p/copy 07/04
Mary

Journal of Arid Environments (1979) **2**, 263–271

Pre-adaptation and speed mimicry among Namib Desert scarabaeids with orange elytra

E. Holm* & J. F. Kirsten*

The unique occurrence of a complex of true scarabs with orange elytra in the Namib Desert is explained through speed mimicry. Alate species are argued to converge to orange elytra to distinguish themselves from the predominantly black and apterous diurnal beetles in the area in a Müllerian system, while one apterous scarab joins this complex with Batesian mimicry. An explanation is offered for the parallel occurrence of orange elytra prior to their selection for aposematic and mimetic advantage.

Observation

The Scarabaeini species with remarkably similar orange-brown elytra occur in a limited area in the central Namib Desert. The different genera to which these species belong are represented outside the Namib Desert by black species only (Fig. 1(a)–(d)). Two of the species, *Scarabaeus rubripennis* Boheman (Plate 1(d)) and *Drepanopodus proximus* (Péringuey) (Plate 1(e), (f)), are alate, while the third, *Pachysoma denticolle* Péringuey (Plate 1(a), (b)), is apterous. *S. rubripennis* always has orange elytra, but a closely related species which occurs throughout the arid parts of Southern Africa (*S. flavicornis* Boheman—Plate 1(c)) is always black, and reaches parapatry with *S. rubripennis* in the marginal central Namib. *D. proximus* has black (Plate 1(e)) and orange (Plate 1(f)) forms with occasional intermediates, and all forms apparently occur throughout the limited distribution range. *P. denticolle* has the elytra orange (Plate 1(b)) in most of its distribution range, but intermediate and completely black (Plate 1(a)) forms occur in a very limited area on the coast north of Sandwich Bay (Fig. 1(c)). While Ferreira (1953) commented on the convergent colour of these three species, she did not offer an explanation for the supposed mimicry.

In addition to the above three species, there are at least two other species of the *Scarabaeus parvulus* group in the Namib Desert which have forms with visibly reddish elytra. One of these, *S. knobeli* Ferreira, is known from only one specimen with moderately orange elytra from Moçamedes (northern Namib) (Plate 1(i), (j)). The other species with black to moderately orange elytra occurs in the marginal central Namib. Black members of the *S. parvulus* group are widely distributed in Southern Africa (Plate 1(j)). The otherwise black *S. bohemani* Harold also has brownish specimens in the marginal central Namib (Plate 1(g)).

The Buprestidae of the drier parts of South West Africa show parallel cases of species with brown to brick-red elytra, while their congeners elsewhere in Africa are black to viridescent. This phenomenon is most pronounced in the julodine genera *Julodis* (see Ferreira & Ferreira, 1958), *Neojulodis* (*Protojulodis*) and *Julodella* (see Holm 1979).

), black
icornis;
orange
; (i) S.
l black

page 263]

---

* Department of Entomology, University of Pretoria, Pretoria 0002, South Africa.

