

The biology of the stoat (*Mustela erminea*) in the National Parks of New Zealand

V. Moulting and colour change

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Abstract Moulting and colour change were recorded independently from the flat skins of 1298 stoats. A moulting cycle begins when hair follicles enter the anagen phase and begin to accumulate melanin (visible on the 'skin' side as black patches) and ends when the old hair is shed. Growth of the hair was inferred from the disappearance of the anagen follicles, and shedding was inferred from colour change. On average in New Zealand, the spring moulting begins in August and ends in December and the autumn moulting begins in November and ends in July (the moulting periods will be shorter at any given locality). The spring moulting is later in the south (44-45°S) than in the north (39-40°S), and is synchronised with the breeding season, but is not later at higher altitude. The autumn moulting is earlier in the south. The proportion of male stoats turning white is significantly related to minimum temperatures and to numbers of days with ground frosts, but not to mean temperature, number of days with snowfall, or duration of snow-lie. Both altitude and latitude influenced whitening. These data are consistent with hypotheses developed from experimental work on animals in captivity that moulting and breeding are controlled by daylength (i.e., latitude but not altitude) but that winter whitening is controlled by temperature (i.e., latitude and also altitude). Three anomalous specimens were possible examples of pituitary malfunction.

Keywords *Mustela erminea*; New Zealand National Parks; trapping; pelage; moulting; colour change

INTRODUCTION

The moulting of a mammal begins with the anagen or preparatory phase of the follicle cycle and ends when the old hair is shed (Ling 1972). The term 'moulting' therefore includes both growth and shedding, but it is the latter which most influences the external appearance of the animal. Earlier data on the moulting of stoats have all been inferred from observation of the intact animal in high northern latitudes, where stoats always turn white in winter (Hamilton 1933, Salomonsen 1939, Hall 1951, van Soest & van Bree 1969, Müller 1970). This indirect method has the disadvantages that it cannot distinguish between moulting and colour change, which are separate processes initiated and controlled by different mechanisms, and it cannot be applied to stoats which do not regularly turn white in winter. Its great advantage is that living animals can be followed through the process (Müller 1970), and may be subjected to experimental manipulation (Rust 1962, 1965, Rust & Meyer 1969). These studies have provided much useful information on the physiological control of moulting and colour change in captive animals.

In the present study the patterns of moulting and colour change in wild stoats were recorded independently, and much additional information about the same animals was obtained. Further, because the total sample is large and drawn from a wide range of environments, it has enabled us to test predictions arising from previous work concerning the relationships between such variables as moulting and daylength, colour change and temperature, and moulting status and reproductive condition. The moulting in stoats living in climates where they do not always turn white has previously been studied only by Salomonsen (1939), who did not distinguish between the effects of temperature and daylength.

MATERIAL AND METHODS

Dated skins were available from 1298 stoats (750 males, 548 females) of the 1599 collected from 14 study areas in New Zealand, representing a range of habitats, altitudes, and latitudes (King & Moody 1982a). The animals were accumulated without

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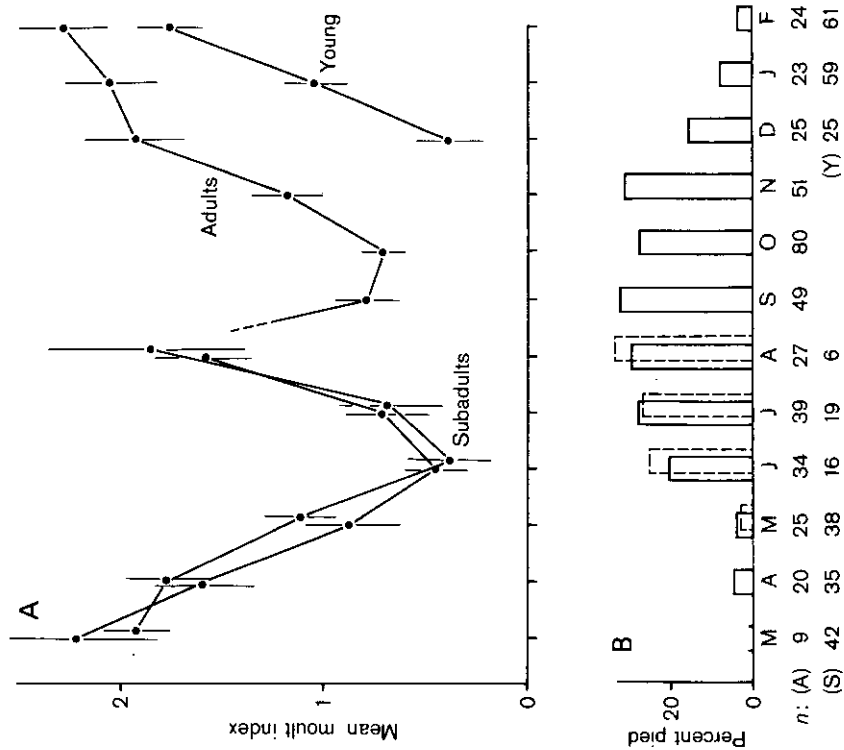


Fig. 2 (A) mean moult index, $\pm SE_{\bar{x}}$, for male stoats. (B) Percentage of adult males and subadults (pecked lines) pied, omitting anomalies listed in text.

