physiological and behavioural adaptations to high temperature and low moisture availability (e.g., Crawford, 1981; Louw and Seeley, 1982).

I was originally asked to contribute a discussion on the role of abiotic and biotic factors in shaping the character and diversity of species in a desert ecosystem. I have chosen to concentrate on the role of a particular biotic factor, predation, which I have considered in relation to the common and conspicuous tenebrionid fauna of the Namib Desert, particularly in the dune habitat. This has only slight bearing on the nature of species and speciation events (the main topic of this volume), but is relevant to discussions concerning the importance of biotic factors in determining patterns of desert adaptation and species diversity.

I have examined these questions in the Namib Desert dunes, using as a model the common and conspicuous tenebrionid beetles found there. For this group of beetles the relative number of species increases along a gradient of increasing aridity until they become one of the numerically dominant groups in very arid areas such as the Namib Desert dunes (Koch, 1962). The predominantly diurnal tribes Adesmiini and Zophosini are particularly well represented, with 46 species in the central Namib alone. Of these, 24% are restricted to the dunes and 83% do not live beyond the borders of the Namib. In contrast, the ranges of 80% of the 20 potential predators extend over much of southern Africa.

The adult forms of many tenebrionid species are found on the open slopes of the dunes. While more than half their time is spent below the sand surface, they must spend the remainder on the surface gathering food in the form of wind-blown plant detritus and water from fog condensation (Seely, 1983). Wind-blown detritus is usually gathered on warm days, while fog-water is collected during cool nights (Seely *et al.*, 1983). These species are potentially exposed to predation whenever they are on the surface of the dunes. Yet none of the tenebrionids of the Namib Desert dunes shows evidence of adaptation for predator avoidance. For example,

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members of the genus *Onymacris* are shiny, black, diurnal species, several centimetres long, and they are very conspicuous against the background of the vegetationless or lightly vegetated orange dune sands (Penrith, 1975). Why are these species so conspicuous and why do they behave in such a way as to attract the attention of potential predators? I propose two contrasting hypotheses that attempt to explain the conspicuous colour and behaviour of these beetles. The hypotheses involve determination of the intensity of predation and the possible adaptive roles that colouration and behaviour play in these organisms.

1. The selective value of predation is strong, and the conspicuous colour and behaviour are related to predator avoidance.
2. The selective value of predation is neutral, and the conspicuous colour and behaviour represent an evolutionary legacy from wetter and more vegetated habitats, or the conspicuous colour and behaviour have physiological significance, or both of these explanations.

These hypotheses represent the extremes of a continuum, for the selective value of predation is probably intermediate and the conspicuous colour and behaviour represent a compromise between predator avoidance, evolutionary legacy and physiological requirements. These hypotheses are not new, and variations of the alternatives have been discussed previously (e.g., Hamilton, 1973; Cloudsley-Thompson, 1979). To evaluate the two hypotheses, I use observational evidence based largely on my experience in the Namib Desert. I first present arguments as to the intensity of predation within the Namib Desert dunes.

There are a number of potential predators living in or near the Namib dune sea which prey on the adults of the dune tenebrionids (Table 1). Only seven of the twenty species listed are permanently resident in the dunes. The number of invertebrate predators may be underestimated. The other species occupy the richer surrounding areas of coastal beach or vegetated dry river course or pro-Namib grassland and only enter the dune field occasionally. Eight of the potential predator species are active during the day. The quantitative impact of any of these predators on the populations of the adult tenebrionids is unknown.

For example, Stuart (1976) mentions that Coleoptera were present in over 50% of the jackal scats he examined from the central Namib, but does not mention their importance in terms of biomass. Tilson and Le Roux (1983) and several authors quoted by them mention the presence of tenebrionids in pellets of two species of owl collected at various Namib localities, but their contribution to the total prey biomass was negligible. In contrast, the mean annual representation of tenebrionids in the diet of the Namaqua chameleon was found to be 60% for an inland desert population and 90% for a coastal desert population (Burrage, 1973). Other species are included in the list of predators because either I have observed them feeding on tenebrionids, or the observed evidence was irrefutable (e.g., numerous tenebrionid exoskeletons in trap-door spider burrows) or their recorded habitats suggested that these desert tenebrionids probably constitute at least occasional prey.

