

# The biology of the stoat (*Mustela erminea*) in the National Parks of New Zealand IV. Reproduction

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**Abstract** The gonads of 528 female and 821 male stoats were examined. The weights of ovaries and testes in adults peaked simultaneously in October, the season of births and of post-partum oestrus. Of 73 females, 78% had even numbers of nipples, mostly 8 or 10. The mean number of embryos in 13 pregnancies was 8.8 (6-13), and embryo weights ranged from 0.005 g to 2.9 g. Of 11 pregnant females, 8 contained fewer embryos than corpora lutea, and there was evidence of transuterine migration of blastocysts in 6. All but 2 of 451 females caught in December-July inclusive carried corpora lutea of delay. Few adult and no young females were found in oestrus in September-October, though adult males were fertile from August to February (no first-year males were fertile). There was some evidence that the breeding season started later at more southerly latitudes in both males and females. The mean number of corpora lutea per female was 9.7 ( $n = 439$ ), and there was a significant inverse correlation between counts for the 2 ovaries of one individual. There was generally no significant variation in fecundity of females with age, body weight, or year. Of 11 females which were considered to have lost their litters, 10 were collected in beech (*Nothofagus*) forests. Four females and 9 males had abnormal gonads; the most severe abnormality was an ovarian teratoma of unknown pathology.

**Keywords** *Mustela erminea*; New Zealand National Parks; trapping; reproductive cycle; fecundity; gonads.

## INTRODUCTION

The reproductive cycle of the stoat in the Northern Hemisphere has been described from histological, experimental, and behavioural studies by Deanesly (1935, 1943), Watzka (1940), Wright (1963), Kopein (1965), Müller (1970), Rowlands (1972, 1974), Danilov & Tumanov (1972, 1975), Gulamhusein & Tam (1974), and Gulamhusein & Thawley (1974). Male stoats do not mature until nearly a year old, and adult males have a well defined fertile season from spring to midsummer. Adult females come into oestrus and are fertilised shortly after parturition; young females are sexually precocious, and mate before weaning, at about 5-8 weeks of age. Ovulation is believed to be induced, and virtually all females, young and adult, are impregnated during the breeding season in early summer. A long period—9-10 months—of delayed implantation follows. About 2 months after the winter solstice the blastocysts implant, and gestation proper takes 4 weeks. It is of interest to determine whether New Zealand stoats, from a stock introduced late in the 19th century, have adjusted their reproductive cycle and fecundity to the different conditions in the Southern Hemisphere.

## MATERIALS AND METHODS

A total of 1599 dead stoats were collected, and the gonads of 1349 (821 males, 528 females) were examined. The study areas and the composition of the samples are described in King & Moody (1982a).

### Laboratory procedures

Field collection methods precluded removal of gonads before the trapped stoats were stored frozen. At autopsy, thawed gonads were trimmed of surplus fat and stored in 75% ethanol. Later, uteri were weighed with the ovaries intact, and then both ovaries were decapsulated and weighed together. Paired testes were weighed with epididymes attached. Weights cited here therefore refer to the paired, preserved organs. The material was suitable only for gross histological examination, but we

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**Table 1** The annual cycle of reproductive condition in female stoats of all ages, all collection areas pooled (percentage per month in parenthesis).

	In delay	Implant- ation	Visibly pregnant	Post- pregnant	'Failed'		Not classified
Dec	47(98)				1(2)	48	21
Jan	72(100)					72	17
Feb	105(99)				1(1)	106	20
Mar	61(100)					61	13
Apr	49(100)					49	10
May	53(100)					53	11
Jun	34(100)					34	6
Jul	28(100)					28	6
Aug	14(88)	2(13)				16	1
Sep	7(28)	4(16)	8(32)	1(4)	5(20)	25	1
Oct	0(—)	1(5)	5(24)	9(43)	6(29)	21	4
Nov	11(73)			4(27)		15	3
	481	7	13	14	13	528	113

found that the effects of freezing and of post-mortem changes were seldom sufficient to prevent diagnosis of breeding condition.

Both ovaries of all females preserved in relatively good condition were embedded in paraffin wax and serially sectioned at 15  $\mu$ m. The complete ribbon of sections was divided by eye into 8 equal portions, and 2 adjacent sections were taken from each. These 16 sections were mounted in order on a slide and stained with haemotoxylin and eosin. There was 160–290  $\mu$ m between adjacent pairs of mounted sections. The corpora lutea of delay measured 550–750  $\mu$ m, so every one appeared in at least 2 and up to 4 adjacent pairs of sections. By plotting the appearance and disappearance of each corpus luteum through the series, the number of corpora lutea could be counted. This procedure was rarely unsuccessful, since corpora lutea are large and obvious even in only moderately preserved material.

In all females not visibly pregnant the 2 ovaries were stored together, and are referred to (non-discriminately) as A and B. The ovaries of uteri with visible foetuses were stored separately, so that the number of corpora lutea could be related to the number of foetuses on each side.

A 1 mm strip of uterus was removed from each female and embedded, and about 6–10 consecutive sections were mounted. These slides helped in determining reproductive condition, even though detailed examination at cellular level was not usually possible. In some, collapsed unimplanted blastocysts could be seen. Serial sectioning to count blastocysts was not attempted, and the material was not fresh enough to attempt to flush blastocysts out of the uteri for counting. No uterine scars were seen.

Selected testes were also embedded, and enough sections from each were mounted to determine whether spermatozoa were present in the seminiferous tubules and/or epididymes.

### Classification of reproductive condition

**FEMALES.** Six classes were defined, as follows.

1. *In delay.* Females caught between November and August inclusive, with ovaries showing the typical small (0.4–0.6 mm) corpora lutea of delay and with a quiescent (0.05–0.15 g) uterus.
2. *Implantation.* Females caught from August to October, with enlarged corpora lutea (0.9–1.4 mm) and uteri (0.15–0.36 g).
3. *Visibly pregnant.* Females with distinct uterine swellings.
4. *Post-pregnant.* Females which were lactating, with regressing corpora lutea or none; or lactating and in oestrus; or in immediate post-oestrus with a new generation of corpora lutea, with or without lactation continuing. This class, though heterogeneous, was so small (total 14) that subdivision was not worthwhile. There is no overlap of successive generations of corpora lutea.
5. *Failed.* (a) During the period of delay: females with no corpora lutea (assumed to have failed to ovulate or to find a mate). (b) In September or October: females with or without corpora lutea, which had apparently not successfully produced or reared a litter (see below for further details).
6. *Unknown.* Females for which there was not at least one set of ovary sections.