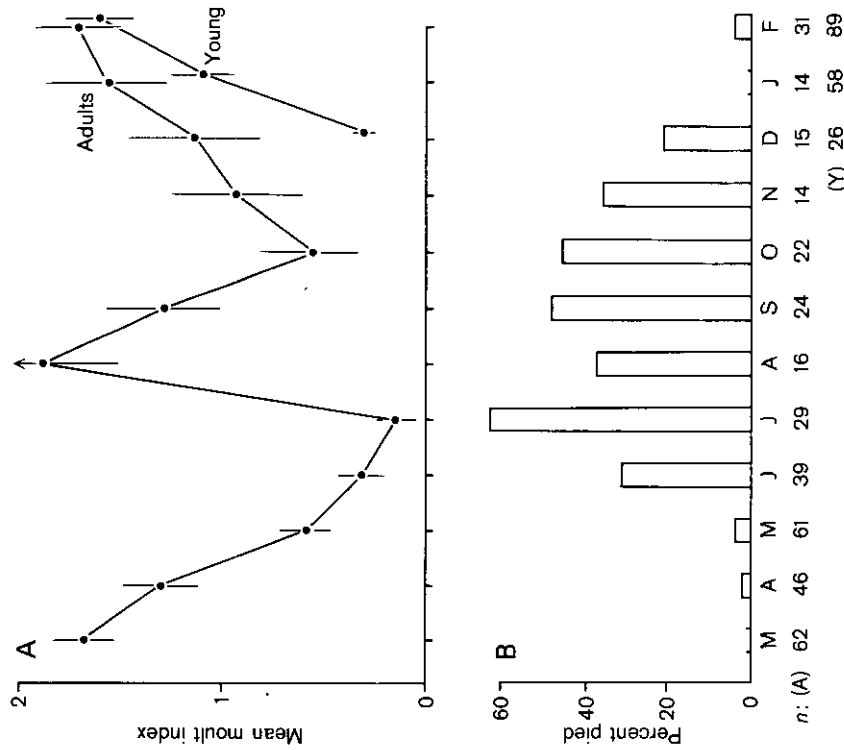


Fig. 1 (A) Mean moult index, $\pm SE_{\bar{x}}$, for female stoats. (B) Percentage of adult females pied.

selection for appearance, though a few trappers may have retained the occasional outstanding ermine specimen.

After mid-ventral incision from throat to anus, each skin was removed whole except for that on the nose and feet, pinned out flat, and air-dried. Dry skins were scraped free of fat and stored, without preservative or further treatment, in polythene sleeves.

Definitions of categories of moult

The extent of moult activity in each animal was determined by examining the inside of the dry skin. In the anagen phase of the cycle the follicles become active, enlarge, and extend deep into the dermis (Ebling & Hale 1970). In conditions favouring the growth of brown hair the follicles then begin to accumulate melanin (Schwalbe 1893), and become visible as dark flecks, usually aggregated into patches. Santisteban (1949) stated that in *M. frenata* these moult patches appear about 18 days before any change can be detected in the fur. It may be many days later that the new hairs are fully grown, and weeks before they entirely replace the old ones, since the old coat is not necessarily shed at the same time as the new one is grown (Ling 1970); indeed, successive cycles of hair growth and shedding can overlap (see below). Environmental temperatures influence shedding, and possibly also growth, whereas the follicle cycle appears to be controlled principally by daylength (Ebling & Hale 1970). It is therefore more appropriate to date the start of each new hair cycle from the presence of anagen follicles than from the onset of shedding, although seasons of 'moult' defined by the 2 methods are not identical; anagen follicles represent the early stages and shedding the late stages of the moult cycle. Anagen follicles about to produce white hairs are not detectable, so all the analyses of moult cycles described below were repeated, excluding animals showing any colour change.

The status of the anagen follicles was defined as follows:

- 0 - clear skin;
- 1 - anagen follicles present but distributed in indefinite pattern and at low density;
- 2 - anagen follicles densely distributed over less than half the skin;
- 3 - anagen follicles densely distributed over more than half the skin.

The status of moult activity represented by category 1 is uncertain, but as it is relatively constant (averaging 12% per month in both sexes) and varies with season in harmony with the other categories, it probably represents the very early and/or the very late stages of a moult. Only the area of the skin producing brown hair in summer was considered, and the proportion of this area covered by dark

follicles was estimated by eye. The 4 categories have been treated as a graded scale, the 'moult index', the mean of which indicates the intensity of moult activity in a given sample.

Definitions of categories of colour change

Van Soest & van Bree (1969) illustrated the process of winter whitening in Dutch stoats. First, white hair appears on the tail immediately anterior to the black tip; then the edge of the brown fur, normally low on the flanks, moves upwards towards the spine; the residual stripe of brown becomes narrower, then confined to a cap on the head, and finally to rings around the eyes. The return to brown in spring follows the same route in the other direction. The New Zealand animals conform in all respects, and for the purposes of this study the process has been arbitrarily divided into sequential stages, as follows: 0 - no dorsal white (i.e., no white on areas brown in summer);

1 - white hair on tail only;

2 - white hair on less than half the body area brown in summer;

3 - white hair on more than half the body area brown in summer.

Stage 3 is not subdivided, as very few stoats reached the pristine ermine condition. All stoats with any colour change (stages 1-3 inclusive) are therefore referred to as 'pied'.

'Colour change' here means change between brown and white. Seasonal or local differences in the shade of the brown hair were not examined.

RESULTS

Moult

Seasonal variation in hair growth and shedding in adults. Since the complete process of moult runs from the beginning of the anagen phase to the end of shedding, it is important to correlate observations on both sides of the skin to determine the length of the whole cycle.

Fig. 1 and 2 show the monthly variation in the intensity of moult activity, as estimated by the mean moult index, and the monthly variation in the proportion of pied stoats observed. The cycles are similar in both sexes. Preparations for the spring moult begin soon after the winter solstice, and are most intense in August. From then until October the declining moult index shows that the stored melanin is being used up in the growth of new brown hair, and from September to December the old white hair (and presumably also old brown hair) is shed. As soon as the summer fur has finished growing, the follicles begin to accumulate melanin for the production of the winter fur and the moult index rises again from November to a peak in February-

March. The decline in the moult index from March to June marks the growth of the winter hair, and from April onwards, as the summer fur is shed, white fur appears on some animals.