I have observed only two instances of heavy predation on these tenebrionid beetles. During one foggy morning in the northern Namib, 80 fog-basking *Onymacris unguicularis*, approximately 15% of the population of 13 isolated barchan dunes, were eaten by an unidentified rodent (Seely, 1979). No similar occurrence has been observed in hundreds of nights of observation of their fog-basking behaviour in the central and southern Namib (Seely *et al.*, 1983). This fact and the observation that fog-basking is a common behaviour pattern in these beetles suggest that predation levels are not intense enough to select against fog-basking on the surface as opposed to some other mechanism of gaining water. A second observation involves the great increase of plants and animals following the unusual (>100 mm) rains of 1976 and 1978, the first rains of this magnitude in the central Namib since 1934 (Seely and Louw, 1980). In 1977, Ludwig's bustard moved, in great numbers, into the Namib dunes from the interior, preying almost exclusively on *O. plana* on the dune slopes. These bustards remained throughout most of the next four years, after which they disappeared from the dune habitat. Such sporadic events do not appear to be frequent enough to have selected for nocturnal behaviour or cryptic colouration, which would seem to be a logical consequence of the selective impact of predation by these bustards.

From the evidence available it is apparent that predation is a factor to be considered with respect to the Namib dune tenebrionid beetles, but its impact is unknown. I have examined the originally proposed hypotheses in more detail.

1. The selective value of predation is strong, and the conspicuous colour and behaviour are related to predator avoidance.

If predation pressure is heavy, adaptations to avoid predation are to be expected. Conspicuousness rather than crypsis or submergent behaviour is characteristic of the diurnal Namib dune tenebrionids. Cloudsley-Thompson (1979) concludes that the black colouration of desert animals probably has an aposematic function, as most black desert insects, even if non-toxic, have extremely hard integuments or may be distasteful in other ways. There are several pieces of evidence, however, which suggest that this conclusion is not applicable to the Namib dune tenebrionids. None of these species is known to use defensive secretions as described by Tschinkel (1975) for tenebrionids elsewhere. A few species, however, use the head-down posture, used by species with defensive secretions, when confronted by a potential predator. This behaviour, however, would facilitate rather than deter capture by providing a conspicuous, non-moving, non-toxic target to a predator. Observations of beetle remains in the scats and pellets of a number of mammal and bird species indicate that these beetles are apparently not distasteful. They may be consumed in large numbers for extended periods of time if the opportunity to do so presents itself to a predator. Fi-

Table 1

Potential predators on adult Namib dune tenebrionids*

	Activity Period	*Habitat*	*Prey Size*	*Evidence*
Mammals				
Crocuta crocuta spotted hyaena	Nocturnal	Periphery	Large	Suspected
Hyaena brunnea brown hyaena	Nocturnal	Periphery	Large	Suspected
Canis mesomelas black-backed jackal	Diel	Periphery	Large	Observed
Vulpes chama Cape fox	Nocturnal	Periphery	Large	Suspected
Otocyon megalotis bat-eared fox	Diel	Periphery	Large	Suspected
Gerbillurus spp. gerbils	Nocturnal	Dunes	Large	Observed
Eremitalpa granti namibensis golden mole	Nocturnal	Dunes	Small	Observed
Birds				
Corvus albus pied crow	Diurnal	Periphery	Large	Observed
Corvus capensis black crow	Diurnal	Periphery	Large	Observed
Falco rupicoloides greater kestrel	Diurnal	Periphery	Large	Observed
Falco tinnunculus rock kestrel	Diurnal	Periphery	Large	Observed
Melierax canorus chanting goshawk	Diurnal	Periphery	Large	Observed
Neotis ludwigii Ludwig's bustard	Diurnal	Transient	Large	Observed
Bubo africanus spotted eagle owl	Nocturnal	Periphery	Large	Observed
Tyto alba barn owl	Nocturnal	Periphery	Large	Observed
Reptiles				
Chamaeleo namaquensis Namaqua chameleon	Diurnal	Dunes	Large/ Small	Observed
Aporosaura anchietae sand-diving lizard	Diurnal	Dunes	Small	Observed
Invertebrates				
Carparachne alba trap-door spider	Nocturnal	Dunes	Large/ Small	Observed
Leucorchestris arenicola trap-door spider	Nocturnal	Dunes	Large/ Small	Observed
Opistophthalmus flavescens scorpion	Nocturnal	Dunes	Large/ Small	Observed

*Holm and Scholtz (1980) and personal observations.

nally, aposematic colouration is directed toward vertebrate predators, usually birds (Matthews and Matthews, 1978), and is often correlated with clumped distributions and high population densities of prey. Neither of these two conditions is found in the dune tenebrionids.