The term 'fecundity' is used to refer to the number of corpora lutea per mated female, and 'fertility' refers to the number of embryos per pregnant female. Most of the data here concern fecundity.

**MALES.** The relationship between the weight of testes and their reproductive condition is well known, and the fertility of males can be classified from weight alone if an adequate series of testes is first sectioned to calibrate the scale. For this purpose, 1 testis from each of 205 male stoats of all

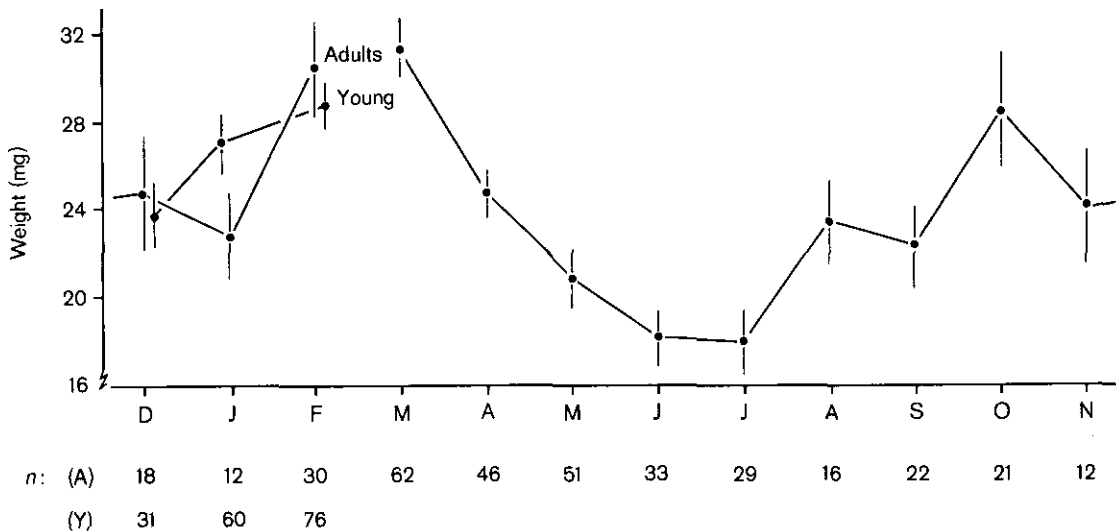


Fig. 1 Monthly mean weights of decapsulated ovaries  $\pm$  SE $\bar{x}$ .

ages were sectioned; 30 were from Tongariro, 87 from Craigieburn, and 88 from Westland. From these data, the male reproductive categories were defined as follows:

- Infertile - testes < 0.6 g;
- Intermediate - testes 0.6–1.0 g;
- Fully fertile - testes > 1.0 g.

#### Estimation of birth date

Hugget & Widas (1951) showed that the growth of the foetuses of many mammalian species can be expressed by the formula

$$\sqrt[3]{W} = a(t - t_0)$$

where  $W$  is the average weight of the foetuses of a given litter,  $a$  is the specific foetal growth constant, and  $t$  is the age of the foetuses from conception. The plot of weight against age of the foetuses is linear from time  $t_0$ , the intercept on the time axis.

The total active gestation period of the stoat, excluding the period of delay in implantation, is unknown. In the closely related *M. frenata* the period from conception to the beginning of delay is about 2 weeks, and that from implantation to birth is 27 days (Wright 1948). In the stoat the latter period is similar (Rowlands (1972) states 4 weeks), so for present purposes we assume that the former period is too, and we use Wright's (1948) figure of 40 days for total active gestation.

Hugget & Widas (1951) found that in mammals with a gestation period of less than 50 days  $t_0$  is usually  $\approx 0.4 \times$  (gestation period), so for the stoat  $t_0 = 16$  days. The specific growth constant,  $a$ , has not been measured, but since the foetuses are known to grow to about 3.5 g (Deanesly 1935, Tumanov et al. 1970)  $a$  can be found by rearranging the formula:

$a = \sqrt[3]{3.5 / (t - t_0)}$ , i.e.,  $a = 1.52 / (40 - 16) = 0.063$ . Then the age of a given set of embryos, as a negative value, 'days before birth', can be determined from their mean weight by the relationship

$$t = (\sqrt[3]{W / 0.063}) + (16 - 40)$$

## RESULTS

### Seasonal changes in sex ratio

The sex ratio of stoats caught (King & Moody 1982b) shows a seasonal shift from a slight majority of females in late summer (43% males in March) to a great majority of males in spring (77% males in October). This is characteristic of samples of *M. erminea*, and is important because it means that samples of females in oestrus, pregnant, or lactating are usually small, whereas females in delay are well represented (Table 1).

### The annual reproductive cycle in females

**Ovary weight.** Fig. 1 shows the monthly variation in the mean weight of the paired, decapsulated ovaries. In adults there is an irregular increase from July to October (spring), then a stasis or slight decrease for 2 months before a second, larger peak in March, followed by a sudden drop in autumn by about 40% back to the winter low. The August increase may be associated with the reactivation of the corpora lutea before implantation, when they reach their maximum development; and the lower peak in October probably reflects the onset of oestrus. The greater enlargement after the breeding season, in February and March, is caused by a temporary increase in the atretic follicles and interstitial cells, which regress during the winter