In general, therefore, the complete cycle of the spring moult from anagen to shedding takes 6–7 months, from July to December or January, but the complete cycle of the autumn moult takes longer, from November to May or June. Most of this extra time is in the anagen phase, which is 4–5 months for the autumn moult but only 1–2 months for the spring moult. This is partly a statistical result of averaging the different spring patterns over the whole country (see below). It could perhaps also be partly because the winter coat is thicker, and hence the skin takes longer to accumulate enough melanin to make it; or possibly the anagen phase of the autumn moult is retarded by some inhibitor, perhaps one connected with reproductive condition, so that individual follicles spend longer in the anagen phase in breeding animals (October–January) than in non-breeding animals (July–August). The overlap of the 2 seasonal cycles is possible because growth and shedding of hairs are independent, even within an individual follicle. However, in any given locality the period of moulting will be slightly shorter, and the cycles may not necessarily overlap in individual animals.

Variation in moult activity with age and sex. Young stoats tend to be later than adults in preparing for their first moult in autumn. Their moult index is lower on average than in adults, up to January in females and February in males (Fig. 1 and 2). After February the moult index in subadult and adult males is similar.

When young are excluded, the mean moult index is higher in males than in females for all months except August and September (difference significant at $P = 0.04$ in a 2-tailed signs test). As females more often turn white than males, this could be because some monthly samples include animals with undetectable white anagen follicles, which might reduce the mean moult index for the group. But the pattern is similar even when all pied animals are excluded, although then the males have a higher moult index in every month except August. This may be attributed to sampling error: the August sample contains an unusually large proportion of female stoats from Egmont, which would have a relatively high moult index (see below).

Variation with latitude and altitude in the time of initiation of the moult. The 14 study areas were divided into 4 groups by latitude, and monthly moult indices (omitting young) were plotted. Fig. 3 shows the pattern in the pooled data for both sexes; plots for the sexes separately are similar. Stoats from the

furthest south (region 4) are always the last to increase moult activity in November and the first to grow new hair in May. In November, December, April, and May (the periods of most rapid change between summer and winter coats) the mean moult index for region 4 is lower than that for region 1 in all of 7 comparisons controlled for month and sex ($P = 0.016$, 2-tailed signs test) (Fig. 4A).

The effect of altitude on initiation of the moult was checked by examining 3 pairs of collections, representing a higher and a lower altitude at the same latitude (Tongariro cf. Mount Bruce, Craigieburn cf. Westland, Eglinton Valley cf. Milford; for locations, see King & Moody (1982a)). For the November, December, April, and May data 7 of 11 sex/altitude/month comparisons show less intensive moult activity at higher altitude, which is not significant ($P > 0.5$) in a 2-tailed signs test (Fig. 4B).

Colour change

Rather few stoats are classed in the 3 categories (i.e., 1–3) of colour change—respectively 9%, 5%, and 5% of 375 adult females and 11%, 4%, and 3% of 562 adult and subadult males. Of the 36 stoats of both sexes in category 3 only 8 are in almost full ermine, and even these have a few brown hairs around the eyes. The numbers are small because the stoats most likely to be pied are females collected in winter from colder areas; but snow obscured the traps, and females are always more difficult to catch, in winter (King & Moody 1982b).

Seasonal variation in the extent of colour change by age and sex. Fig. 1, 2, and 5 show the seasonal variation in occurrence of pied stoats. Fig. 1 and 2 plot the percentage of stoats in each monthly sample showing any colour change at all (categories 1–3 pooled); Fig. 5 shows the monthly distribution of the colour change categories for each sex.

Among 361 females only 4, all adults collected between January and May, are pied. The proportion of white adults is highest for July (Fig. 1 and 5A), mainly because there was an exceptionally large proportion of stoats from Fiordland, in the far south, in July. The proportion of white females declines steadily to zero from September to January.

The seasonal variation in males shows approximately the same timing as in females, but with a smaller amplitude (Fig. 2 and 5B). Apart from a single young male collected at Mount Bruce in December (see below, 'Anomalous specimens'), no young or subadult male shows any colour change until May. From then on the subadult males behave in the same way as adults (Fig. 2).

In midwinter samples a smaller proportion of males (33%) than of females (63%) shows any colour change, and fewer males than females reach

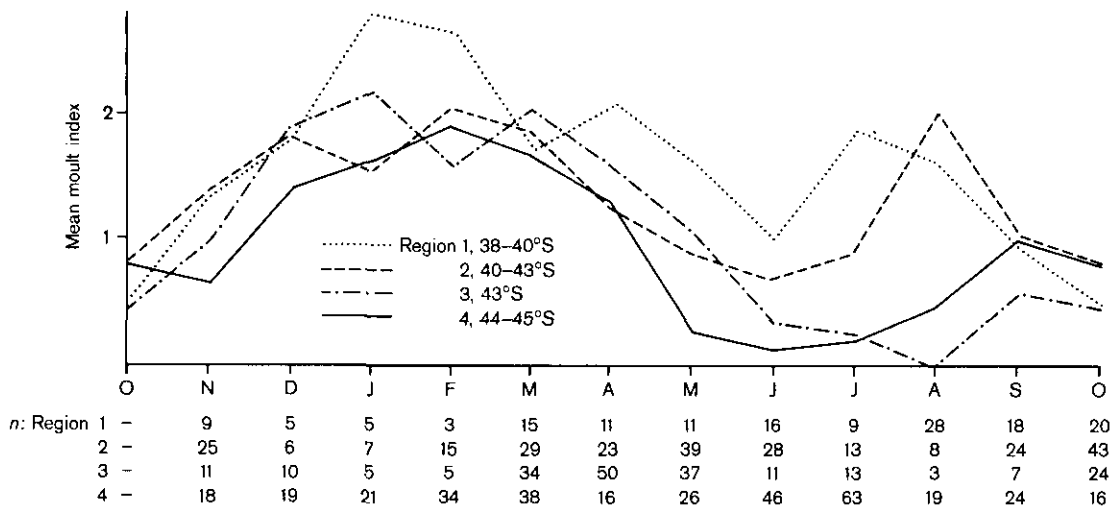


Fig. 3 Regional variation in the seasonal cycle of moult activity (excluding young); sexes pooled.