0140–1963/79/030263+10 $02.00/0

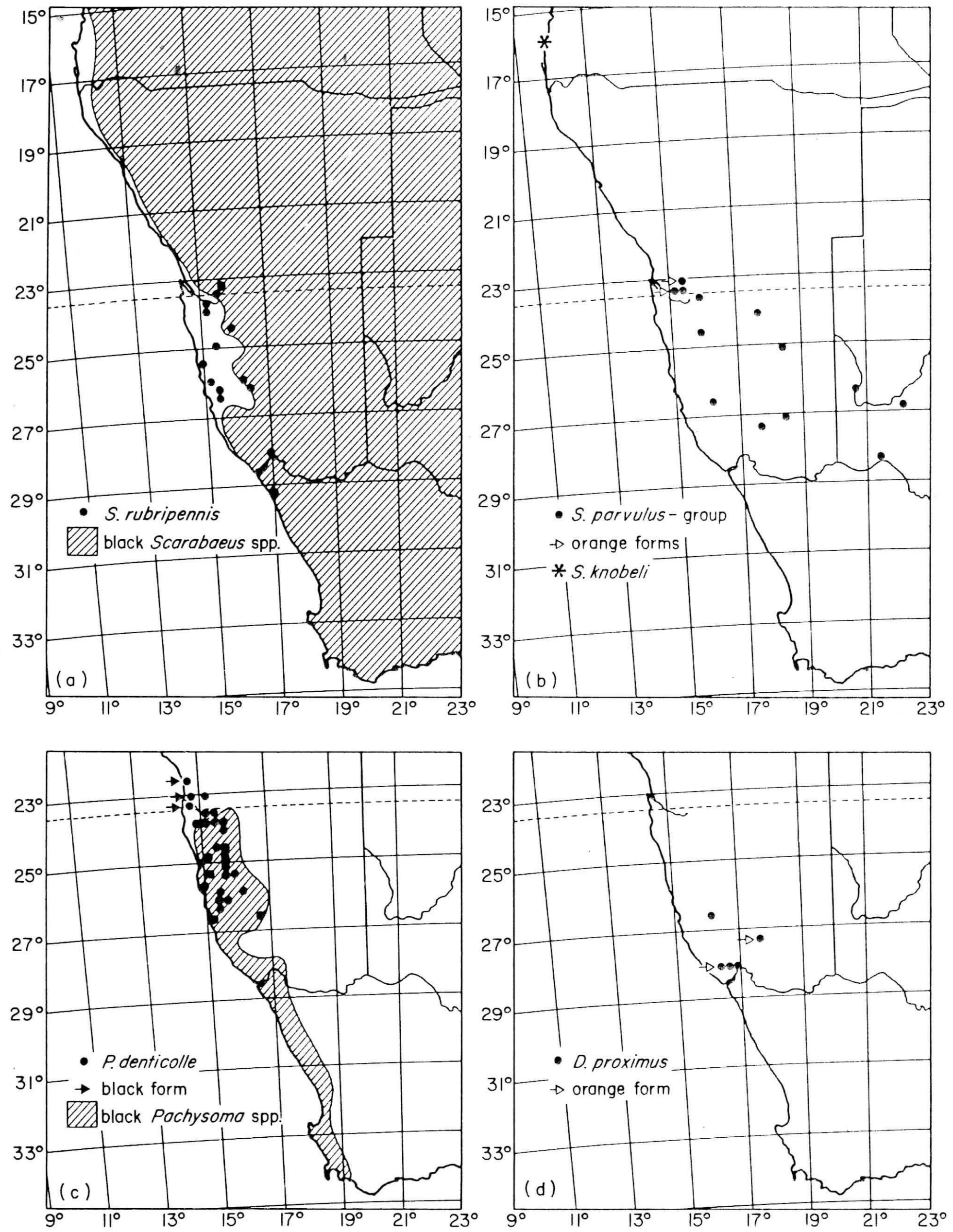


Figure 1. Distribution of the Scarabaeinae with orange elytra and their relatives in south western Africa. (a) Recorded distribution of *S. rubripennis* and black *Scarabaeus* species; (b) recorded distribution of the *S. parvulus* group; (c) recorded distribution of *P. denticolle* and black *Pachysoma* species; (d) recorded distribution of *Drepanopodus proximus*.

Hypotheses

We propose the following explanations of the situation described above:

(1) The orange colour arises primarily through a lack of (black) melanin, caused physiologically by high temperatures (and possibly also by dry conditions).

(2) The disad
body part
of the mel
black cont
(3) The unme
and thus a
(i) *Prep*
S. ru
black
This
by ot
slowe
partly
(ii) *Batesi*
aptere
which
resem
mimi
with
(iii) *Crypsi*
elytra

It is well know
Bernardi, 196
tion protects
other hand, bl
desert insects,
deserts (Cloud
protects inter
perties of mel
and metabolic
these organs a
increases body
held to be del
ences due to
to differences
(1973, 1975) p
their quest to
energy turnov
brionid specie
integuments, a
sematic (Clou
ably demonstr
desert tenebric
all seem to be
lizard stomach
may contribute
1975; Cloudsle
Thompson co
melanin may a

(2) The disadvantages of an unmelanized cuticle are minimized by zoning melanin to the body parts where it is most crucial. This zoning may become heritable independently of the melanin available, allowing completely black forms to co-exist with forms with black confined to zones.

(3) The unmelanized orange zones acquire a positive function unrelated to heat or drought, and thus act as pre-adaptations for:

  (i) *Preponderantly Müllerian mimicry among the alate scarab species.* In this system, *S. rubripennis* 'advertises' its superior agility and speed compared to the otherwise black and apterous diurnal beetle fauna in the area by means of its orange elytra. This 'low reward for effort' code for predators would protect, and be reinforced by other alate species with orange elytra, like *D. proximus*. The latter is larger and slower than *S. rubripennis*, and the mimicry between them would probably be partly Batesian, partly Müllerian.

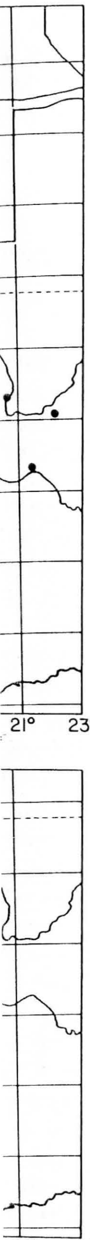
  (ii) *Batesian mimicry of* S. rubripennis *by* P. denticolle. The latter species is the only apterous species that has 'broken the code', and is also the only apterous scarab which is sympatric with *S. rubripennis*, and comparable in size. It shows the closest resemblance to *S. rubripennis* (and must therefore benefit considerably from the mimicry), while non-mimetic black and intermediate forms occur in allopatry with *S. rubripennis*.

