

SELECTION FOR MELANISM AND FOR LOW REPRODUCTIVE RATE IN *TRICHOSURUS VULPECULA* (MARSUPIALIA)

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SUMMARY: Agouti grey pelage, as found in the opossum and many other mammals, is a generalised concealing coloration. In dense vegetation melanic pelage also is concealing, but the melanic phase displaces the grey one in rain forests where, in the current absence of predation, selection is not for colour. This local dominance suggests close linkage of genes for melanism with ones for toleration of humidity.

Since food trees of the opossum are killed by heavy browsing, a low birth rate conserves limited resources. Elimination of surplus young would not be effective in this because there is a long period of maternal protection, and young do not face direct competition for food before reaching an age of one and a half years.

Increase of reproductive rate is beneficial to the species when vacant habitat is available, but such an increase is dangerous unless curbed after population establishment. Field evidence in New Zealand shows that, despite abundance of food, a low reproductive rate is usual. This would be expected if the pioneer and the established opossum belong to alternative genetic phases, analogous to the visually distinct melanic and grey ones.

INTRODUCTION

The basic colour of the brush-tailed opossum is agouti grey. This form of pelage, with banding of colours on individual hairs, is common in primitive mammals and it serves for generalised concealment (Herskovitz 1968). In specialised mammals, such as the opossum, social markings are developed (Kean 1967, Herskovitz 1968) and body colour becomes varied according to habitat (Troughton 1965) with a change towards reddish brown in northern latitudes of Australia. As an alternative to the varied greys, a melanic phase occurs in humid forests.

The usual reproductive rate of the opossum is one young reared per year but this rate may increase when foods are abundant. It is the frequent absence of such increase that requires explanation.

Comparison of two forms of selection, for melanism and for low reproductive rate, may help to indicate the processes involved.

MELANISM

Grey opossums were brought to New Zealand from mainland Australia and black ones from Tasmania, but, because secondary liberations resulted in mixing of the two stocks (Pracy 1962), many populations in New Zealand consist of

hybrids between the Tasmanian sub-species and one or more of the Australian ones.

The grey and melanic phase opossums interbreed freely but intermediates are not found in Tasmania and they have not been reported from the Australian mainland (Guiler and Banks 1958). However, in New Zealand, intermediates occur and are classified in the fur trade as "moles". Such animals are never very common and they are found only in sub-specific hybrid populations. In the Orongorongo valley, near Wellington, about two per cent of the animals examined during the years 1953-61 were intermediates—a usual proportion for hybrid populations, although the figure is only approximate because colours vary and observers differ in deciding which ones should be excluded from the permissible range for greys and melanics. Grey and melanic pelage can form a coarse mosaic in a single animal but this is rare. I have heard of a few such opossums but have seen only one, sent from Rotoehu Forest, near Rotorua. It seems that speciation in Tasmania has proceeded far enough to impair an all-or-none switch mechanism when the Tasmanian sub-species is crossed with a mainland one.

In Tasmania, frequency of blacks increases with increasing humidity, as shown by vegetation type rather than by rainfall (Guiler and Banks 1958). For example, Buckland-Nugent with 30 in. (76 cm.) rainfall has 100% blacks, and Lake Margaret area with 120 in. (300 cm.) has 100% greys; but the former area carries tall forest while the latter

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has few trees except for gullies with dense scrub, unacceptable as opossum habitat (Guiler and Banks 1958, L. T. Pracy *pers. comm.*).

In New Zealand, distribution of the two colour phases shows the same correlation with humidity as in Tasmania, but the pattern first determined by the early liberations has not yet fully conformed to climate (Pracy 1971). Populations near Auckland and on Kawau Island have remained 100% grey; those of the large Urewera Forest are 100% black (Pracy 1971). This would be expected according to climate. Either the pioneers were homozygous for colour or climate eliminated progeny of the alternative phase. Some populations have not conformed to expectation. A purely melanic population in warm open country extends from slightly north of Gisborne, south to Mahia Peninsula (Pracy 1971).

Conversely, in the Wanaka region of the South Island, greys extend from the Wilkin valley, south of Lake Wanaka, northwards to the catchment of Lake Ohau (Pracy 1971). The area is largely suitable for greys but it flanks the Southern Alps, and the opossums have failed to penetrate the country where rainfall reaches or exceeds 200 in. (500 cm.). Elsewhere in New Zealand predominantly grey populations have readily occupied equally humid forests, as on Mt. Egmont, in Taranaki. This geographical limit suggests that the Wanaka population lacks genes which permit toleration of humidity, with or without the incidence of melanism. The Gisborne and Wanaka populations appear to be homozygous for their respective colour phases.

