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Cryptic colouration and melanism in the sand-burrowing beetle Chaerodes trachyscelides (Coleoptera: Tenebrionidae)

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Cryptic colouration and melanism in the sand-burrowing beetle *Chaerodes trachyscelides* (Coleoptera: Tenebrionidae)

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The flightless, sand-burrowing beetle *Chaerodes trachyscelides* White is confined to the intertidal zone of sandy marine beaches in New Zealand. The dorsal surface varies from black to pale whitish-yellow, and most specimens closely match the colour of the sand they live on. On a beach with pale sand, about 98% of specimens are whitish on the dorsal surface, and about 1% are black. Conversely, on a beach with black sand, about 96% are black and about 1% are whitish. The beetles live under cast-up marine algae on which they feed, and burrow beneath it in the sand. When predatory sea birds pick up such algae, invertebrates, including *C. trachyscelides*, fall out, run a short distance, and burrow into the sand. I suggest that a higher proportion of beetles coloured less like the sand are eaten by seabirds, and that these predators exert differential selection (genetic or phenetic) against non-cryptically-coloured individuals. However, there is as yet no way of telling whether the genetic mechanism is the same as in the classical example of industrial melanism in the pepper moth *Biston betularia*.

Keywords: Cryptic melanism, sandy marine beaches, Chaerodes trachyscelides, *Coleoptera.*

INTRODUCTION

Colour and pattern in animals may be determined by the interaction of several different types of selection, of which thermoregulation, intraspecific communication and evasion of predators are the most significant (Endler, 1978). Numerous investigations involving visible genetic polymorphisms have paid attention to the pleiotropic effects of the genes for colour pattern, as well as the primary adaptive significance of the colour pattern of the phenotype (Ford, 1975; Kettlewell, 1973). In New Zealand, many species of insects display environmental melanism. Harris (1974, 1987) showed that several species of endemic Pompilidae (spider-hunting wasps), active as adults throughout New Zealand but generally only in sunlight, become progressively darker southwards with decreasing mean annual temperature and decreasing solar radiation. Harris (1974) showed that predictable degrees of melanism could be induced in some species by variably lowering the temperature experienced by the pupa during the period of pigment deposition in the cuticle. This melanism is related to thermoregulation in adults; conversely, melanism in *Chaerodes trachyscelides* appears to be a means of predator avoidance through cryptic coloration.

Chaerodes trachyscelides White is a highly convex, rotund flightless beetle about 7 mm long, greatly modified for burrowing in sand. It is confined to the intertidal zone of sandy marine beaches on New Zealand's three main islands. the adults live under the cast-up marine algae upon which they feed. Unlike the false wireworm larvae of most Tenebrionidae, the larva is white and u-shaped. The adult beetle is nocturnal.

If seaweed such as "flap jack" (*Carpophyllum maschalocarpum*), partially buried in sand, is pulled up during the day and shaken, adult beetles fall out, run along the beach a short distance and then burrow rapidly in the sand. Large numbers of adult beetles often congregate in the sand at depths of up to 150 mm below cast-up seaweed.

The beetles vary greatly in colour. While the undersurface of adult beetles is always uniform pale whitish yellow, the dorsal surface is highly variable, ranging from uniform