  (iii) *Crypsis, optical form disruption and thermoregulation.* These functions of orange elytra probably play a minor part, but may add to their selective advantage.

Discussion

The origin of unmelanized forms in the Namib Desert

It is well known that Glogers' rule also applies to poikilotherms in deserts (see, for example, Bernardi, 1962, 1963; Rettenmeyer, 1970), and it was generally believed that light coloration protects desert animals from excessive radiation heat and through crypsis. On the other hand, black melanization of the cuticle has several advantages, particularly to diurnal desert insects, and the relative proportion of black diurnal insects actually increases in deserts (Cloudsley-Thompson, 1977). Melanin adds to the hardness of the cuticle and protects internal organs against chemo-active UV radiation (Neville, 1975). These properties of melanin may be the reason for the heavy melanization above muscle insertions and metabolically active organs, rather than the consequence of the metabolic activity of these organs as proposed by Wigglesworth (1974). Melanin also absorbs IR radiation and increases body heat (Edney, 1971; Hamilton, 1975). While heat absorption was generally held to be deleterious to desert animals, Edney and others argued that temperature differences due to colour are negligible (Edney, 1971; Cloudsley-Thompson, 1977) compared to differences due to niche and behaviour (Edney, 1971; Holm & Edney, 1973). Hamilton (1973, 1975) proposed that black colour may be a positive advantage to poikilotherms in their quest to reach and maintain 'maxithermy' and consequent maximal metabolism and energy turnover, and Henwood (1975) demonstrated the principle on two Namib tenebrionid species. Cloudsley-Thompson (1977) rejected the 'maxithermy' theory of black integuments, and maintained that the primary function of black in desert beetles is aposematic (Cloudsley-Thompson, 1965, 1975, 1977). Such a aposematic function is admirably demonstrated by Doyen & Somerby (1974) in a Müllerian complex of American desert tenebrionids, but does not seem to explain the black diurnal Namib beetles, which all seem to be palatable to predators (judging from jackal and crow droppings, owl pellets, lizard stomach contents and several years of field observations by one of us, E. H.). Melanin may contribute to the water impermeability of the cuticle and prevent water loss (Hamilton, 1975; Cloudsley-Thompson, 1977 and references), but neither Hamilton nor Cloudsley-Thompson considers this to be the prime function of melanin in desert beetles. Lastly, melanin may also confer resistance to bacterial attack (Hackman & Goldberg, 1968).



s in south
us species;
. *denticolle*

:d physio-

The white tenebrionids of the relatively cool and moist coastal Namib dunes and plains have received much attention and are not discussed in the present paper because they do not constitute unmelanized forms, since the white elytral covering is on a dark base (Hamilton, 1975). The various coverings of light wax, scales and hair on black diurnal tenebrionids may be ways of combining the advantages of a melanized cuticle with a light coloured surface, and may have several functions in the thermoregulation, water conservation and general niches of these insects.

Lack of black pigmentation, on the other hand, is much more prevalent among nocturnal beetles in the Namib Desert than among their mesal counterparts and, as we have mentioned, occurs in a number of diurnal species which have exclusively black counterparts elsewhere. For the purpose of this discussion we presume the black of the beetles' integument to be caused by melanin. A combination of melanin with other dark pigments such as dark omochromes would not alter our arguments much, since the latter behave physiologically similarly to melanin in relation to temperature (Bellamy, 1958).

There is a considerable body of evidence to suggest that high temperatures inhibit melanization of the cuticle without affecting sclerotization. Uvarov (1966) ascribed the colour differences between solitary and gregarious locusts primarily to differences in metabolic rates, and Husian & Ahmed (1936) indicated a steep reduction in melanization of *Schistocerca gregaria* at breeding temperatures from 24 °C to 44 °C. Albino locusts may be reared at very high temperatures. Gortner (1911) found that formation of melanin in the elytra of *Leptinotarsa* is inhibited by high temperatures.

There are also some suggestions that low humidity may inhibit melanization (Bodenheimer, 1954). Owen (1966) recorded apparently environmentally induced colour differences in wet and dry seasonal forms of African butterflies, and Joly (1960) concluded from his work on locusts that low humidities may inhibit melanization.

Locusts produce melanistic forms after grass has been burnt (Hocking, 1964; Burtt, 1951) but the mechanism by which this melanization is induced is not known (Edmunds, 1974). Other factors affecting melanization may exist, but temperature and humidity are those which have been indicated most conclusively.