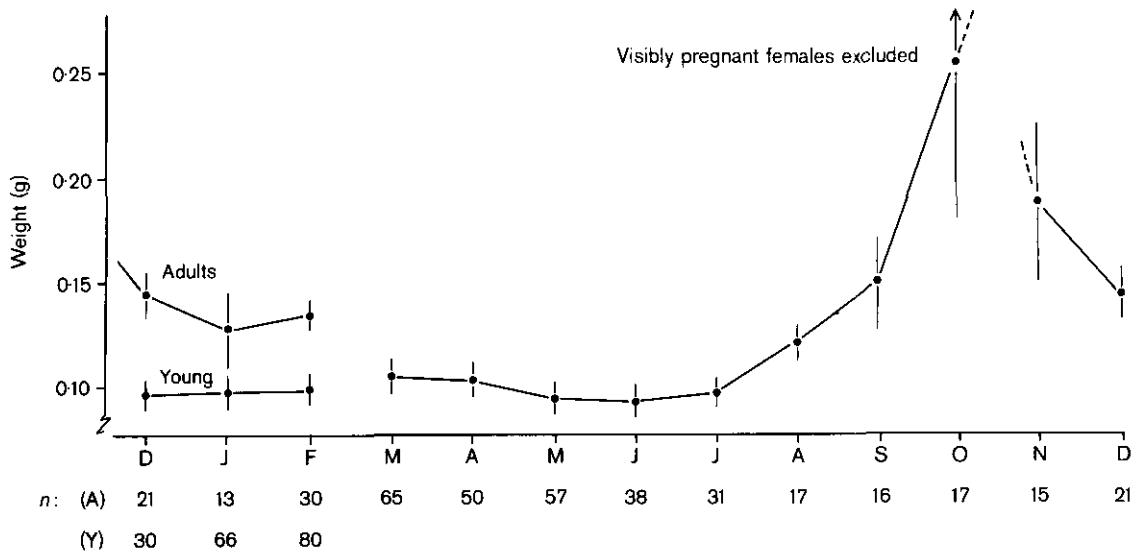


Fig. 2 Monthly mean weights of uterus plus ovaries  $\pm$  SE<sub>x̄</sub>.

months, and was also observed (in August, Northern Hemisphere) by Deanesly (1935).

The ovaries of young females are not systematically different in weight from those of adults, even though the young do not reach adult body weight until March (King & Moody 1982b).

**Uterus weight.** Fig. 2 shows the monthly variation in the mean weight of the uterus plus ovaries, excluding females which were visibly pregnant. In adults the uterus weight is low through the winter, then rises rapidly from August onwards. Both the mean and the standard deviation are high for spring samples, because of the mixture of animals in various phases of early pregnancy and oestrus.

Uterus weights for young females are uniformly low in summer; none was caught which still showed any sign of oestrus.

**Nipples.** Visible nipples were recorded during autopsy on 79 adult females, in all months except June, July, and August (winter). In September and October 17 of 46 females examined had nipples, of which 4 were visibly pregnant, 10 post-pregnant, and 3 'failed'. In November, 8 of 15 examined had nipples, of which 3 were post-pregnant and 5 already in delay. From December to February, 33 of 226 had nipples, and from March to May, 9 of 163 had them, all in delay. The remaining 12 either were not dated or their reproductive condition was unknown. Of the 79, only 10 were definitely lactating, all collected in September or October.

Most females (78% of 73, excluding 6 with suspect counts) had equal numbers of nipples on the left

(mean  $4.2 \pm 0.95$  SD) and right (mean  $4.1 \pm 0.87$ ) sides. A frequency distribution shows that most females had either 8 or 10 nipples (mean total  $8.23 \pm 1.97$ ). We could not always distinguish between functional and non-functional nipples.

**Embryos.** Table 2 gives details of the 13 pregnancies observed. The mean total number of embryos per female is 8.8 (range 6–13). In 5 of the 12 uteri preserved in good condition at least 1 embryo was resorbing (defined as an embryo conspicuously smaller than the rest). Total simultaneous resorption could not be detected, since if all embryos were of even size total resorption could not be distinguished from post-mortem decay. However, in 1 female 7 of the 8 embryos were reduced to simple swellings, leaving only 1 as a large, normal embryo. Normal embryos ranged in weight from about 0.005 g to 2.9 g.

Table 2 shows that the number of embryos often differed from the number of corpora lutea, both in total and in distribution between the horns of the uterus. In 11 instances in which both were counted, the total number of embryos was fewer in 8 and there was evidence of intra-uterine migration of blastocysts in 6.

It is disappointing that in so large a sample of females so few pregnancies were observed, and there is no possibility of checking for seasonal or geographic variation in fertility, as opposed to fecundity. Nor do we have any information on litter size, since nests of young were never found. Fitzgerald (1964) found only 3 pregnancies, of 7, 12, and 12 embryos.

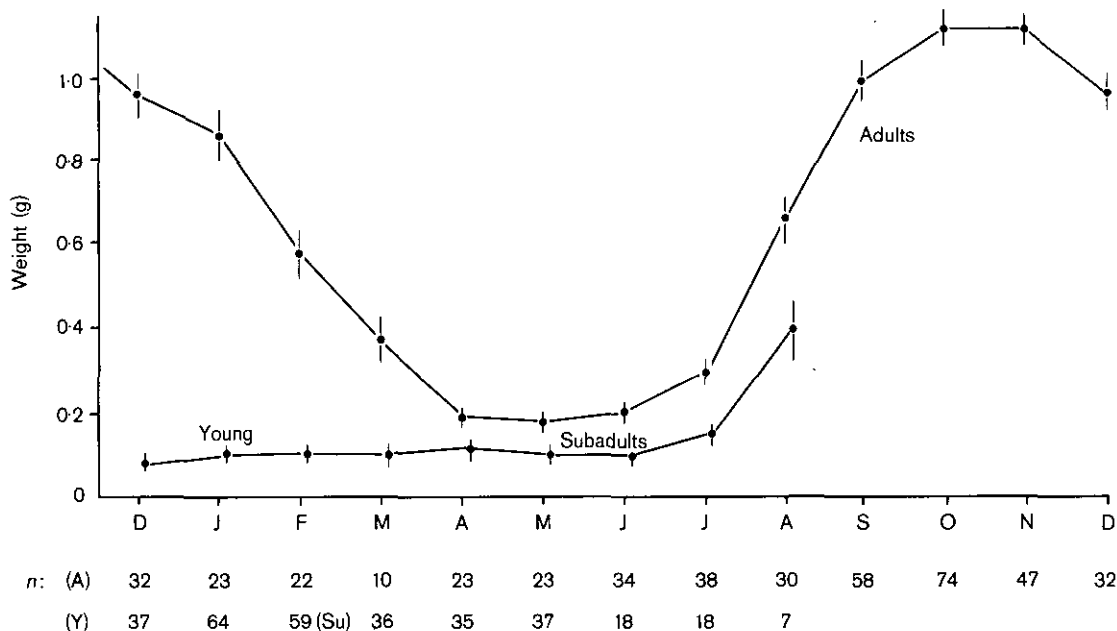


Fig. 3 Monthly mean weights of paired testes with epididymes  $\pm$  SE $\bar{x}$ .

*Seasonal distribution of categories of reproductive condition.* All but 2 of the 451 females caught from December to July inclusive carried the small corpora lutea of delay (Table 1). The exceptions, classed as 'failed', were a young female from Kaikoura in December and an adult from Craigieburn in February.