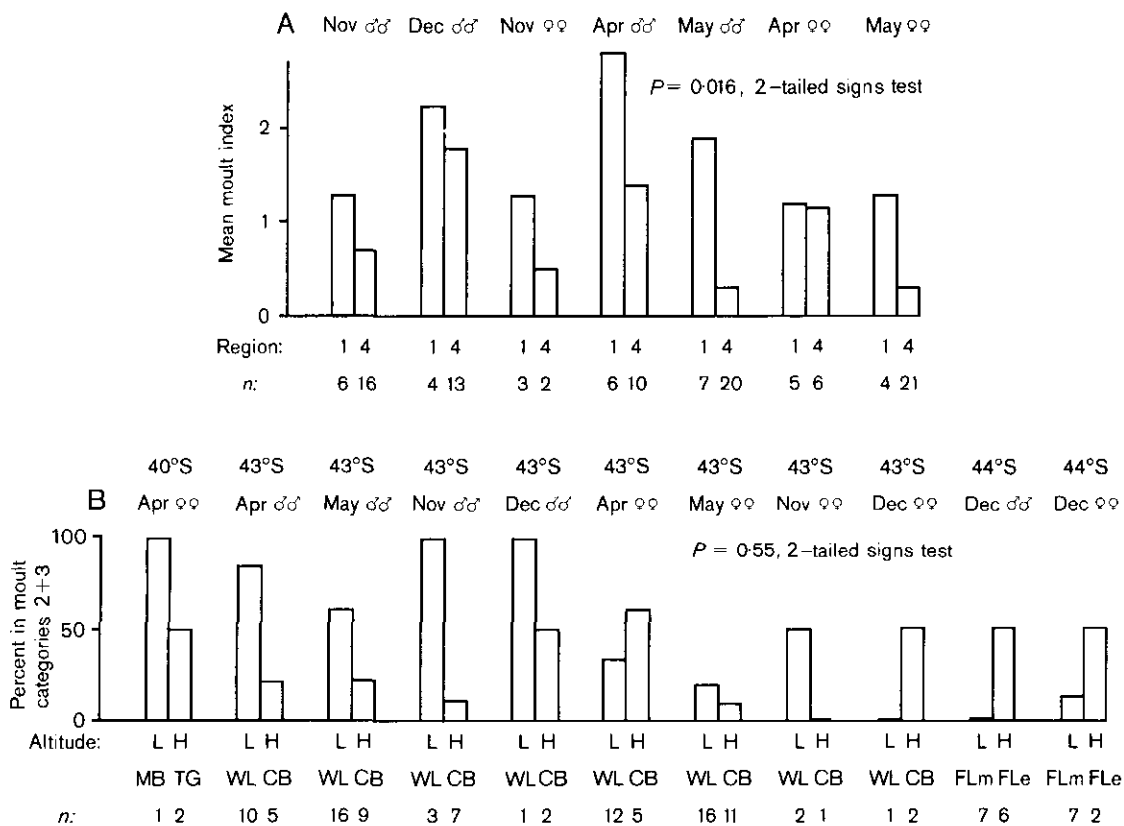


Fig. 4 Variation with (A) latitude and (B) altitude (L, low; H, high) in time of initiation of moult. For actual altitudes and full names of study areas, see King & Moody (1982a).

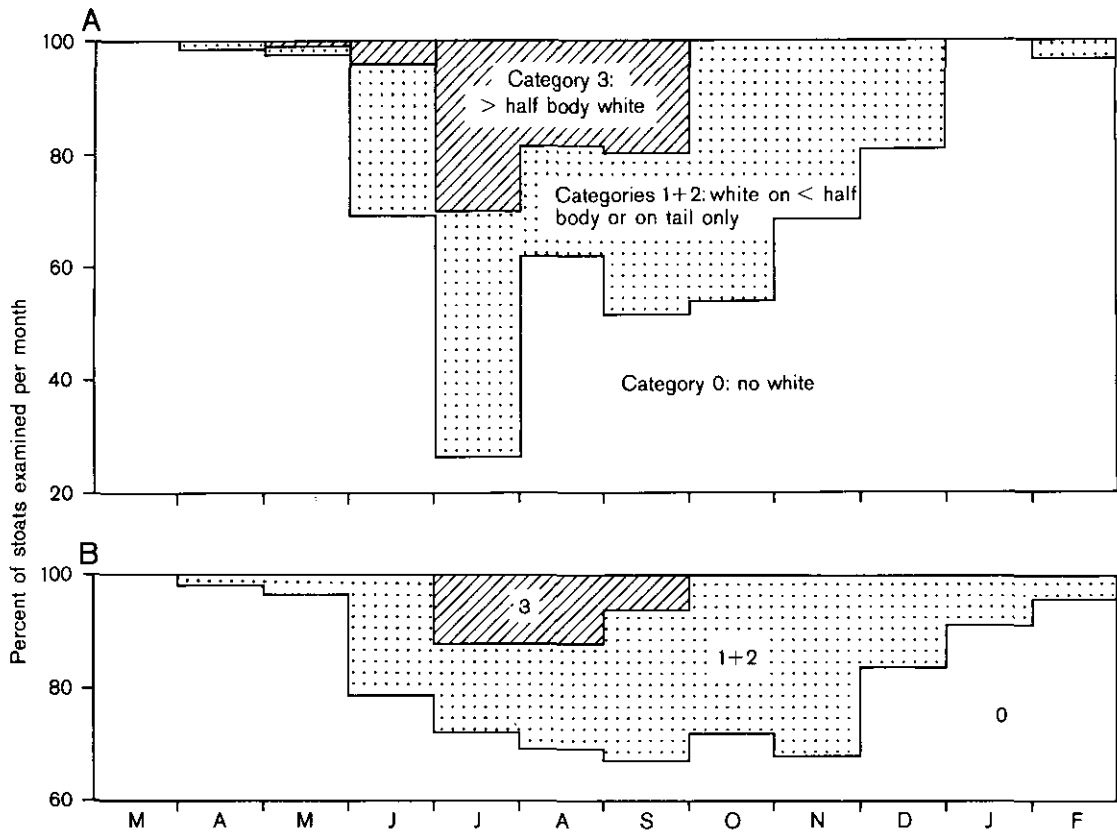


Fig. 5 Seasonal variation in proportion of (A) females and (B) males found in each category of pelage colour (excluding young).