Tasmanian blacks were liberated on Kapiti Island in 1893, but opossums of the Tasmanian grey type emerged, and by 1918 they formed about 68% of the population. The phenotypically black pioneers were evidently heterozygous for colour, and the colony switched to grey according to the proportions of open country and humid forest occupied during the early part of the century (Pracy 1962, 1971).

Huxley (1942) and Guiler and Banks (1958) discussed the association of melanism and tolerance of humidity in mammals, but no common selective advantage was found. Heat exchange does not seem important in either hot or cold climates. Kelly *et al.* (1954) found that reflectance of direct sunlight was 51% in white pigs and only 7% in black ones, but the practical difference is

far less than these figures suggest. Reflectance was less for the longer wavelengths, and at 3μ it was equal from both black and white. Diffuse solar radiation of long wavelength, although forming only 34% of the radiation received by the earth, emanates from a hemispherical sky and so is available to most of the body surface, whereas direct sunlight illuminates only half the body, and much of it is oblique with consequent reduction of intensity. Loss of body heat, all of infra-red emission, was not affected by coat colour.

Hamilton and Heppner (1967) pointed out that many basking homiotherms (and poikilotherms) direct black surfaces so as to receive sunlight, and that nocturnal animals could recuperate heat loss at dawn. However, such behaviour has not been observed in the nocturnal opossum.

Barber (1954, 1956) found that rabbits (*Oryctolagus cuniculus*), introduced into Tasmania 150 years previously, showed clines in melanism like those found by Guiler and Banks for the opossum. (The highest proportion of blacks in rabbit populations was only 37%, but this would be expected because rabbits do not live in dense forests). Time required for correlation with climate was short — from a possible 20 years to a maximum of 50. Barber reached no conclusion as to selective advantage.

The grey and melanic phases are concealing against light vegetation of arid or mesophytic environments, and against dark tones of humid vegetation, respectively. Intermediate colours would not be cryptic in any usual habitat. Concealing coloration would result from selection by predation and, although Guiler and Banks (1958) discount effective predation in Tasmania today, Gill (1955) suggested that it was formerly heavy enough to cause extinction of some Australian marsupials. If so, brush-tailed opossums would have been vulnerable, since they spend much time on the ground (Broom 1898, Guiler 1957, Kean 1967) where they can move only slowly.

Juvenile melanics are black but fading commences in males at one and a half years and it continues to a light rust shade in old age. Fading starts about a year later in females and does not proceed very far. Juveniles, the easiest prey, have the most concealing pelage, and females always have some protection; but males, of least value to the species, have cryptic coloration only while young.

The light brown of old males has no known function; it appears to have resulted from relaxation of selective pressure. This colour is presumably due to deposition of phaeomelanin, associated with reduced physiological expenditure. Either form of melanin can be produced by the same cell, but dark eumelanin requires the greater mitotic activity (Searle 1968).

Benson (1933) found that the mouse *Perognathus apache* had light pelage where it occurred on white gypsum sand, and that *P. intermedius* had melanistic pelage on dark lava flows in arid New Mexico. Here there is no association of melanism with humidity.

Adaptation to background in the opossum is similar, if less striking. The greys and blacks are appropriate for a nocturnal animal; predators may have night vision, but low intensity of light reduces colours to monochrome. Natural predation on the opossum is virtually absent in New Zealand forests (but not in rural areas) and protective coloration confers no advantage there. Superiority of either phase depends only on pre-adaptation to climate.

Procryptic coloration is of value only in appropriate situations. Since greys and blacks which occurred in vegetation of contrasting colour tone would have been susceptible to predation, behaviour patterns appropriate to colour should by now have become established. Such behaviour, as in habitat preference, has not been demonstrated but there are differences in temperament. Among 46 healthy adult black opossums none were easy to handle in captivity, but of 61 greys, two thirds were reasonably tractable. Since the Orongorongo population, from which these animals were taken, is a hybrid one with about 40% of blacks, it is unlikely that the captive blacks were homozygous for colour. Black and grey siblings, then, usually differ in temperament according to colour.

Guiler and Banks (1958) stated that in all cases the transitional region between high percentages of one phase and high percentages of the other was very narrow in Tasmania. This is true for New Zealand also, but in the absence of predation phase has been determined by humidity, and the close association of tolerance with melanism can be attributed only to linkage of genes. Probably genes conferring appropriate behaviour patterns share the same linkage.