Edney, Cloudsley-Thompson and others have repeatedly warned against generalizations on environmental conditions in deserts, since any animals' microclimatic environment may differ vastly from the macroclimate, while the effect of the environment is further modified by behaviour. Yet there is reason to believe that the diurnal desert scarabs are indeed (at least for times within their minimal daily activity cycle) exposed to hotter and drier conditions than their mesal counterparts. These exposures would encompass the slow process of sclerotization and melanization, which occurs after emergence. (It should be noted that recently emerged unmelanized specimens can easily be recognized by their lack of sclerotization. In the present investigation, such specimens were not considered to be unmelanized forms.)

Prosser (1960) summarized the evidence demonstrating that the first response of animals to a new environmental pressure is physiological, and that the resulting phenotype only subsequently becomes incorporated in the genetic make-up of the population, and consequently susceptible to adaptation and selection. While unmelanized body parts are certainly genetically fixed in such species as *S. rubripennis*, there are reasons to believe that the reddish elytra of some *S. parvulus* group specimens are still only physiologically determined. In these cases insects can be found showing a complete gradation from heavily to weakly melanized (especially on the elytra). Often the least melanized specimens are so inconspicuously lighter than their black counterparts that a selective advantage through the effect of the colouring of the phenotype seems extremely unlikely.

The zonation of melanin

In the scarabs with well-developed orange elytra the pronotum, head and underside are invariably black. The same situation is found in many of the nocturnal tenebrionid species, and also in the white tenebrionids of the Namib. Hamilton (1974) mentioned that this phenomenon could be explained by the need for protection of vital organs against UV radiation (as suggested by Porter, 1967) in the cases of the head and pronotum, but not for the underside. Protection against UV also fails to explain why nocturnal species (e.g. *Uniungulum hoeschi* Koch, *Vernayella pauliani* Koch, and *Ograbies testaceus* Solier) have darker heads and pronata than elytra. It should be noted that the elytra (and to a lesser extent the legs) are also the only body parts with reduced melanization in the South West African buprestids mentioned above.

For other plausible explanations for zonation of melanin we have to look at the other functions of this pigment. The strengthening property would call for a concentration in the body parts which are most susceptible to abrasion and carry the most vital muscular attachments. The water-conserving property would be least needed in the elytra above the sub-elytral cavity (although the water-conserving function of this cavity has been questioned, see Edney, 1971). Finally, in a case of short supply of melanin, the extremities might be deprived first simply because they are least provided with chemicals through the haemolymph. It is therefore probably no coincidence that lack of melanin affects the elytra first and most severely in virtually all under-pigmented Namib beetles, with the appendages (between joints where strength for muscle attachments is least needed) in second place.

It follows that, when melanin is at a premium, it would logically not be evenly spread, and the elytra could be expected to suffer the first and most severe reduction.

Possible advantages of orange elytra

Bock (1959) gave a sensible explanation of evolutionary pre-adaptation, by stating that a character evolves under selection pressure A to a point where selection pressure B takes over, and then B may completely change the significance and direction of development of the character. In the case of the orange Namib scarabs, A would be an environmentally induced physiological pressure (not a selection pressure on the genotype), resulting in a physiological reduction in melanization through hot and dry conditions. Once this was expressed by orange (or moderately orange) elytra, it offered a phenotype which *could* acquire advantages in a new context, B, and (after genetic fixation) be selected for by pressure of B. In this case, as in Bock's model, A may be quite unrelated to B. Since well-developed and probably genetically fixed orange elytra occur in some Namib scarabs, we can here assume B to have selected positively for orange elytra. The possibilities of a selective advantage for B which occurred to us are the following:

(1) Orange elytra may become useful for thermo-regulation.
(2) They may be cryptic and/or form-disruptive (on the reddish sands of the Namib dunes).
(3) The colour may be employed for social functions, such as mate recognition or territoriality.
(4) The orange elytra may be aposematic if one or more of the orange species are distasteful or noxious to predators.
(5) They may be aposematic if one or more of the species possess effective escape mechanisms.

Of these possibilities, only the fifth holds much promise for explaining the orange elytra of Namib scarabs. The first possibility is counter-indicated by the very small temperature differences we measured under black and orange elytra. With electric probes inside the sub-elytral cavities of dead beetles in direct insolation, we found maximal differences below 1 °C between black and orange forms of *P. denticolle*, and black *S. flavicornis* and equal-sized orange *S. rubripennis* (with the black forms hotter in all cases). The average difference at equilibrium was below 0·5 °C (with 12 repetitions). The differences in rates of heat gain were negligible. One of us (E. H.) measured abdominal temperatures of live orange-coloured *P. denticolle* in the Namib dunes. Seventeen specimens were picked at random throughout the day's activity cycle of the beetles, and eleven of the temperatures measured fell between 38 ° and 42 °C (which very closely matches Hamilton's prediction for maxithermy), with the lowest record 26·5 °C and the highest 42·9 °C. It would seem that *P. denticolle* is a maxitherm, but that colour has no significant effect on its temperature. On the other hand, all poikilotherms are maxitherms within the limits of their environment (Cloudsley-Thompson, 1977). The same would undoubtedly apply to the other orange scarabs, and would also preclude the refinement that differentially coloured body parts may be exposed selectively to the sun to thermoregulate (Edney, 1971; Hamilton, 1975).