The 'post-pregnant' category included 5 females which were lactating without sign of oestrus ('pre-oestrus'), 1 (from Westland, 22 October 1974) in full oestrus, and 8 in which oestrus was subsiding and a new generation of corpora lutea was present. The distinction between successive generations of corpora lutea is clear since they do not overlap as they do in weasels.

No young females caught were still in oestrus, or even showing any signs of recent oestrus. Since newly independent young could be caught from the age of about 2–3 months (King & Moody 1982b), this supports the observation—made on captive animals—that young females are usually fertilised before weaning (Müller 1970, Andreewska & Brandesowa 1977).

#### The annual reproductive cycle in males

*Testis weight.* Monthly variation in the testis weights of adults shows a nearly sinusoidal pattern with a maximum at about the end of October and a minimum in May (Fig. 3). The period of increase (July–October) begins after the winter solstice, and the period of peak testis weight corresponds with the

time of year when Gulamhusein & Tam (1974) observed a peak in the concentration of plasma testosterone (February–April in London). There is no significant correlation between body weight and weight of the fully developed testes of adult males in October.

The mean testis weight of young males reaches about 0.1 g in January, and then shows no further change until almost the end of the subadult phase in July, when it increases in parallel with the mean for adults. In winter, the testes of subadult males are consistently smaller than the regressed testes of adults.

The relationship between testis weight and fertility is shown in Fig. 4. Spermatozoa were found in all but 3 testes over 0.6 g; the exceptions contained spermatids. For Craigieburn and Tongariro stoats (mean body weight of adult males  $356 \pm 7$  g and  $355 \pm 13$  g respectively) the maximum testis weight in spring is rather higher than in the Westland sample ( $285 \pm 7$  g). This raises the possibility that the testes of smaller stoats might be fertile at weights lower than 0.6 g. There are 3 possible such individuals from Westland: an adult in July, which had spermatozoa in the testes but not yet in the epididymes; and 2 other adults, 1 in February and 1 in March, which still had spermatozoa in the epididymes but none in the testes. However, the series is incomplete at the critical points, and there is insufficient evidence to show whether or not the smaller Westland males



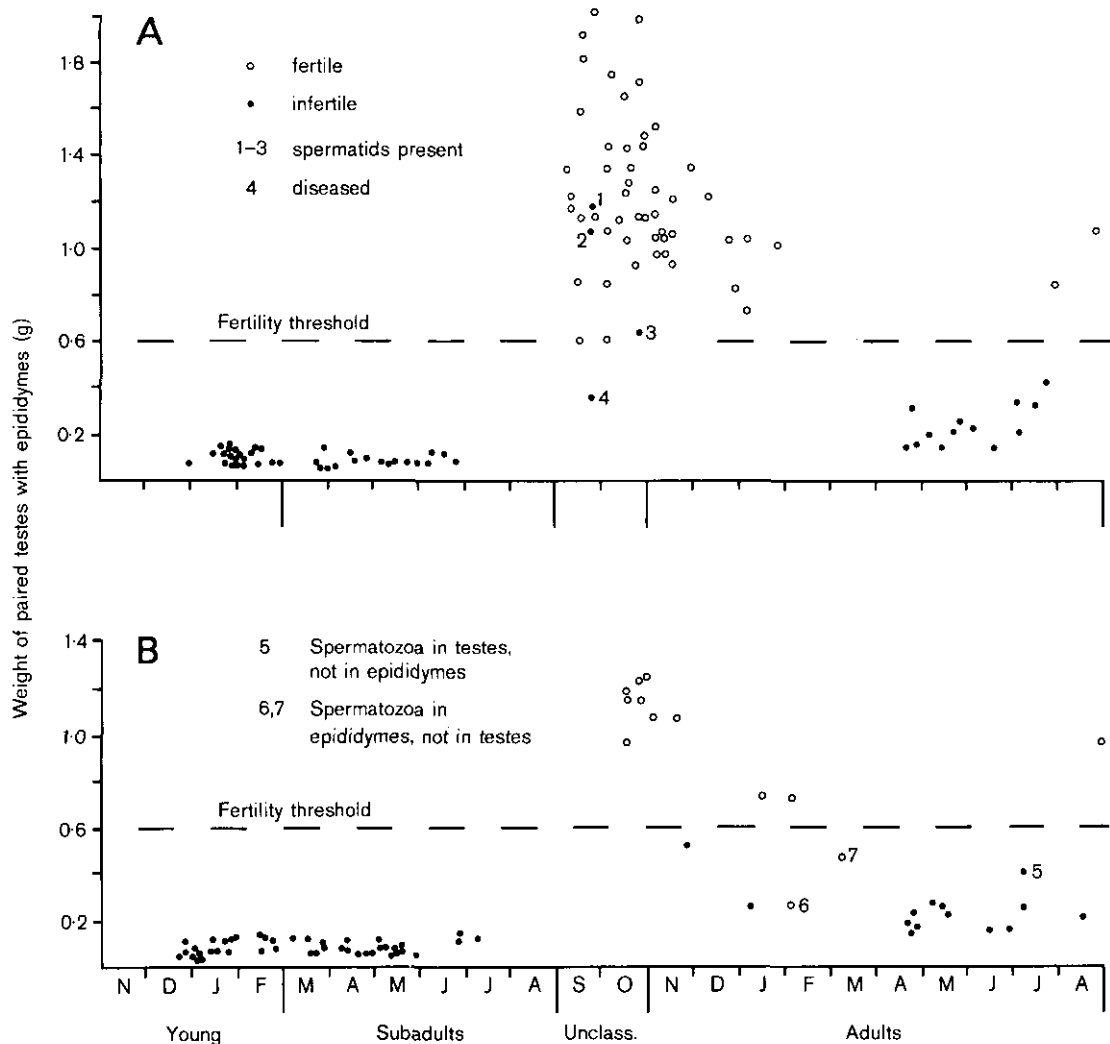


Fig. 4 Relationship between testis weight and fertility for stoats from (A) Craigieburn and Tongariro (populations with large average body size); (B) Westland (a population with small average body size). For definitions of age classes see King & Moody (1982a).

were fertile at lower testis weights. For the same reason it is not possible to say whether the fertile season in the mild lowland climate of Westland is any longer or earlier than that in the cold alpine climate of Tongariro or Craigieburn.

**Baculum weight and length.** Wright (1950) has shown that the development of the baculum in *M. frenata* is controlled by androgens, and that the adult form is not achieved by prepubertal or castrated animals. The development of this bone should therefore be synchronised with that of the testes through the first year. Fig. 5 shows an increase

in the mean weight of the baculum in immature males, by equal monthly increments, from 13 mg in December to 23 mg in March, after which no further change is evident until the onset of puberty, in July. The length of the baculum shows a similar pattern, except that there is less difference between adults and subadults in autumn and there is a less obvious stasis in growth of the young bacula in autumn.