REPRODUCTIVE RATES

Reproductive patterns of *Trichosurus vulpecula* have been found essentially similar in all published studies (Smith *et al.* 1969). There is an autumn breeding season which is commonly supplemented by a spring one in which fewer females breed. Most females rear one young per year, but some females rear two, one in each season. Usually, such fast breeders form only a small proportion of any population, but in two small groups within populations, 11 in 25 adults (Kapiti Island, Kaiwharawhara valley 1958 (L. T. Pracy, *pers. comm.*)) and about 75 in 100 (Mt Egmont, near Mahoe 1957 (E. Brown, *pers. comm.*)) were found rearing spring and autumn young simultaneously. Published records of double breeding (Tyndale-Biscoe 1955, Dunnet 1956, Winter 1963 and Gilmore 1966), and unpublished reports, indicate that double breeders occur only when population densities are low and food supplies plentiful. However, these conditions do not always result in fast breeding; the only common factor is potential expansion of population. For this, annual production of a population has to be removed, either by applied controls, such as trapping, or by continuous dispersal.

In populations limited by winter starvation, obligatory reproduction in both seasons might reduce chances of survival for both young and mother, but this explanation is untenable. In the Orongorongo valley food resources declined slowly. In 1946 the first of the preferred food species were being over-utilised, but basic foods were not seriously affected until 1962. Supplies appeared to be lowest in August, but condition of opossums continued to fall during the next two months (attributed to increased activity and maximal demands in lactation). During these three months in 1953, among 89 suckling females, 29 were excessively fat, 26 were fat, 25 had some fat and nine were without visible fat.

In this population most females reared young, which were suckled for eight months. The spring breeding season was absent. Longevity was about nine years (maximum recorded 11½ years), and population density was about three per acre (Batcheler *et al.* 1967). Among 8,000 females taken during the period 1946–1961, only one double breeder and one female with twins were found. The population remained essentially stable during the study period, even in untrapped areas,

as shown by the slowness of decline of food plants during 15 years; yet the constant reproductive rate provided far more young than were required to balance losses through senility and infrequent disease. Removal of the surplus by dispersal was not possible in the continuous forest. Since young have a long period of maternal protection, competition evidently occurred somewhere between the yearling stage and senility. Such competition seems to have been unfavourable for fast breeders.

Leaves of trees and shrubs form the basic food of opossums, but only a small proportion of forest species are acceptable (Pracy and Kean *in press*). In New Zealand, opossums have denuded many forests of such species (Howard 1965) and have then declined through starvation. Young opossums in New Zealand do not face shortage of food until the end of their first pouch-free winter, at an age of one and a half years. A surplus of such young would impose a considerable strain on a limited food supply before their ultimate elimination, and this can be avoided only by a low reproductive rate.

Some females (as in the Orongorongo valley) could easily rear two young annually in many forests where double breeders are virtually absent. Unless fast breeders are limited by some means, they would steadily increase their own numbers and also the birth-rate. Such an increase would be unfavourable for the species, because spaces left by killed food trees are quickly filled by lateral growth of unpalatable species. Recovery of depleted opossum food resources is very slow in forests.

Shelter and food, if equally shared, may be sufficient to meet the needs of a population, but resources are not equally shared. This is shown, as in the Orongorongo valley, by the simultaneous presence on one trap line of poor conditioned and fat opossums. Inhibition of breeding might have resulted from social behaviour (Kean 1967) but irrespective of its cause in the Orongorongo valley the spring breeding season, as well as double breeding, was absent.

Genes associated with adaptation for wet forests and those for melanism appear closely linked, and it seems necessary to postulate a similar linkage of genes for fast reproduction with ones that are unfavourable for intra-specific competition. The evolution of a slow reproductive rate in *Trichosurus* is a subject beyond the scope of this paper, but it can be considered in outline. Early

Trichosurus was a generalised feeder, as shown by the bunodont teeth which persist today, although selenodont teeth are found in related genera. Diet of the Phalangeridae is basically insectivorous, with the addition of nectar and pollen from blossoms, together with foliage and fruit (Troughton 1959). *Trichosurus* is still not fully specialised for leaf eating, and the present basic diet seems to be a recent development. The early type was evidently dependent on mainly seasonal foods, and probably one long-suckled young was the number most likely to be reared to maturity. This limitation would have been favourable for survival of the individual and its progeny. In changed circumstances, it has come to be favourable only for the species.

Double breeders are probably present in all populations, as indicated by the one in 8,000 females recorded for the Orongorongo area. The proportion rises in expanding or potentially expanding populations where annual increase is removed. The high level recorded locally for Mt. Egmont was attributed to two factors. First, the area had been subject to heavy trapping because it was on the forest margin adjacent to one of the National Park roads, and second, food supplies had been increased by removal of goats and trespassing cattle. On Kapiti Island food supplies were good and Kaiwharawhara valley was the most heavily trapped part of the island because a hut for trappers had been built there. Some double breeding was reported at Rangitira Point, near the caretaker's cottage, but trapping had been less intense there.