Table 1 Incidence of pied stoats (colour categories 1 + 2 + 3), excluding young, in June–November in relation to local climate ($n > 5$ only). For latitudes and altitudes of collection areas, see King & Moody (1982a) * $P < 0.05$.

Collection area	Females		Males		Mean temperature in July ($^{\circ}\text{C}$) ⁽¹⁾		Annual average no. of days with ⁽²⁾				
	<i>n</i>	% pied	<i>n</i>	% pied	Met. station	Min.	Mean	Met. station	Snow-fall	Ground frost	Snow-lie ⁽³⁾
Egmont	19	5	40	0	Stratford Mtn Hse	0.6	3.7	Stratford Dem. Fm	0.6	73.1	0.2
Tongariro	5	80	15	7	Chateau	-1.1	2.5	Chateau	16.1	140.7	10.3
Urewera	6	17	9	0	Onepoto	3.1	6.1	Onepoto	4.2	39.2	5.0
Abel Tasman	—	—	6	17	Riwaka	1.3	7.0	Riwaka	0.5	80.2	2.5
Nelson Lakes	14	50	34	24	St Arnaud	-2.2	3.0	Golden Downs	1.6	116.9	0.9
Arthurs Pass (east side)	8	38	16	56	Bealey ⁽³⁾	-1.7	1.7	Bealey ⁽³⁾	26.1	266.0	20.1
Craigieburn	10	50	43	53	Camp Stream	-2.3	-0.3	Nursery Hill ⁽⁴⁾	c.21	139.3	44.9
Mount Cook	8	38	29	17	Hooker Flat	-5.4	0.8	Hermitage	21.2	130.1	60.8
Westland	9	11	22	9	Franz Josef	2.0	6.7	Franz Josef	0.7	74.8	—
Mount Aspiring	—	—	16	31	—	—	—	—	—	—	—
Takaro Lodge	11	55	13	15	Te Anau	-0.3	3.9	Otautau	3.0	107.1	3.1
Fiordland (east side)	34	71	62	47	Cascade Creek ⁽⁵⁾	-2.4	2.7	—	—	—	c.5.0
Tendency of females to whiten more often than males (subsamples pooled): $\chi^2 = 9.80$, 1 df, $0.01 > P > 0.001$					r_1 - males:	-0.67*	-0.53 NS		0.46 NS	0.72*	0.45 NS
					females:	-0.51NS	-0.34 NS		0.37 NS	0.57 NS	0.36 NS
					N - males:	11	11		10	10	11
					females:	10	10		9	9	10

⁽¹⁾ From temperature normals, 1941–70 (Meteorological Office 1978); July is always the coldest month. ⁽²⁾ From Summaries of Climatological Observations to 1970 (Meteorological Office 1973) (fewer stations than for (1), and some further from collection areas. Blanks show no near or comparable station available). ⁽³⁾ Meteorological Office (unpubl. data). ⁽⁴⁾ From unpubl. records of N.Z. Forest Service, 1973–75 incl. ⁽⁵⁾ Personal observations, 1975–77 incl.

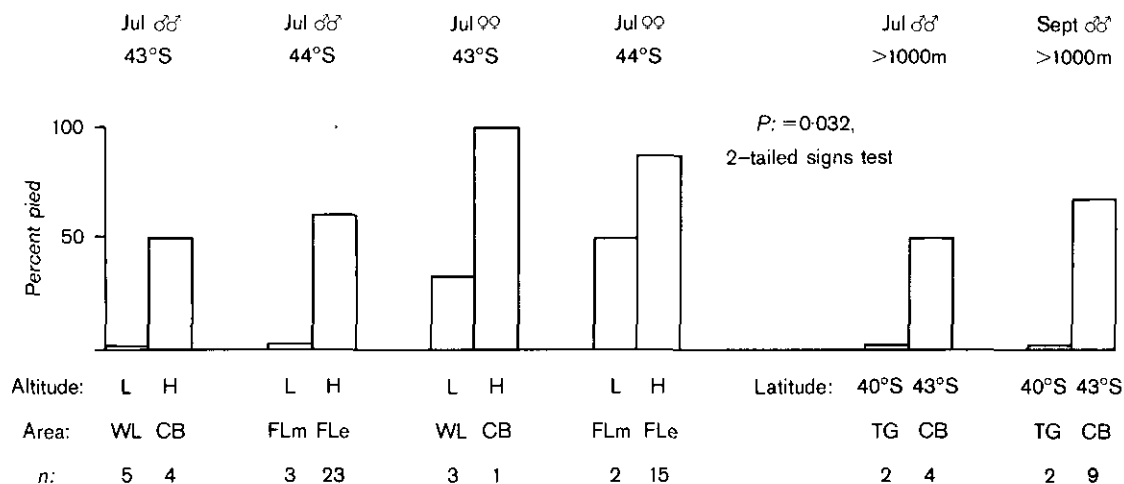


Fig. 6 Effect of altitude and latitude on proportion of pied stoats observed.

the highest category of colour change (Fig. 5). More females than males are pied in 8 of the 10 local subsamples listed in Table 1 ($P < 0.01$), and this is not because more females than males came from higher altitudes.