The mean baculum weight of adults drifts upwards between September and February, probably because of continued growth in newly recruited young adults. After February there is, if anything, a slight decrease in the mean baculum weight of

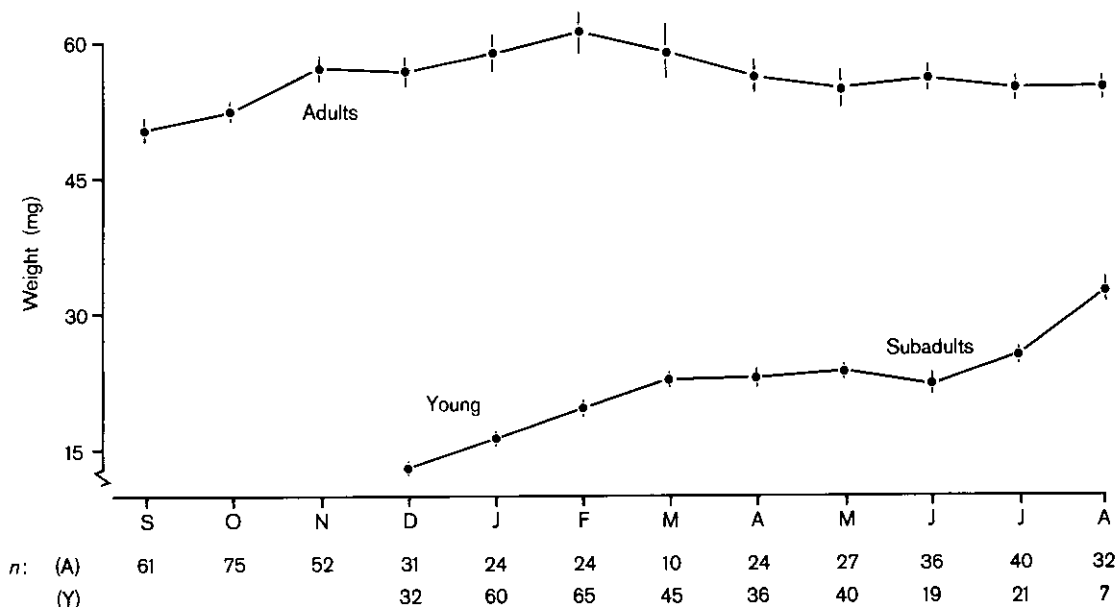


Fig. 5 Monthly mean weights of bacula  $\pm$  SE $\bar{x}$ . The transition from subadult to adult weight beginning in July is very rapid, though the mean baculum weight for the mixed group of young and old adults continues to increase from September to February.

adults. If baculum weight continues to increase with age in adults, as suggested by van Soest & van Bree (1970), this slight decline could represent the gradual loss of older males from the population; it is less likely to be due to a progressive contamination of the sample of adults with misclassified subadults, since the distinction between them in autumn is so reliable (Fig. 5).

**Seasonal distribution of categories of reproductive condition.** Fully fertile adult males are evident from August to February. The peak of the season is in October and November, but even in these months a few adults were apparently still infertile. No young or subadult male had enlarged testes ( $> 0.6$  g) or a developed baculum, so it appears quite definite that males do not mature until the season following that of their birth.

#### Evidence for geographic variation in the reproductive season

**Females.** Because few females were caught in spring, it is difficult to determine precisely the season of births. However, there are 2 lines of evidence which suggest that, on average, births may be slightly later in the far south.

Table 3 gives the reproductive condition of the 77 females caught during August–November in relation to latitude. The figures are small, but in each month the animals from the more northerly latitudes consistently tended to be the first to reach each new stage in the reproductive cycle, while those from the

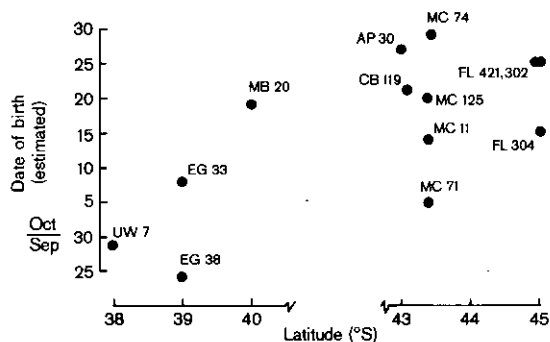


Fig. 6 Correlation between latitude and expected date of birth;  $r_s = 0.52$ ,  $N = 13$ ,  $P < 0.05$ . Figures are the sample numbers of individual pregnant females. For key to sample codes, see King & Moody (1982a).

far south tended to be the last. Northern females reached the implantation stage, in August, first; in September, a northern animal was already lactating while 7 of 10 from the far south were still in delay. The last animals to pass the implantation stage in October and the post-oestrus stage in November were from the far south, and neither of the 2 females from there had got as far as a new cycle of corpora lutea in delay by the end of November, whereas most females from the other 2 regions had.

The date of birth too tended to be later in the South Island than the North Island. Table 2 gives