The second possibility might contribute slightly to selection for orange elytra, especially during the digging of burrows when for a short period only the red abdomen is exposed. The beetles are, however, extremely conspicuous on the bare dunes (at least to humans and therefore presumably also to jackals and birds).

The possible advantage of mate recognition is reduced by the sympatric occurrence of other orange species, and seems unlikely in the two cases which have both well-developed orange and black forms and intermediates (*P. denticolle, D. proximus*). Platt & Brower (1968) found random interbreeding between mimetic and non-mimetic forms of butterflies, and there is no reason to believe that the situation between black and orange forms of scarabs is different. Territoriality may be ruled out, since none of the species exhibit any of the behaviour patterns normally associated with territoriality, and densities are highly clumped on available concentrations of food.

Unpalatability of the orange scarabs is very unlikely, for the same reasons given for black beetles above. Rejected damaged specimens were not found among the hundreds of live specimens and carcasses collected in the dunes.

The last possibility, namely that the orange colour is employed to advertise being 'high investment/low reward' prey to vertebrate predators (or 'frustration learning'—Gibson, 1974), offers a fascinating theory for the evolution of the various orange species in the Namib. Hespenheide (1973) recorded this type of mimicry in a predominantly Müllerian complex involving flies and agile beetles in the American tropics. Rettenmeyer (1970) included an effective escape mechanism in his list of features worth mimicking, and it is also mentioned by Edmunds (1974). Gibson (1974) demonstrated experimentally that birds learn to avoid rapidly escaping prey, and cites two recorded instances of mimicry of rapidly escaping prey. The learning response in the predator is in these cases obviously different from the classical cases of mimicry of unpalatable or noxious specimens, and the Müllerian/Batesian type of distinction may not be adequate. Captured models will not be rejected and will weaken the learning of the predator rather than strengthen it.

In the Namib dune area vertebrate predators are well in evidence. For the diurnal scarabs in particular, the crows, jackals, *Meroles* lizards, chameleons and various small predatory and insectivorous birds may be the most important, the latter particularly on the edges of the dune area and along river beds.

Holling (1963, 1965) demonstrated that the abundance of alternative prey is crucial to the success of any mimetic complex. The high preponderance of black diurnal beetles in the Namib makes the few and not very populous orange species conspicuous rarities. Rettenmeyer (1970) further summarized the requirements for Batesian mimicry as: (1) presence of undesirable properties in the model; (2) a resemblance between model and mimic which is appreciable to the predator(s); (3) Lower abundance for mimic than for model; (4) space/time sympatry between mimic and model; (5) conspicuousness and distinctness of both mimic and model relative to other prey; (6) learning ability of the predator(s). Of these requirements, the third was questioned by Brower (1960) and Holling (1963, 1965). In our situation with the scarabs with orange elytra, all requirements, except (1), (2) and (6), are evidently met, and we shall assume (2) and (6) to be present. Condition (1) is discussed under point (1) below. An aspect of (4), namely that mimetic species become non-mimetic outside the distributional range of their model (Rettenmeyer, 1970), is convincingly illustrated by *P. denticolle* (Fig. 1). Rettenmeyer (1970) drew attention to the fact that invertebrate predators are usually unable to see red, and suggested that aposematic red may have to be broken by black to create a pattern which is visible to them. This, added to form-disruptive effect, may strengthen the zoning aspect of black and orange body parts in the scarabs. Edmunds (1974), however, found no learning response to colour in mantids, and concludes that vertebrate predators are needed to select for mimicry.

The fastest and most agile species among the orange scarabs is *S. rubripennis*. It also seems to have the reddest elytra, and no black forms occur (Plate 1(d)). It is a scavenger on dead animals (e.g. dead beetles, larvae, snakes, lizards and *Gerbillus* species), but also forages on jackal dung. Its food niche, therefore, agrees with that of the Trogidae, which are absent in the main distribution of *S. rubripennis* in the central Namib dunes (Scholtz, 1979). *D. proximus* occurs partly sympatrically with *S. rubripennis* in the south, and has well-marked black and orange forms with occasional intermediates. Orange forms predominate where it is sympatric with *S. rubripennis*. Those specimens of the *S. parvulus* group which have some degree of orange coloration on the elytra occur parapatrically with *S. rubripennis* in the north. Our explanation for this combination of species is as follows:

(1) *S. rubripennis* was most probably the first alate scarab to adapt to the conditions of the Namib dunes by a considerable shift of food niche (made possible by the absence of Trogidae, and necessary by the already-established apterous scarabs in the herbivore-dung niche). This species was also probably the first to develop orange elytra, which were further selected for by the establishment of the association between speed and orange in the predators (meeting condition (1) above).