Geographical variation in the proportion of pied stoats. Table 1 gives the distribution of pied stoats in June–November, for samples from 12 study areas in which there are at least 5 animals (excluding young) of either sex. The proportion of pied male stoats is inversely related to the mean daily minimum temperature in July and positively related to the annual average number of days of ground frost, both significantly. But the proportion of pied males is not significantly related to the July monthly mean temperature, nor to the number of days of snow-fall or snow-lie. The proportion of pied females varies in the same direction as for males, but is not significant in any of the 5 calculations.

Atmospheric temperature is affected by latitude, altitude, and aspect. Westland, at 43°S and 120–150 m altitude, faces onshore winds and has very few pied stoats by comparison with Mount Cook (at the same latitude, but at 690–910 m just on the other side of the Main Divide) or with Tongariro (at 39°S but inland at 1000 m). As might be expected, samples from lower altitudes at a given latitude and from more northerly latitudes at a given altitude have fewer pied stoats in all of 6 area/sex comparisons of July and September data (August samples are often small) ($P = 0.032$ in a 2-tailed signs test; Fig. 6).

Collections at Craigieburn span 3 complete winters, of which 1973 was exceptionally mild (109 days of ground frost in June–November inclusive).

An apparent associated reduction in the proportion of male pied stoats (46% of 13, cf. 64% of 14 in 1975, when there were 125 days of ground frost in June–November) is not significant (in a 2×2 contingency test, $\chi^2 = 0.25$); the samples of females are too small to consider. There is no difference with altitude in the proportion of male pied stoats within the Craigieburn sampling area.

The data are insufficient to show whether there is any geographical variation in the season of colour change, though Fig. 7 suggests that pied stoats appear earlier in autumn in the south.

Anomalous specimens

The only young stoat to show dorsal white was collected at Mount Bruce in December 1975. It has 2 white spots on the head, which could possibly represent regrowth of hair—after a minor injury—from follicles in which the melanocytes were seasonally inactive.

All other anomalous specimens come from Mount Cook. A male collected in October 1973 (a nominal adult) has a curious 'puppy' coat (Fig. 8). Histological sections taken from various parts of the body and upper tail confirm that the pelt contains no guard hairs whatever. Two white males were trapped in summer. One of these was seen around the village at times over about 12 months before being trapped alive in August 1974 and sent to Wellington Zoo, where it lived for another year. Its coat was mainly white, with a mixture of brown hairs on the back, and it remained in this condition for the whole time it was in captivity. It was never included in this collection. Fig. 8 contrasts this pattern with that of a normal individual in the process of colour change. The second white male, killed in March

1974, is similar, and has been omitted from Fig. 2, 5, and 7.

It is remarkable that all 3 anomalous stoat skins observed in this study come from Mount Cook, and all can be explained as cases of pituitary malfunction. Permanently white coats and 'puppy' coats can both be produced experimentally by hypophysectomy (Rust 1965, Ebling & Hale 1970). Further, of 4 females with disorders of the ovary, the most extreme case also comes from Mount Cook; it had a large ovarian cyst or teratoma (King & Moody 1982b). The three abnormal skins and the teratoma from Mount Cook were all found in stoats collected between October 1973 and mid 1974. It could be interesting to follow these observations further, to check whether, for example, environmental toxins could be implicated.

DISCUSSION

Studies of the moult in stoats based on observation of colour change are really only studies of shedding. In this study, moult was detected from observation of anagen follicles and shedding from those individuals which turned white. By considering both together the entire moult cycle can be displayed, at least as an average, and related to other features of the annual cycle of the same animals.

The moult cycle

Bissonette & Bailey (1944) showed that the moult cycle in captive *Mustela* is controlled by daylength, and our results are consistent with that conclusion. Fig. 3 shows that the anagen phase of the spring moult cycle begins conspicuously later in the 2 southern regions (peaks in September) than in the 2 northern regions (peaks in July and August). Fig. 9 shows that, between July and September, localities in the south of New Zealand reach a given daylength later than those in the north. The same difference appears in other characters of the same animals also controlled by daylength, at the same season, i.e., the spring resurgence of the testes and the date of implantation (King & Moody 1982b). The whole cycle of spring activity is later in the south; the rise in the moult index for the southern animals is still later, in November and December (Fig. 3), even though by that time the equinox is past and the southern animals experience a given daylength before the northern ones (Fig. 9). The winter fur starts to grow just after the March equinox, earlier in the south; by this time the southern animals again experience a given daylength first.

Temperature appears to have less effect on this process, since there is no consistent delay in the initiation of anagen at higher altitudes at a given latitude (Fig. 4). In Belorussia spring shedding takes place from early March to late April, when

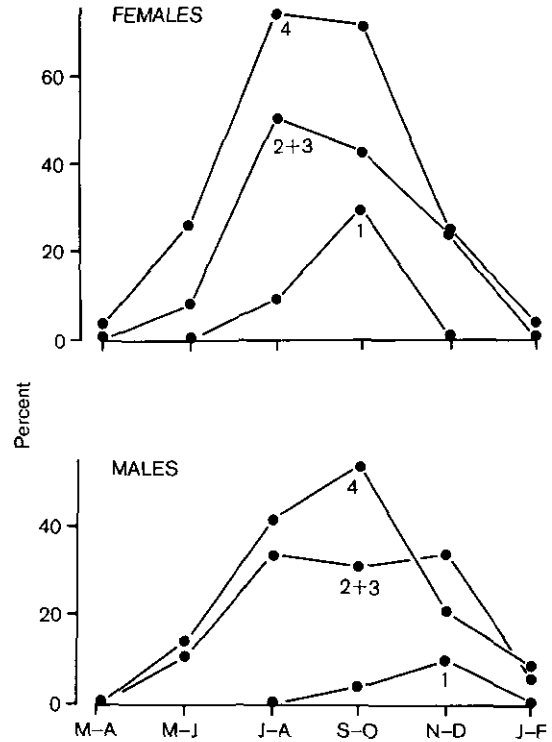


Fig. 7 Regional variation in proportion of individuals showing any dorsal white, by sex (excluding young). Regions defined in Fig. 3.

daylengths increase from 11½ to 14½ h and mean temperatures rise from -2° to +7° (Gaiduk 1977). In New Zealand most stoats shed from early September onwards, beginning at the same critical daylength but at higher average temperatures. At Hooker Flat, Mount Cook, the meteorological station nearest to the coldest area sampled, mean temperatures for September, October, and November are 5.1°, 7.9°, and 10.0°C respectively. Bissonette & Bailey (1944) observed that about 3 months elapsed between a change in experimental lighting conditions and a detectable pelage colour change (i.e., shedding of fur) in captive *erminea*. Fig. 1 and 2 show that shedding of the winter fur starts in September, about 3 months after the rise in the moult index immediately following the winter solstice.