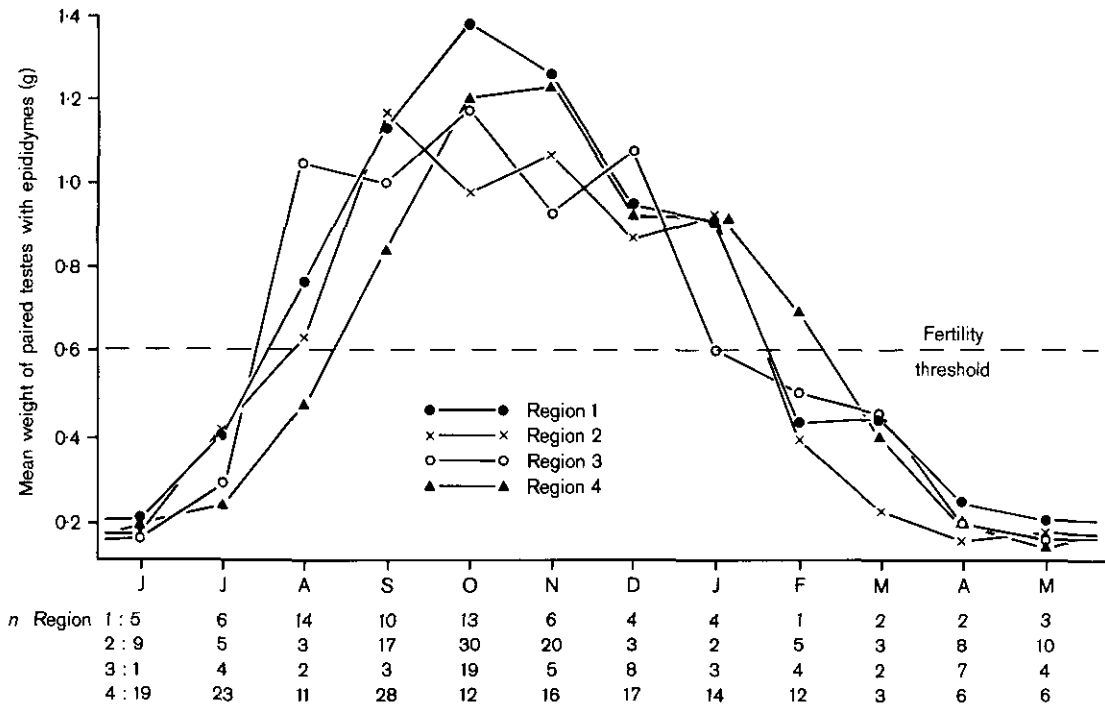


Fig. 7. Latitudinal variation in the annual cycle of adult testis weight. Regions: 1, 38–40°S; 2, 40°S; 3, 43°S; 4, 44–45°S. See King & Moody (1982a) for list of study areas in each region.

the estimated date of parturition for the 13 pregnancies observed. The range of approximate birth dates over the whole country is from 24 September to 29 October. This coincides with the distribution of very early post-partum females, recorded between 29 September and 25 October. The range of estimated birth dates for the 4 North Island females, from latitudes 38–40°S, is slightly earlier (24 September to about 19 October) than that for the 9 South Island females from latitudes 43–45°S (5 October to 29 October). The Spearman rank correlation coefficient between birth date and latitude is significant (Fig. 6). The difference in implantation dates between the North and South Islands is small, perhaps only about 10 days. This coincides with the difference in daylength between north and south at the time of implantation. In the far south (Bluff) the 'daylight' phase of the diel cycle reaches a given length 30 days after it does in the north (Auckland) in July, 20 days later in early August, 10 days later in late August, and, of course, at the same time at the September equinox. A 10-day difference in birth dates between the north and the south presumably reflects a physiological process, controlled by daylength, occurring in late August. This is exactly the time that blastocysts must begin to implant if the young stoats are born,

after 4 weeks' active gestation, from late September onwards.

**Males.** Fig. 7 compares the cycles of adult testis weight in 4 latitudinal regions. There is a suggestion that the onset of spermatogenesis may be delayed in the far south relative to regions further north. By August all but the southernmost males had passed the threshold of fertility, and they appeared to reach their maximum testis weight later than males in the North Island. However, increasing altitude appears not to retard spermatogenesis; an analysis of variance of testis weight in males of 5 altitude classes in October and November (omitting Region 4) gives an F value of 0.88 ( $P > 0.5$ ).

#### Variation in fecundity

The early maturity, induced ovulation, and extended delayed implantation in the stoat conveniently allow both the ovulation rate and the proportion of females fertilised to be estimated for females of all ages collected through most of the year. The ovulation rate (indicated by the number of corpora lutea) is of particular interest, since it gives an estimate of the maximum potential productivity of a population of stoats. The number of young born may be much less, but we have little information on

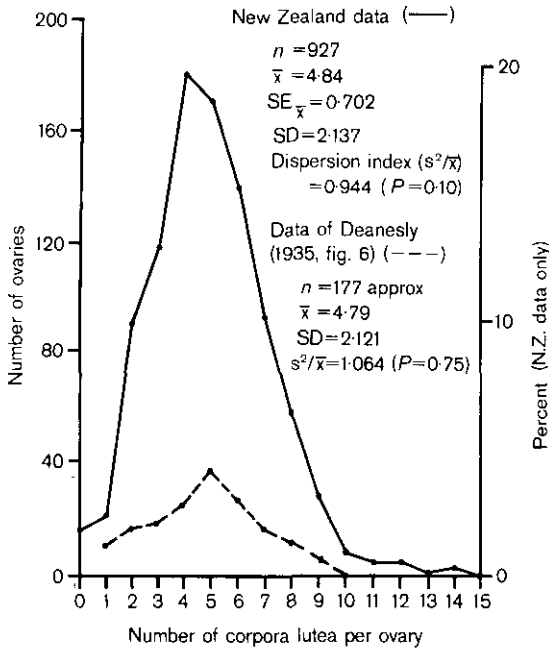


Fig. 8. Frequency distribution of the numbers of corpora lutea per ovary of female stoats in delay.

litter size. King (1981) documents the extent of the variation in the reproductive effort of stoats in 3 of our study areas.

*Incidence of corpora lutea in relation to reproductive condition.* Corpora lutea (illustrated in Deanesly (1935)) were found in the ovaries of females in all categories of reproductive condition. Some females which had presumably failed to ovulate or had not yet been fertilised for the next season are classified 'failed' (see below) or 'post-pregnant', and these had no corpora lutea in either ovary. The mean number of corpora lutea per female is low and the standard deviations are large in the 'failed' and 'post-pregnant' classes ( $6.6 \pm 4.2$  and  $5.3 \pm 4.2$  respectively, both  $n = 10$ ). Counts from the other 3 classes are higher and similar; in particular, there is no systematic decrease in the mean from the period of delay (mean  $9.7 \pm 1.9$ ,  $n = 439$ ) through implantation ( $8.8 \pm 1.6$ ,  $n = 6$ ) to pregnancy ( $10.5 \pm 2.5$ ,  $n = 10$ ).