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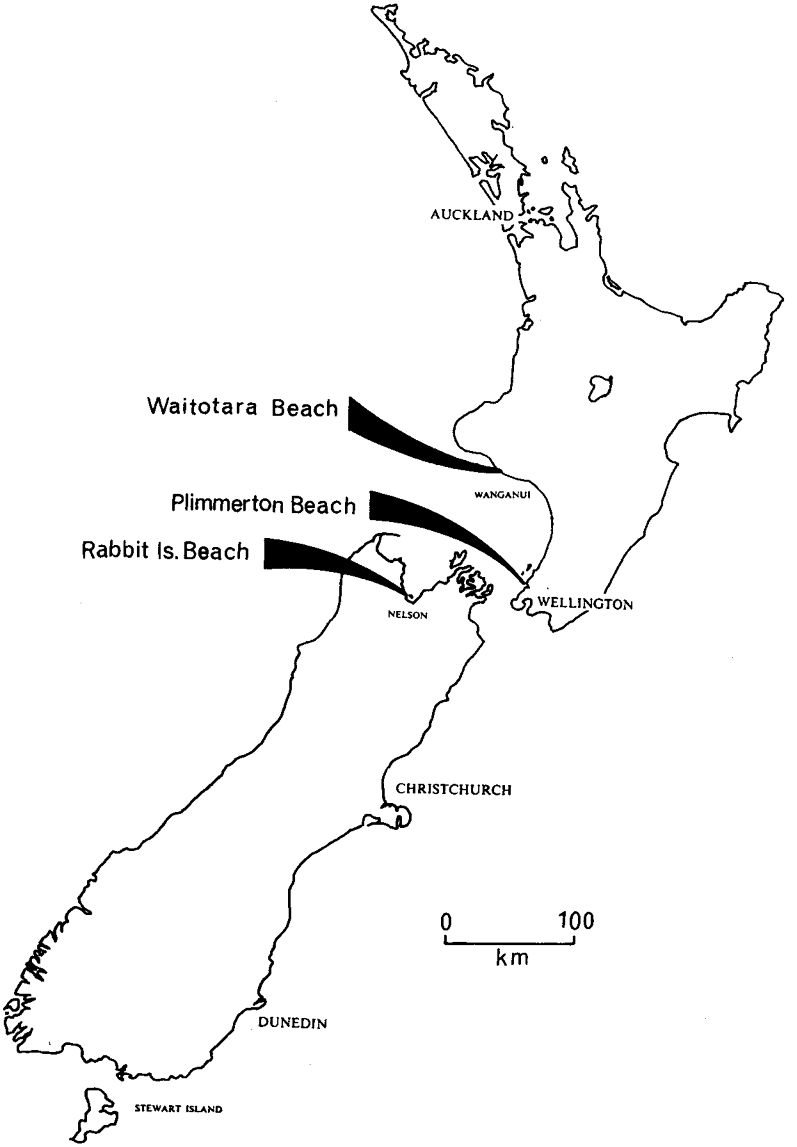


Fig. 1 — Locality map of New Zealand, showing positions of the three beaches from which samples were taken.

pale whitish yellow, through individuals speckled variously with black and shades of brown, to completely black. Generally, the colour of the dorsal surface of most of the individuals resembles that of the sand of their home beach. Nevertheless there are always a few individuals coloured conspicuously unlike the sand. This is very striking on beaches with very black or very pale sand.

Samples of beetles and sand were taken from three beaches (Fig. 1): Waitotara Beach, north of Wanganui (39°52′S, 174°43′E) (black sand); Plimmerton Beach, Wellington (41°05′S, 174°50′E) (light brown sand); Rabbit Island, Nelson (41°16′S, 173°09′E) (very pale whitish-yellow sand).

METHODS

Sand was collected in three 75 × 25 mm vials filled from just below mean high water level on each of the three beaches. The samples were sent to Dr. D. Craw (Geology Dept., University of Otago) for petrographic analysis. Sand from each sample was sprinkled into a glue mounting medium on a glass slide, ground to about 30 μm, and sealed under a cover slip with Canada balsam. The mineral types present were then determined, and their relative proportions were estimated using comparative charts (*e.g.*, interference colour charts for common minerals). The estimates are correct to within about 10%.

The remainder of the three sand samples were sent to Dr. I. Weatherall (Faculty of

Fig. 2 — Beetles from Waitotara Beach: left to right black, speckled, pale.