(2) *D. proximus* was placed under a selective regime already established, and the development of red elytra would have been supported by and would have strengthened this regime. Thus the mimicry between alate species would be partly Müllerian, partly Batesian, as indeed most cases of so-called Müllerian mimicry can be expected to be (Rettenmeyer, 1970).

(3) It is not clear whether the *S. parvulus* group specimens with red elytra are participating in this Müllerian mimicry, but we rather doubt it. Firstly the orange specimens are not yet fully orange, and are rather inconspicuous, and secondly they form a very small minority. It could, however, be predicted that if these species should invade the Namib proper, they would evolve along the same lines as *S. rubripennis* and *D. proximus*.

With the situation established as described above, it is not difficult to envisage the origin of the purely Batesian mimicry by *P. denticolle* of *S. rubripennis*. The two species are sympatric (Figs 1(a), 3(c)), of equal size and active in the same habitat during the same times of day (bimodally diurnal on hot days, unimodally diurnal on cool days). *P. denticolle*, which is black on the coast and has thirteen black congeners elsewhere (Holm & Scholtz, 1979), must have evolved orange elytra (from probably already brownish elytra in the dune populations) under the selective advantage created by *S. rubripennis*. *P. denticolle* is much less frequently found in traps than *S. rubripennis*, but it is difficult to compare densities between the species on account of *S. rubripennis* being so much faster than *P. denticolle*. Effective densities of prey species obviously do not rely on numbers only, but also on their relative vagility and that of the predator. Holling (1962, 1965) predicted that 30 per cent of models will protect 70 per cent mimics, and that this protection would increase with availability of alternative and distinct prey. The biology and relationship of the *Pachysoma* species are further discussed elsewhere (Holm & Scholtz, 1979).

Summary

We have recorded what we believe to be one of the few recorded Batesian and the first recorded Müllerian mimicry complex exclusively based on the agility of the prey. All the species involved belong to the tribe Scarabaeini.

The pre-adaptation which underlies the parallel coloration in all cases is argued to be a physiological consequence of the desert environment.

We wish to thank Dr S. Endrödy-Younga of the Transvaal Museum and Dr G. F. Bornemissa of the Dung Beetle Research Unit, C.S.I.R.O., for the loan of material. We should also like to thank our colleagues, Professor J. J. Matthee and Mr C. H. Scholtz, for useful suggestions. The research was partly financed by a C.S.I.R. grant.

References

Bellamy, D. (1958). The structure and metabolic properties of tissue preparations from *Schistocerca gregaria* (desert locust). *Biochemical Journal*, **70**: 580–589.

Bernardi, G. (1962). La variation géographique du mimétisme chez les Lépidoptéres. *Annales Société Entomologique Française*, **130**: 77–94.

Bernardi, G. (1963). Quelques aspects zoogéographiques du mimétisme chez le Lépidoptères. *Proceedings of the 16th International Congress of Zoology*, Washington **4**: 161–166.

Bock, W. (1959). Pre-adaptation and multiple evolutionary pathways. *Evolution*, **13**: 194–211.

Bodenheimer, F. S. (1954). Problems of physiology and ecology of desert animals. In Cloudsley-Thompson, J. L. (Ed.). *Biology of Deserts*, pp. 162–167. London: Institute of Biology. 224 pp.

Brower, J. V. Z. (1960). Experimental studies of mimicry. 4: The reactions of starlings to different proportions of models and mimics. *American Naturalist* **94**, 271–282.

Burtt, E. (1951). The ability of adult grasshoppers to change colour on burnt ground. *Proceedings of the Royal Entomological Society of London* (A) **26**: 45–48.

Cloudsley-Thompson, J. L. (1965). Microclimate and desert adaptation in Arthropoda. *Proceedings of the 12th International Congress of Entomology*, London, 1964, p. 404.

Cloudsley-Thompson, J. L. (1975). Adaptations of Arthropods to arid environments. *Annual Review of Entomology*, **20**: 261–272.

Cloudsley-Thompson, J. L. (1977). The black desert beetle paradox. *Entomologists' Monthly Magazine*, **113**: 19–22.

Doyen, J. T. & Sommerby, R. E. (1974). Phenetic similarity and Müllerian mimicry among darkling ground beetles. *The Canadian Entomologist*, **7**: 759–772.

Edmunds, M. (1974). *Defence in Animals*. Harlow, Essex: Longman. 357 pp.

Edney, E. G. (1971). The body temperature of tenebrionid beetles in the Namib Desert of Southern Africa. *Journal of Experimental Biology*, **55**: 253–272.

Ferreira, M. C. (1953). Monografia dos Escarabaeideos da Africa do Sul. *Bolletim da Sociedade de Estudos de Mocambique*, **23** (80): 1–81.