*Frequency distribution of counts.* The frequency distribution of corpora lutea per ovary during the period of delay in implantation is unimodal, with the variance approximately equal to the mean (Fig. 8). The data of Deanesly (1935), included in Fig. 8, also show a unimodal distribution with variance equal to mean. The probability of a single ovary containing a particular number of corpora lutea within the

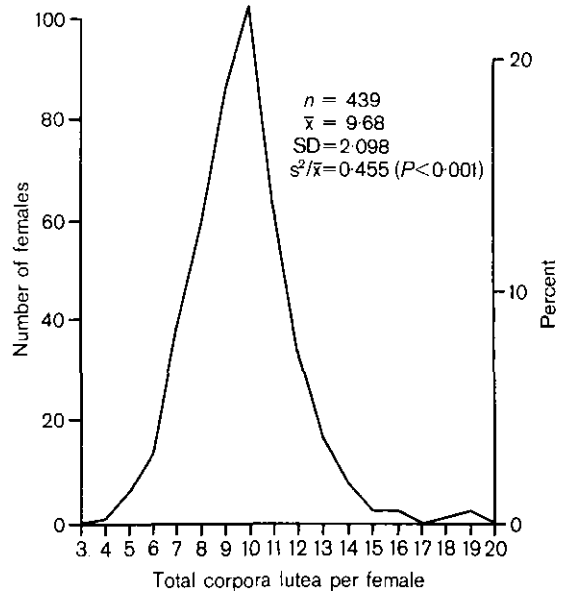


Fig. 9 Frequency distribution of the numbers of corpora lutea per female in delay, excluding 49 for which counts from only one side were available.

observed range is therefore best described by a Poisson (random) distribution.

The frequency distribution of the total number of corpora lutea per female is also unimodal, but the ratio of variance to mean is significantly less than unity (Fig. 9), which implies that the distribution of corpora lutea numbers is narrower than would be expected by chance.

*Relationship between counts for the two ovaries of one individual.* The numbers of corpora lutea in the A and B ovaries of one individual are inversely related: if one contains more than the average number, the other is likely to contain less than the average (Table 4). The inverse correlation is significant for all seasons except spring; the spring sample is small, and the pattern is likely to be confused by the degeneration of corpora lutea in post-pregnant individuals.

*Variation with season.* The mean and standard error in number of corpora lutea per female for each month are shown in Fig. 10. Most of the variation can be traced to a few exceptional animals. No corpora lutea were found in the 2 trapped in February and December which are presumed to have failed to ovulate, nor in several taken in October which were not yet fertilised for the next season; very high counts (15–19) were obtained from a few individuals scattered throughout the

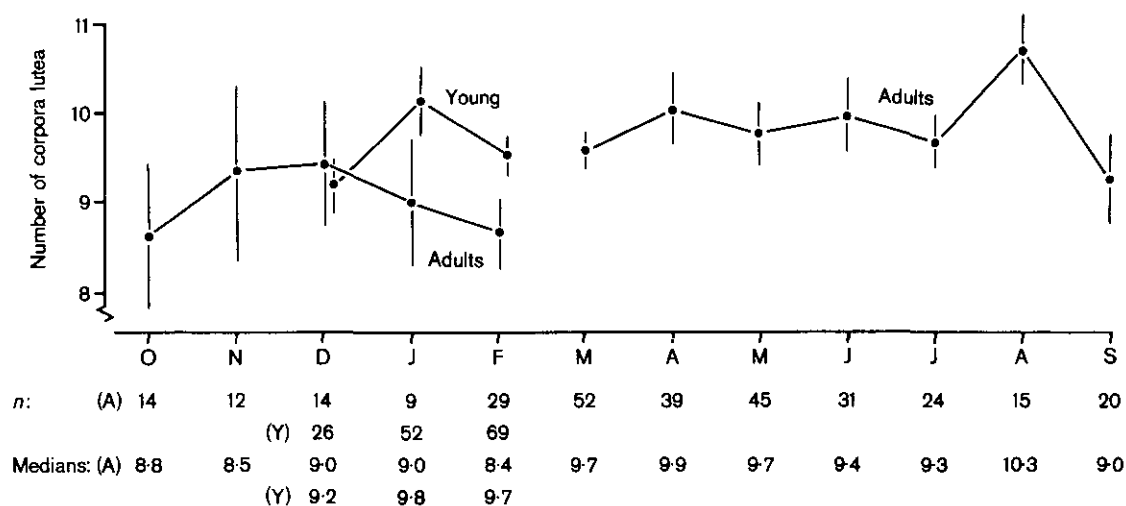


Fig. 10 Monthly mean numbers of corpora lutea per female  $\pm$   $SE_{\bar{x}}$  (all reproductive categories).

period of delay. The large variability in the counts suggests that the median may be more useful than the mean, but in fact the series of monthly medians shows much the same pattern of variation as that of the means. The August peak in the mean, which occurred also in body weight (King & Moody 1982b), may be a sampling error related to the smallness of the sample or to monthly variation in the proportions of females from different environments. There is no correlation between mean body weight and mean fecundity (in 19 samples of adults from separate years in 6 localities,  $r_s = 0.08$  NS).

**Variation with age.** Fig. 10 also shows that young females in January and February (but not in December) appear to have about 10% more corpora lutea per female than adults in the same months. This effect can not be examined rigorously for samples taken later in the year, as first-year females can not be distinguished with certainty after February. However, it is possible to make an approximate classification into 2 year-classes between March and August using the comparative method of King (1980), based on known-age material of the closely related *M. nivalis*. There is no consistent difference in corpora lutea count between the year classes defined by this method. Likewise, Deanesly (1935) found no difference in the number of corpora lutea per ovary in parous and non-parous (first-year) stoats in Britain. Extended sampling at Craigieburn and in the Eglinton and Hollyford valleys confirmed that young females tend to be more fecund than adults in summer, but again, the difference is not significant (King 1981).

**Variation with area and year.** Table 5 shows the statistics of geographic and annual variation in the number of corpora lutea per female during the period of delay (January-August). The means of all samples of 4 or more females lie within 1 standard deviation of the overall mean for all stoats in delay.

The significance of the variation between year/area samples in ovulation rate was tested with a 1-factor analysis of variance. However, Bartlett's test shows significant heterogeneity of variance ( $P < 0.01$ ), even if samples containing less than 10 females are omitted. A plot of standard deviation against mean number of corpora lutea per female identifies a single sample (Craigieburn 1975) as unusually variable. When the test is repeated with this sample omitted, the variance becomes homogeneous. The analysis of variance then gives an F-ratio more reliably showing no significant annual or geographic variation in corpora lutea counts in the remaining year/area samples.

Variation between years and places may still occur, but in the present data it is masked by the large variation within a local population (the coefficient of variation within year/area counts is about 22%).

The larger variance for Craigieburn stoats mated in 1974 and sampled for corpora lutea from January to August 1975 (see Table 5) is due to the occurrence of some exceptionally high counts among that generation of corpora lutea (up to 19; the maximum in 3 other years was 13). Reasons for this are discussed by King (1981).