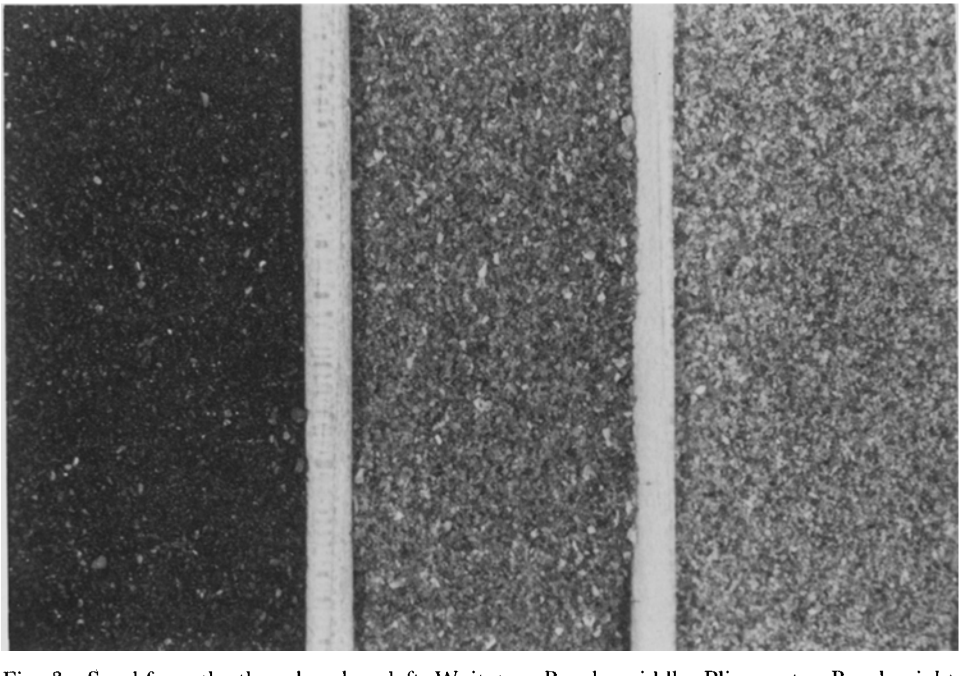
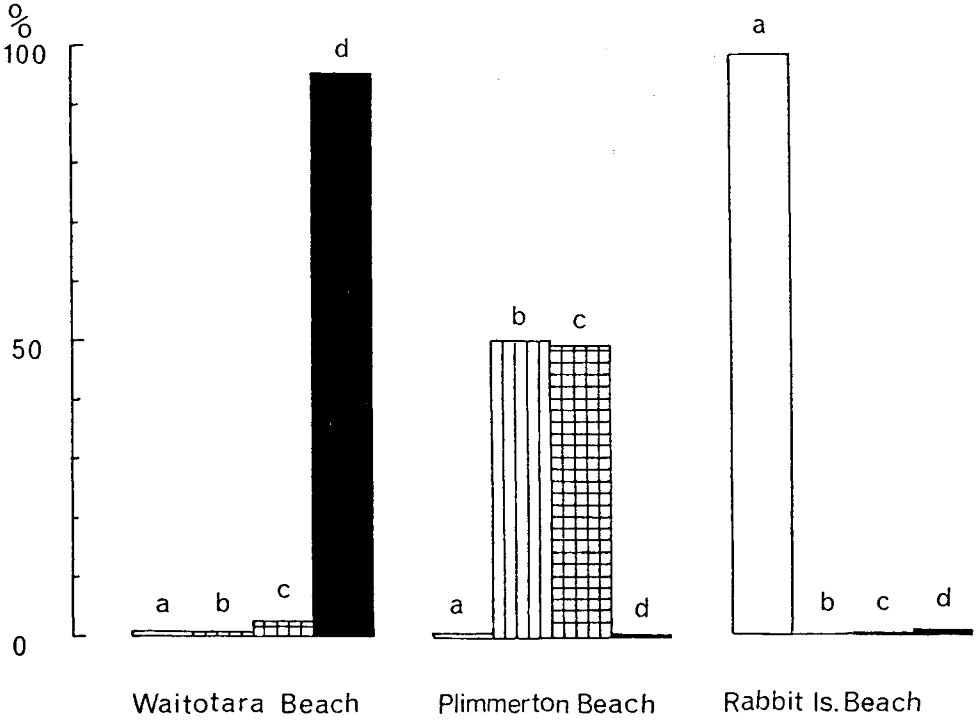


Fig. 3 — Sand from the three beaches: left, Waitotara Beach; middle, Plimmerton Beach; right, Rabbit Island Beach.



KEY
Colour of dorsal surface of beetle

- a pale straw colour
- b light speckled
- c dark speckled
- d black

Fig. 4—Percentage of beetles with dorsal surface black, speckled, or pale on each beach. Number of beetles collected: Waitotara, 88; Plimmerton, 214; Rabbit Island, 276.

Home Science, University of Otago). The absorbance spectrum of each was measured with a Pye Uniscan SP8-400 UV-VIS spectrophotometer equipped with a Philips integrating sphere. Measurements were made from 700 to 400 nm, in total diffuse reflectance mode.