2. The selective value of predation is weak or absent, and the conspicuous colour and behaviour represent an evolutionary legacy from wetter and more vegetated habitats, or the conspicuous colour and behaviour have physiological significance, or both of these explanations.

If black colouration and conspicuous behaviour were, indeed, only evolutionary legacies in the Tenebrionidae, all desert tenebrionids would be expected to have such characters. Evidence against this is to be found in the presence of Namib dune tenebrionids that are predominantly white, brown or combinations thereof (e.g., Koch, 1962; Penrith, 1975). Other black Namib desert tenebrionids secrete a wax cover (McClain, 1982; McClain *et al.*, 1985) which to a lesser or greater degree alters their colour to entirely or partially white, yellow, blue or beige, simultaneously altering their thermal properties and perhaps also conferring the advantages

of camouflage. Furthermore, the basically day-active behaviour of the tribe Adesmiini is not evident in all species of this tribe. Members of the genus *Epiphysa* are crepuscular and are very slow walkers (their elytra, however, are the hardest of all known species). *Metriopus depressus* is another adesmine species that moves very slowly and is not active during sunny conditions, apparently preferring reduced light and rocky crevices. Such apparently 'submergent' behaviour could actually expose these species to predation from both nocturnal and diurnal predators (e.g., Jaksic, 1982). Thus the idea that conspicuous colour and behaviour are an evolutionary legacy in adesmine tenebrionids (to which the genus *Onymacris* belongs) is not supported.

Tenebrionids of the Namib dunes consume windblown plant detritus and water condensed from fog. While neither food (Seely and Louw, 1980) nor water is limiting, surface behaviour is necessary for their procurement. Because the foraging and water-imbibing behaviour of dune tenebrionids makes them more conspicuous, it could be suggested that the behaviours have evolved under somewhat relaxed conditions of predation. In a more general context, Oksanen *et al.* (1981) point out that efficient use of forage conflicts with adaptations that make a herbivore (or detritivore) an elusive or submergent prey.

Selection also acts on factors other than mortality, for example, on productivity and energy efficiency (Hamilton, 1973). Thus, while the absolute amounts of food may not be limiting to Namib tenebrionids, the rate at which food can be processed (digested) may be a limiting factor. Diurnal behaviour may contribute to increasing the amount of food located and consumed, while the thermal consequences of the conspicuous black colouration could contribute toward increasing processing rates.

In a desert environment, physiological constraints may be imposed on potential predators (Louw and Seely, 1983 and references therein). Whereas the larger mammalian and avian predators must tolerate adverse temperature and moisture conditions or move to more equable climates, the smaller tenebrionid prey need only escape below the sand surface to find moderate conditions (Seely, 1983). As an example, even during peak population densities of the dune tenebrionids, Ludwig's bustard was absent from the sand sea during the few hottest months of the year.

Other examples of conspicuous colouration and behaviour under what are thought to be relaxed conditions of predation have been proposed or observed. Crawford (1981) suggests that sun-basking in cicadas is likely to be hazardous unless it coincides with diminished predator activity. Hamilton (1973) summarizes descriptive data that suggest that relaxation of predation on Mediterranean islands off the coasts of Yugoslavia and the Sorrento Peninsula may have led to the island lizard *Lacerta serpa* becoming nearly black with a blue belly, conspicuous colouration used in visual displays. The black colouration of *Lepus insularis* (Hamilton, 1973 quoting Bryant, 1891), a jackrabbit living on Espiritu Santo Island in the Gulf of California and closely related to the camouflaged *Lepus californicus* of the nearby mainland, may also be the result of a relative paucity of predators or of the cool island climate.

Conclusion

By considering the possible selective value of predation on tenebrionid beetles with very conspicuous colour and behaviour in the Namib Desert dune environment, tentative ideas concerning the relative importance of predation versus environmental factors as selective agents on this fauna may be derived. I suggest that the selective value of predation has not been as marked as the selective value of the desert environment and that the conspicuousness of the fauna is a result of an evolutionary legacy reinforced by selection for physiological adaptations.