These data confirm the findings of van Soest & van Bree (1969) that growth and shedding pass across the body together in a 'wave'. Shedding begins on the head in spring but on the belly in autumn. Gaiduk (1977) suggested that the various parts of the body shed at certain critical temperatures, higher for the ventral side than for the dorsal. In spring, when temperatures are rising,



Fig. 8 Left to right: normal pelt; 'puppy' pelt with no guard hairs; diffuse pattern of colour change; normal pattern.

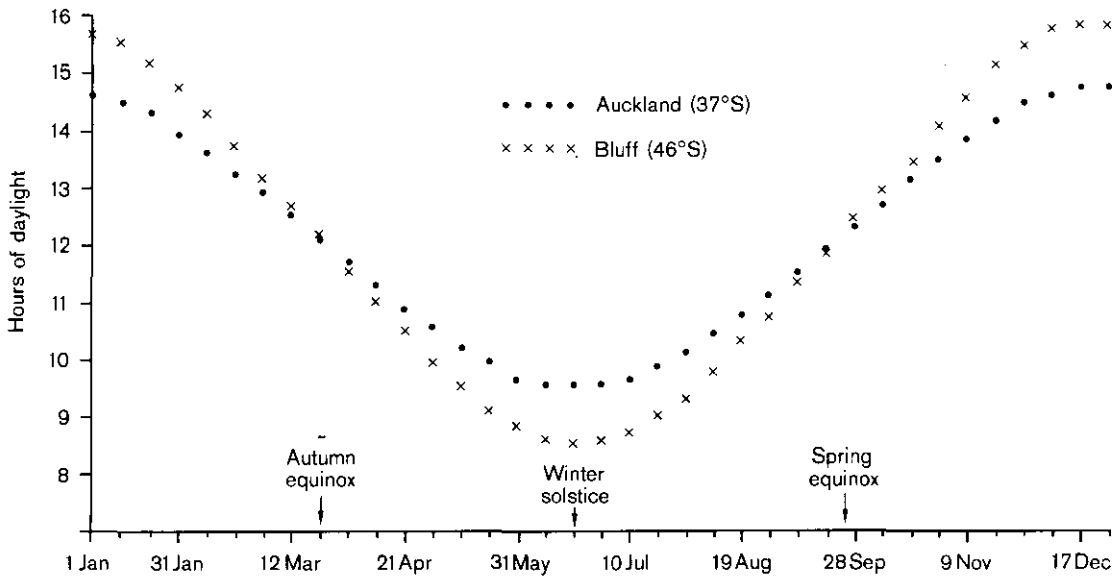


Fig. 9 Difference in annual cycle of daylength at the northern and southern ends of New Zealand, plotted at 10-day intervals.

the head and back reach their threshold temperatures first, and vice versa in the falling temperatures of autumn. It could be an advantage for a short-legged terrestrial animal living in a cool climate if the belly is the last to lose its extra insulation in spring and the first to obtain it in autumn (Ling 1970).

Seasonal cycles in moult and reproduction are co-ordinated through the neuro-endocrine system, of which the hypothalamus is the pivot. In the lengthening days after the winter solstice, gonadotropins released by the hypothalamus stimulate both hair follicles and gonads. This was demonstrated experimentally by administration of gonadotropin to hypophysectomised male *frenata* (Wright 1963) and *erminea* (Rust 1965), and may be inferred for the present material by the simultaneous rise in the moult index and gonad weights in both sexes (King & Moody 1982b). For the males this synchronisation is so close in early spring that the moult index and testis weights, plotted by month and region, are significantly correlated (Fig. 10; see also Wright (1942)). In both sexes summer fur grows during spring, when plasma concentrations of steroid sex hormones are high (Gulamhusein & Tam 1974, Gulamhusein & Thawley 1974), dormant blastocysts are reactivated and implanted, and males achieve peak testis weight. However, when the winter fur begins to grow, almost all females are in a new cycle of delay and both adult and young males are sexually quiescent. Ling (1972) stated that the spring moult can proceed almost regardless of reproductive condition, but that the autumn moult, involving the growth of a heavier pelage, "does not, and probably cannot take place except during anoestrus". Earlier (1970) he surmised that both spring and autumn moults in female stoats are initiated during the free blastocyst stage. Our results are consistent with both opinions. Van Soest & van Bree (1969) suggested that female stoats go through their spring moult more quickly than males, in order to grow their summer coat before implantation. In the present material both the period of growth of summer fur (inferred from the decline in the moult index) and the period of shedding (used by van Soest & van Bree (1969) as an indicator of moulting) are similar in the two sexes (Fig. 1 and 2); and of 13 pregnant females, 5 still showed anagen follicles up to about 19 days after implantation (data on pregnancies given by King & Moody (1982b)). If there is any difference in the moult cycle between male and female stoats, it is apparently not because moult and pregnancy are metabolically incompatible; neither are they in weasels, *M. nivalis* (King 1979).