Beetles were collected by shaking the sand around and beneath cast-up marine algae through sieves of various sizes. Clumps of marine algae were also shaken over sieves. Beetles were removed from the sieves and mounted. Each beetle was classified as dark, speckled (this category could be subdivided into dark speckled or light speckled) and pale (Fig. 2)

RESULTS

The sand from Waitotara beach is very dark; that from Rabbit Island very pale; and that from Plimmerton intermediate (Fig. 3). These distinctions are clearly shown in the

Table 1 — Petrographic analysis of sand (% composition) from the three beaches sampled

	Waitotara	Plimmerton	Rabbit Is.
Dark grains			
hornblende/pyroxene/magnetite	80	5	5
illmenite	15		
unidentified	5	30	35
green phyllosilicates			4
opaques, epidote etc.			<1
Light grains			
quartz		35	45
feldspar		15	10
calcite		15	1
Ratio dark to light	100:1	35:65	45:55
Total diffuse reflectance	0.95%	0.67%	0.61%

spectrophotometer results: sand from Waitotara beach (black) had an absorbance ranging from 0.94 at a wavelength of 400 nm to 0.98 at wavelength 740 nm. Plimmerton beach sand (pale) had an absorbance ranging from 0.82 at wavelength 400 nm to 0.61 at wavelength 760 nm. Rabbit Island beach sand (very pale) had an absorbance ranging from 0.71 at wavelength 400 nm to 0.54 at wavelength 760 nm. Results of the petrographic analysis combined with total absorbance are given in Table 1. The distribution of dark, speckled and pale beetles collected from each beach is shown in Fig. 4.

DISCUSSION

Cryptic melanism has been studied intensively in the U.K. by E. B. Ford, H. B. D. Kettlewell, D. R. Lees and others. The best known study is Kettlewell's investigation of industrial melanism in the pepper moth *Biston betularia*. Before 1850, a dark form (*carbonaria*) was known but rare (about 1% of individuals). In the late nineteenth century the frequency of *carbonaria* increased to over 90% in woods near industrial cities such as Birmingham. Kettlewell found that trees, once covered with whitish lichen, were now almost lichen-free and black with soot. In experiments, he released equal numbers marked white (*typica*) and black (*carbonaria*) forms of the moth and watched them from a hide. Birds ate many of the moths, choosing many more of the conspicuous white moths than the well-camouflaged black ones. He repeated the same experiment in an unspoiled wood in Dorset, and this time more of the black forms (conspicuous on lichen) were taken by birds. In light-traps a few days later he re-captured far fewer of the forms coloured unlike the background. Thus natural selection, through differential predation, favoured the survival of the melanic (*carbonaria*) form in darkened, industrial areas, and the light (*typica*) form in non-industrial regions. Haldane (1924) estimated that the average selection disadvantage of the *typica* form in the Manchester area during the period 1848-1898 was 30%.

Although this classic study is still the subject of some dispute (*e.g.*, by Mikkola, 1984), new examples of the phenomenon are constantly being reported, and interpreted in the same general terms. Industrial melanism has recently been reviewed by Bishop and Cook (1980) and Lees (1981).

Melanism in *Biston betularia* involves one gene locus, five alleles and dominance. In some other insects, melanism is polygenic. In the case of *Chaerodes trachyscelides*, continuous variation is shown on some (but not all) beaches of intermediate brownish-grey, suggesting that two or three alleles may be involved. Specimens on such beaches were mostly speckled. Some had the elytra with dark speckling, and the pronotum pallid, while others had the pronotum dark-speckled but the elytra light. However, it is not known whether this variation is genetic or phenetic.

The match between beetles and sand is very striking, especially on beaches that are either very black (Fig. 5) or very pale (Fig. 6). Visual observation on the beaches at Waitotara,