Ferreira, M. C. & Ferreira, da V. (1958). Contribuição para o estudo dos Buprestides da subregiao natural da Africa do Sul I. *Revista de Entomologia de Mocambique*, **I** (1): 1–136.

Gibson, D. O. (1974). Batesian mimicry without distastefulness ? *Nature*, **250**: 77–79.

Gortner, R. A. (1911). Melanin and colour pattern: *Leptinotarsa* Col. *American Naturalist*, **45**: 743–755.

Hackman, R. H. & Goldberg, M. (1968). A study of a melanic mutant of the blowfly *Lucilia cuprina*. *Journal of Insect Physiology*, **17**: 335–347.

Hamilton, W. J. III (1973). *Life's Color Code*. New York: McGraw-Hill. 238 pp.

Hamilton, W. J. III (1975). Coloration and its thermal consequences for diurnal desert insects. In Hadley, N. F. (Ed.), *Environmental Physiology of Desert Organisms*, pp. 67–89. Stroudsburg: Dowden, Hutchinson & Ross. 283 pp.

Henwood, K. (1975). A field tested thermoregulation model for two diurnal Namib Desert tenebrionid beetles. *Ecology*, **56**: 1329–1342.

Hespenheide, H. A. (1973). A novel mimicry complex: beetles and flies. *Journal of Entomology* (A) **48**: 49–56.

Hocking, B. (1964). Fire melanism in some African grasshoppers. *Evolution*, **18**: 332–335.

Holling, C. S. (1963). Mimicry and predator behaviour. *Proceedings of the 16th International Congress of Zoology*, Washington, **4**: 166–172.

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, **45**: 1–60.

Holm, E. (1979). Revision of the genera *Amblysterna* Thomson, *Neojulodis* Kerremans and the African species of *Julodella* Semenow. *Entomology Memoirs Department of Agricultural Technical Services Republic of South Africa*. (In press.)

Holm, E. & Edney, E. B. (1973). Daily activity of Namib Desert arthropods in relation to climate. *Ecology*, **54** (1): 45–56.

Holm, E. &
and *Neopo*
its genera (
42 (2). (In
Husian, M.
temperatur
crowded.
Joly, P. (196
Zoologique
Neville, A.
Owen, D. F.
Platt, A. P.
population
Porter, W. P.
on desert
Prosser, C.
after Darw
629 pp.
Rettenmeyer,
Scholtz, C. H
in South W
Uvarov, B. (1
481 pp.
Wigglesworth
and Hall. 8

Holm, E. & Scholtz, C. H. (1979). Revision of the species attributed to *Pachysoma* M'Leay and *Neopachysoma* Ferreira with an evaluation of the subtribe *Pachysomina* Ferreira and its genera (Coleoptera: Scarabaeini). *Journal of the Entomological Society of Southern Africa,* **42** (2). (In press.)

Husian, M. A. & Ahmed, T. (1936). Studies on *Shistocerca gregaria* Forsk. VI. Influence of temperature on the intensity and extent of black patterns in the desert locust hoppers bred crowded. *Indian Journal of Agricultural Science,* 6: 624–664.

Joly, P. (1960). Un cas de gynandromorphisme chez *Locusta migratoria* L. *Bulletin Société Zoologique Française.*

Neville, A. C. (1975). Biology of the arthropod cuticle. Springer-Verlag, Berlin. 448 pp.

Owen, D. F. (1966). *Animal Ecology in Tropical Africa.* San Francisco: Freeman.

Platt, A. P. & Brower, L. P. (1968). Mimetic versus disruptive coloration in intergrading populations of *Limenitis arthemis* and *Astyanax* butterflies. *Evolution,* **22**: 699–718.

Porter, W. P. (1967). Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. *Ecological Monographs,* **33**: 273–296.

Prosser, C. L. (1960). Comparative physiology in relation to evolutionary theory. *Evolution after Darwin.* 1: *The Evolution of Life,* pp. 569–594. Chicago: University Chicago Press. 629 pp.

Rettenmeyer, C. W. (1970). Insect mimicry. *Annual Review of Entomology,* **15**: 43–74.

Scholtz, C. H. (1979). Taxonomic revision and distribution of the genus *Trox* (Col.: Trogidae) in South West Africa. *Cimbebasia.* (In press.)

Uvarov, B. (1966). *Grasshoppers and Locusts,* Vol. I. Cambridge: Cambridge University Press. 481 pp.

Wigglesworth, V. B. (1974). *The Principles of Insect Physiology, 7th edition.* London: Chapman and Hall. 826 pp.