Rural opossums are subject to various forms of predation, and they are tolerated only in small numbers around houses and gardens. In such places, selection favours a higher reproductive rate.

It was expected that sustained trapping in the Orongorongo valley would lead to the emergence of double breeders in the better locations, but this did not occur, even around the field station, where free-living opossums were given supplementary food. Here the population density was controlled by box trapping. Marked opossums were freed; unmarked ones were killed.

Sharman (1955) found that the wallaby (*Setonix brachyurus*), after one year in captivity, had shortened periods of anoestrous, and some females continued having oestrous cycles throughout the whole year. This change from the wild

pattern did not occur in Orongorongo opossums, and even second generation captive females continued to become anoestrous at the end of August.

The explanation for persistence of the low reproductive rate in the Orongorongo opossums appears to be that the population was never a rapidly expanding one. Goats were numerous but they were restricted to the high country which was not good opossum habitat. At lower altitudes the vegetation was too dense for opossums and it was not thinned out by deer until 1940. By that time the opossums had become well established and settled, although numbers were not high in comparison with other forests. Deer arrived too late, in the lower end of the valley, to induce as rapid an increase of opossums as occurred, for example, in parts of Westland where opossums established after deer instead of before.

Increase of the reproductive rate of opossums in the Orongorongo apparently could not be increased by trapping or feeding. Evidently a high incidence of fast breeders required selection for genetical types; it cannot be induced somatically. The required genotypes were too few to permit perceptible change during 16 years trapping of the central part of the study area.

CONCLUSION

Agouti grey pelage occurs in mammals as a generalised colour for concealment. Modification of colour, as explained by Herskovitz (1968) frequently takes the form of conspicuous markings, permitted by low predation pressure. Melanism in the opossum cannot be explained in this way, because social markings of the grey opossum (Kean 1967) are suppressed by melanism. The alternative possibility is that melanism, like agouti grey, is procryptic in the appropriate habitat.

Today melanism is often not adaptive but is associated with humidity. Its persistence in New Zealand rain forests is accounted for by close genetical linkage of genes for melanism with ones for humidity tolerance, and probably for associated behaviour patterns. Such linkage is sufficiently close to ensure that the black phenotype displays all attributes appropriate to the colour, but conceals those required by the alternative grey phase. In the absence of geographical barriers, local incidence of melanism may reach 100%

within populations that are largely grey. Non-cryptic intermediates in pelage colour are reported only in Tasmanian-Australian hybrids.

The inheritance of groups of genes, rather than single ones, and the associated all-or-none switch, which fits a heterozygous phenotype for either a dry or a humid habitat, is necessary for the individual, and individual selection can explain its occurrence.

Supplementary spring breeding is fairly common, but double breeders seldom form a high proportion of the population. Absence of double breeders from populations with ample food requires the hypothesis that genes for high reproductive rates are linked with ones that are unfavourable for intra-specific competition.

Low reproductive rate is not easily explained today by individual selection. It requires many females to rear less than their potential number of young. This potential is indicated by the rearing success of double breeders. Since food resources of the opossum can be permanently impoverished by over-utilisation, breeding "restraint" is beneficial to the species.

As stated by Wynne-Edwards (1963): "In the context of the social group . . . the homeostatic control of population density frequently demands sacrifices of the individual; and while population control is essential to the long-term survival of the group, the sacrifices impair fertility and survivorship of the individual." Wynne-Edwards introduced the concept of group selection or the partial breeding isolation of some animals within a population which permits selection of genetic systems instead of alleles. It explains the establishment of attributes which are favourable for the species although possibly unfavourable for the individual. This could explain the origin of a low reproductive rate in the opossum, or the present rate could be favourable for the individual in some as yet undetermined way. If this were so, opossums did not become adapted to their present diet of leaves; they would have been pre-adapted. The usual low reproductive rate of the opossum is necessary for conservation of food resources, but it alone does not regulate population density.

Expanding populations are equivalent to pioneer ones, and in them rapid increase is favourable provided it is curbed after establishment. Field observations show that such restriction

actually occurs, and it is explainable by the postulate that the pioneer and the established opossum represent alternative genotypes. Close linkage of associated genes would be a necessary condition for this. Such linkage is found in the melanic and the grey phases. The pioneer and the established opossum seem to be different (although intermediates occur) and like melanics and greys, each is well adapted to its different environment.

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