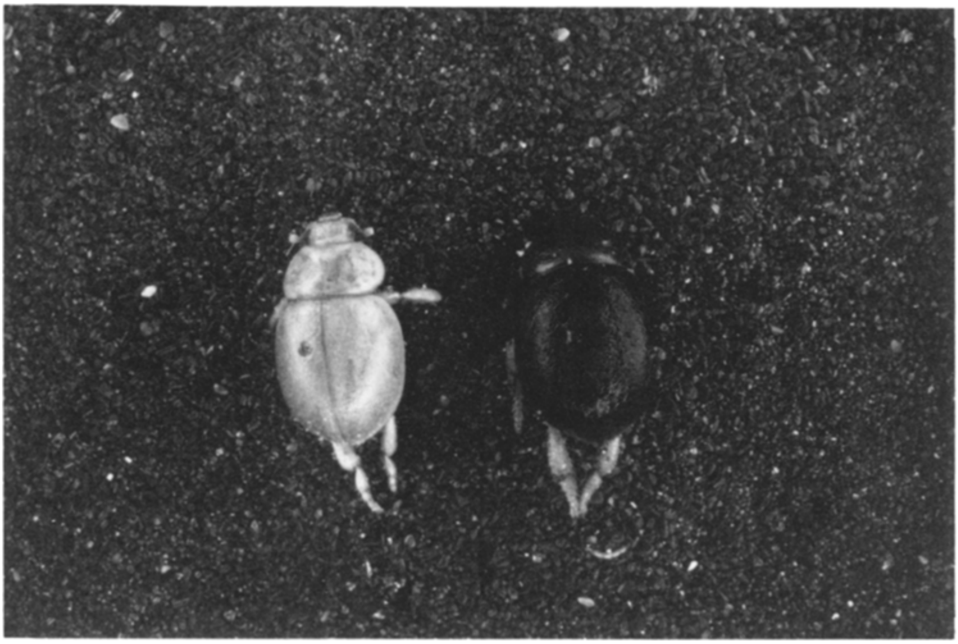


Fig. 5—Sand with pale and black beetles from Waitotara Beach.

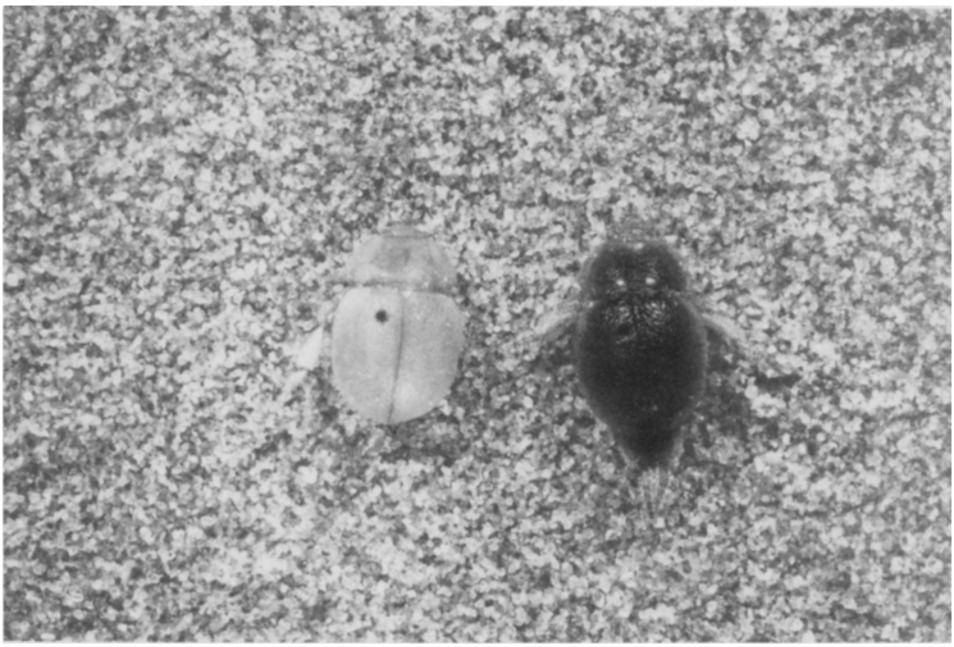


Fig. 6—Sand with pale and black beetles from Rabbit Island Beach.

Plimmerton and Nelson suggests that the main avian predators of *Chaerodes trachyscelides* are oyster catchers (*Haematopus finschi, H. unicolor*) and banded dotterels (*Charadrius bicinctus*). In addition to probing into the sand with their bills, oyster catchers and gulls sometimes pull up seaweed partially buried in the sand, shake it, and eat the invertebrates that drop out. Beetles would run on the surface a short distance before burrowing into the sand. I suggest that the birds take a higher proportion of beetles coloured unlike the sand, because they are more conspicuous.

C. trachyscelides is flightless, and populations on beaches can be isolated on all sides. This is offset to an unknown degree by the fact that these beetles survive rafting quite well; when a high tide takes dead seaweed, and the beetles feeding on it, out to sea, the seaweed and its retinue of beetles may be deposited somewhere else. Nevertheless, vagility is likely to be low, and this would favour the local persistence of the ratio of light to dark beetles favoured at that site.

Before the genetic basis of melanism in *C. trachyscelides* can be understood, offspring of black, white and speckled beetles will have to be reared, and back-crosses and intercrosses made. Another useful experiment would be to release equal numbers of marked black and whitish beetles on white sand beaches and on black sand beaches, and to perform capture-recapture experiments, in order to determine the relative survival rates of individuals coloured unlike the surrounding sand or not.

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