In England at 51–55°N weasels almost never whiten, and observation of anagen follicles has revealed 2 quite distinct moults (King 1979),

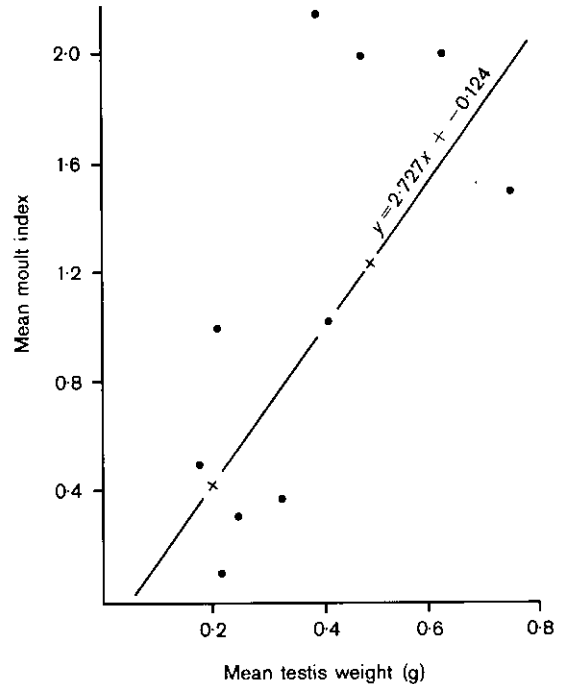


Fig. 10 Correlation between moult index and testis weight in winter and early spring: $r = 0.430$, 158 df, $P < 0.01$. All pairs, both $n > 3$. Each point represents the values of the moult index and testis weight for adult male stoats from 1 of the 4 regions (see Fig. 3) in June, July, or August.

separated by 1 month in winter (February) and 1 in summer (July) when all weasels had clear skins. In the New Zealand stoat skins anagen follicles are present in every month, and the patterns formed by the migrating moult patches are much less clear. For this reason the categories of moult used here are less specific than those used by King (1979). The 2 annual moult cycles in New Zealand (38–45°S) could overlap, because daylength changes over a smaller amplitude and more slowly here than in Britain. Slower moulting in New Zealand could also explain the lower density of anagen follicles observed, particularly in moult category 1.

Colour change

Gaiduk (1977) suggested that there is a critical temperature determining whether new hair grows brown or white, lower for the dorsal surface than for the ventral. In temperate countries such as New Zealand, stoats frequently fail to complete the full change to white. Such animals are not necessarily all caught in the process of moulting. If ambient temperature fell below the threshold for whitening of the lower part of the body but not the rest, new

hair would grow white on the tail and flanks and brown on the head and back. Blood flowing to the tail cools rapidly, which may be why the tail is the first—and, in this study, often the only—part of the body to turn white. The feet and ears have not been considered, as they are often wholly or partially white anyway.

The role of temperature in determining the extent of colour change among stoats of a local population has long been suspected from the geographic distribution of white and pied individuals. Fewer white stoats were recorded from below 305 m than from above in Yorkshire by Flintoff (1935); on the coast as against inland in the western U.S.A. (Hall 1951); and in southern or south-western European latitudes relative to northern or north-eastern latitudes (Salomonsen 1939, van Soest & van Bree 1969, Hewson & Watson 1979). Experimental work has established that production of brown hair depends on melanocyte-stimulating hormone (MSH); in cold climates in autumn the synthesis of MSH by the pituitary is inhibited. The central nervous system apparently monitors environmental conditions and controls the production of MSH or its inhibitor directly (Rust & Meyer 1969). Hence, we may expect a fairly close relationship between temperature and winter whitening, though it is still not clear exactly which characteristics of climate the stoats respond to. Salomonsen (1939) suggested that pied stoats are found only when the mean temperature of the coldest month is below 4.5°C, but pied stoats were collected from several areas in New Zealand with no months colder on average than this (Urewera, Mount Bruce, Abel Tasman, and Westland). Hewson & Watson (1979) found that the greater proportion of white stoats in the north-east of Scotland, relative to the south-west, was correlated with the slightly lower minimum temperature in the north-east, but not with the mean temperatures, which were similar in both areas. The New Zealand data support this finding. There are significant correlations with July minimum temperatures and with the number of days of ground frost, probably the most relevant measure of minimum temperature from the stoat's point of view (Table 1). The effect is significant only for males (samples of females are smaller); Hewson & Watson (1979) did not distinguish the sexes of the stoats they observed. The inverse relationship between temperature and altitude had the expected effect in both New Zealand and Yorkshire (Flintoff's data, re-analysed by Hewson & Watson (1979)).

Scottish mountain hares (*Lepus timidus scoticus*) respond to both temperature and snow-lie (Jackes & Watson 1975), and Hewson & Watson (1979) stated that Scottish stoats do the same. When separate rank-correlation coefficients are calculated from the

New Zealand data, the effect of neither snow-fall nor snow-lie is significant for either sex, in contrast to the effect of minimum temperature; but these tests do not control for the interrelation between snow and temperature. Multiple regression analysis of more extensive and precisely controlled data is required.

Hamilton (1933), Flintoff (1935), Hall (1951), and Müller (1970) have remarked that female stoats tend to turn white more readily than males. The data in Fig. 7 and Table 1 support this suggestion, at least for southern New Zealand. Hewson & Watson (1979) pointed out that the lighter sex of both rock ptarmigan (*Lagopus mutus*) and mountain hare regularly begins to whiten first, and that the same could apply to the stoat, in which sexual dimorphism in body weight is very pronounced. An intriguing alternative explanation put forward by Hutchinson & Parker (1978) is that this is an instance of a rare type of sex-linked genetic polymorphism. Where climatic variations are liable to alter the direction of selection for or against whitening, possibly quite rapidly and unpredictably, if whitening is controlled by one or more genes that are dominant in one sex and recessive in the other, there will always be a small number of momentarily less adapted phenotypes ready to take advantage of a reversal in selective pressure. Such sex-linked genetic control could explain the predominance of white females in variable environments, such as the central U.S.A., Britain, and New Zealand, and the persistence for several generations of whitening in stoats translocated from constantly snowy environments to mild ones (Rothschild & Lane 1957).

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