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References

Branch, G. and Branch, M., 1981. *The living shores of southern Africa.* C. Struik, Cape Town.

Burrage, B. R., 1973. Comparative ecology and behaviour of *Chamaeleo pumilus pumilus* (Gmelin) and *C. namaquensis* A. Smith (Sauria: Chamaeleonidae). *Annals of the South African Museum* **61**: 1–158.

Cloudsley-Thompson, J. L., 1979. Adaptive functions of the colours of desert animals. *Journal of Arid Environments* **2**(2): 95–104.

Crawford, C. S., 1981. *Biology of desert invertebrates.* Springer-Verlag, Berlin.

Emlen, J. M., 1973. *Ecology: an evolutionary approach.* Addison-Wesley, London.

Hamilton III, W. J., 1973. *Life's color code.* McGraw-Hill, New York.

Holm, E. and Scholtz, C. H., 1980. Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. *Madoqua* (Windhoek) **12**(1): 3–39.

Jaksic, F. M., 1982. Inadequacy of activity time as a niche difference: the case of diurnal and nocturnal raptors. *Oecologia* (Berlin) **52**: 171–175.

Janzen, D. H., 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* **2**: 465–492.

Koch, C., 1962. The Tenebrionidae of southern Africa XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum* **24**: 61–106.

Lloyd, M. and Dybas, H. S., 1966. The periodical Cicada problem. II. Evolution. *Evolution* **20**(4): 466–505.

Louw, G. N. and Seely, M. K., 1982. *Ecology of desert organisms.* Longman, London.

McClain, E., 1982. The role of the cuticle in the adaptation of tenebrionid beetles to the Namib Desert. *Zoological Society of Southern Africa Occasional Bulletin* **2**: 31.

McClain, E., Seely, M. K., Hadley, N. F. and Gray, V., 1985. The occurrence, distribution and lipid composition of wax blooms in Namib Desert tenebrionid beetles: correlations with the physical environment. *Ecology* **66**: 112–118.

Maiorana, V. C., 1976. Predation, submergent behaviour and tropical diversity. *Evolutionary Theory* **1**: 157–177.

Matthews, R. W. and Matthews, J. R., 1978. *Insect behaviour.* John Wiley & Sons, New York.

Noy-Meir, I.,1979/80. Structure and function of desert ecosystems. *Israel Journal of Botany* **28**: 1–19.

Oksanen, L., Fretwell, S. D., Arruda, J. and Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**(2): 240–261.

Penrith, M.-L., 1975. The species of *Onymacris* Allard (Coleoptera: Tenebrionidae). *Cimbebasia* (Windhoek) (A) **4**(3): 47–97.

RICKLEFS, R. E., 1973. *Ecology*. Thomas Nelson and Sons, London.
SEELY, M. K., 1979. Irregular fog as a water source for desert dune beetles. *Oecologia* (Berlin) **42**: 213–227.
SEELY, M. K., 1983. Effective use of the desert dune environment as illustrated by the Namib tenebrionids. *In:* LEBRUN, P., ed., *New trends in soil biology*, pp. 357–368. Dieu-Brichart, Belgium.
SEELY, M. K., LEWIS, C. J., O'BRIEN, K. A. and SUTTLE, A. E., 1983. Fog response of tenebrionid beetles in the Namib Desert. *Journal of Arid Environments* **6**(2): 135–144.
SEELY, M. K. and LOUW, G. N., 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *Journal of Arid Environments* **3**: 25– 54.
STUART, C. T., 1976. Diet of the black-backed jackal *Canis mesomelas* in the central Namib Desert, South West Africa. *Zoologica Africana* **11**(1): 193–205.
TILSON, R. L. and LE ROUX, P., 1983. Resource partitioning in coexisting Namib Desert owls, *Bubo africanus* and *Tyto alba*. *Madoqua* (Windhoek) **13**(3): 221–227.
TSCHINKEL, W. R., 1975. A comparative study of the chemical defensive system of tenebrionid beetles: chemistry of the secretions. *Journal of Insect Physiology* **21**: 753–783.
WALLWORK, J. A., 1982. *Desert soil fauna*. Praeger, New York.
WICKLER, W., 1968. *Mimicry in plants and animals*. World University Library, London.