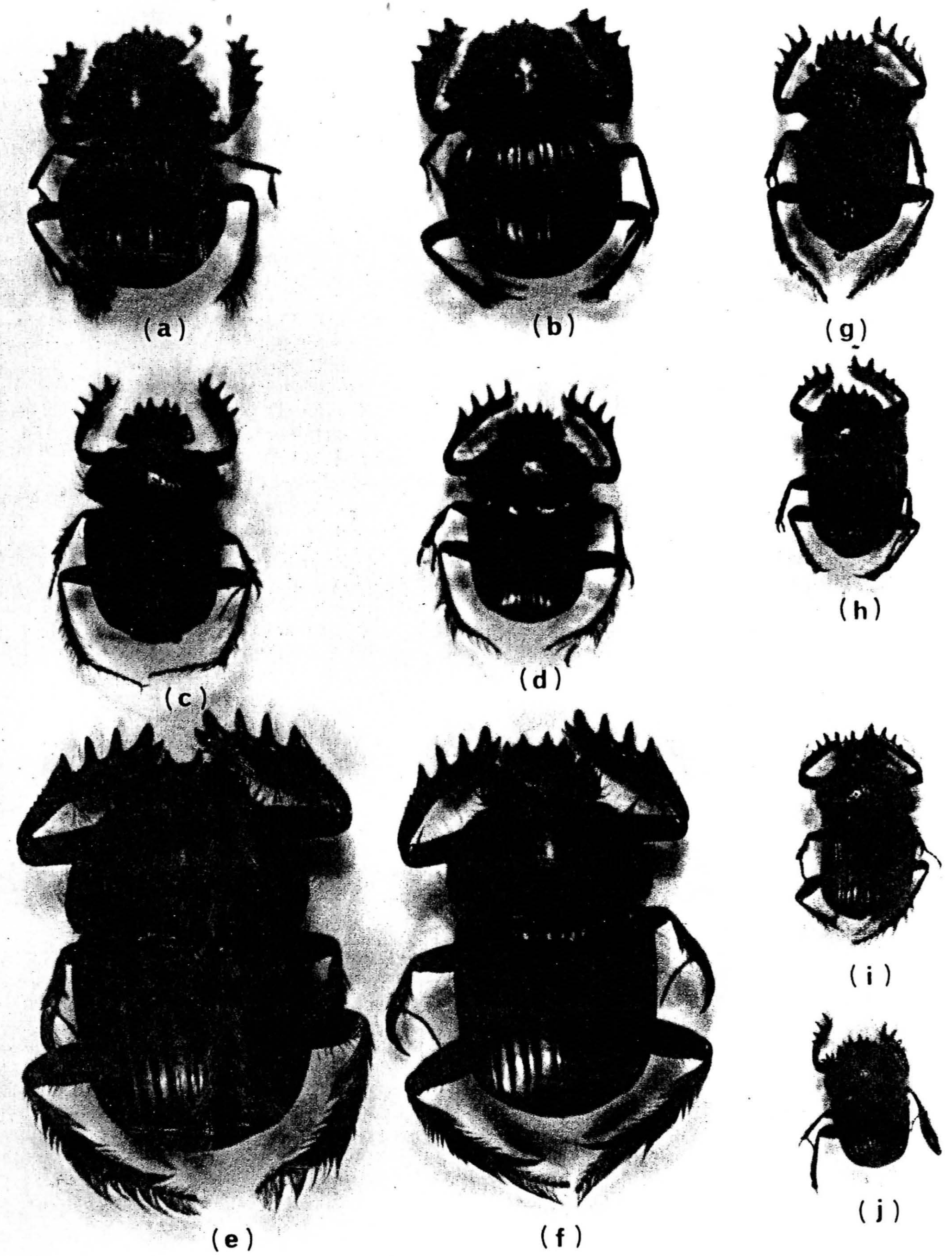


Plate 1. The Scarabaeinae of the central Namib dune area. (a) *Pachysoma denticolle*, black variety from Walfish Bay; (b) *P. denticolle* with orange elytra; (c) *Scarabaeus flavicornis*; (d) *S. rubripennis*; (e) *Drepanopodus proximus*, black variety; (f) *D. proximus* with orange elytra; (g) *S. bohemani*, extreme of orange elytra; (h) *S. bohemani*, normal black form; (i) *S. parvulus* group species, extreme of orange elytra; (j) *S. parvulus* group species, normal black form).

[*facing page 263*]

Pre-adapt

The v
elytra
specie
selves
the a
compl
occurr
mimet

The Scarabaeini
area in the centr
represented outsi
species, *Scaraba*
guey) (Plate 1(e)
1(a), (b)), is apte
which occurs thr
1(c)) is always b
Namib. *D. proxi*
intermediates, an
P. denticolle has
mediate and com
north of Sandwi
colour of these t

In addition to
baeus parvulus g
One of these, *S.*
elytra from Moç
to moderately or
S. parvulus grou
black *S. bohema*
(Plate 1(g)).

The Buprestid
with brown to l
viridescent. This
Ferreira & Ferre

---

* Department o

0140-1963/79/03026