**Table 5** Geographical and annual variation in numbers of corpora lutea per female.

Collection area	Jan-Aug of years†	n	No. of corpora lutea per female	
			$\bar{x}$	SD
Egmont	1974	7	10.9	2.04
	1975	7	9.9	2.27
	1974	6	9.5	1.38
	1974	10	10.3	1.70
Tongariro	1973	5	9.2	—
	1974	16	8.8	1.97
	1973	6	9.3	1.75
Nelson Lakes	1974	4	9.0	—
	1975	21	10.8	3.63
	1976	19	9.3	1.76
	1974	15	10.9	2.10
Arthur's Pass	1975	14	9.2	1.63
	1976	25	9.7	1.91
	1973	8	10.1	1.89
Craigieburn	1974	16	9.8	2.02
	1975	26	9.4	2.73
	1973	16	9.8	1.52
	1974	4	9.8	—
Mount Cook	1973	13	9.8	1.42
	1974	13	10.2	1.79
	1975	20	9.7	1.76
Westland	1976	5	10.2	—
	1975	48	9.5	1.74
	1976	4	7.8	—
	1973	5	10.4	—
Takaro	1974	16	9.8	—
	1973	13	9.8	—
	1974	13	10.2	—
Fiordland, Eglington Valley	1975	20	9.7	—
	1976	5	10.2	—
	1975	48	9.5	—
Fiordland, Hollyford Valley	1976	4	7.8	—
	1973	5	10.4	—

Tests for variation in corpora lutea per female between the above year/area samples.

Test No.	Bartlett's test for homogeneity of variance		One-way analysis of variance		P
	$\chi^2$	df	F	df	
1	49.16	29	0.01	31	0.2
2	35.00	13	0.001	13	0.2
3	13.53	12	0.35	12	0.4

†1976, Jan-Mar only

**Table 4.** Relationship between numbers of corpora lutea in the two ovaries of one individual.

Corpora lutea in ovary B		Corpora lutea in ovary A													
		0	1	2	3	4	5	6	7	8	9	10	11	12	
0	1														
1	2														
2	3														
3	4														
4	5														
5	6														
6	7														
7	8														
8	9														
9	10														
10	11														
11	12														
12	13														
13	14														
14															
		7	12	45	63	91	77	65	38	22	13	3	1	2	439

Spearman rank correlation coefficients for the relationship between number of corpora lutea in the A and B ovaries of females in delay (null hypothesis: there is no correlation).

	$r_s$	n	P
Summer	-0.521	200	<0.001
Autumn	-0.610	136	<0.001
Winter	-0.623	69	<0.001
Spring	-0.258	16	0.167

**Table 6** Details of 11 female stoats failing to rear a litter (all over 11 months old); for reasoning, see below.

Code No.	Lat. (°S)	Habitat	Date	Uterus wt (g) <sup>(1)</sup>	Nipples <sup>(2)</sup>	Corpora lutea Size (mm)	Corpora lutea Condition	Remarks
UW8	38	Mixed forest	13 Sep 73	0.084	2 + 0	0.65	fresh	Expected to be at implantation or early pregnancy stage, but no sign of enlarged corpora lutea or uteri <sup>(1)</sup>
NL5	41	Beech forest	28 Sep 72	0.078	NV	0.69	fresh	
NL6	41	Beech forest	28 Sep 72	0.090	NV	0.50	fresh	
NL11	41	Beech forest	29 Sep 72	0.098	4 + 2	0.60	fresh	
NL14	41	Beech forest	29 Sep 72	0.107	3 + 3	0.50	fresh	
NL1	41	Beech forest	30 Oct 72	0.102	NV	0.46	fresh	Expected to be pregnant or lactating
AP3	43	Beech forest	20 Oct 72	0.074	NV	degenerating		
AP43	43	Beech forest	7 Oct 72	0.082	NV	regressing		
AP36	43	Beech forest	Oct 72	0.121	NV	fresh		
TK174	45	Beech forest	11 Oct 73	0.091	NV	0.50	fresh	Expected to be at implantation stage or pregnant
TK180	45	Beech forest	8 Oct 73	0.082	NV	—	fresh	

<sup>(1)</sup> At implantation stage, mean uterus weight = 0.21 g ( $n = 7$ ); corpora lutea 0.9–1.4 mm

<sup>(2)</sup> None associated with functional mammary glands (NV, not visible)

### Evidence for failure in reproduction

The seasonal cycle of reproductive condition in female stoats from implantation to post-oestrus is rather synchronised and predictable (Table 3). However, there were 11 females caught in September and October whose condition can best be interpreted by assuming that all had failed to produce young in the season in which they were caught (Table 6).

Five females collected at the end of September—1 from Urewera (in the north) and 4 from Nelson lakes (central)—all contained the small corpora lutea of delay. These could represent the ovulation either of the previous breeding season, in which case these females should be about to implant and bear a late litter, or of the current breeding season, in which case they must have had early litters and passed post-partum oestrus already. Neither explanation fits. The only other females still in delay in September were those from the far south (Table 3); all the other females collected from Nelson Lakes and northward in September were already pregnant, including another female collected at Urewera on the day after the one mentioned above. Moreover, none of the 5 showed any signs of preparing to implant (see Materials and Methods), although 3 had partially developed nipples. On the other hand, if the 5 had already had successful litters, the time required for gestation, lactation, and the subsidence of oestrus would have delayed the reappearance of their condition (small corpora lutea of delay, no enlarged uterus) until November at the earliest, and they would have had enlarged nipples. It seems reasonable to suggest that all 5 had lost their litters, either by total resorption of foetuses or at birth or soon after, and all had already been fertilised for the next season.

All but 6 of the females caught in October can be classified into one of the stages of active reproduction, from post-oestrus in northern animals to implantation in southern ones; none had yet reached the stage of a new generation of corpora lutea. The 6 exceptions showed no signs of reproductive activity; 2 had only regressing corpora lutea, and 4 had fresh corpora lutea of delay. None had enlarged nipples. It appears that all had lost their litters, and 4 had been fertilised for the next season.

This interpretation of the status of these 11 females is valid only if (a) the latitudinal variation in breeding season suggested in Table 3 is real; (b) fertile males are available in September; (c) there is evidence that total or near-total resorption may occur; (d) there is a reasonable explanation for the distribution of failures being distinctly non-random (8 of the 11 came from beech forests in 1972).

If there is no latitudinal variation in the breeding season, the 5 September females could simply be in late delay. However, the balance of the evidence—both from males and females in this study and in the literature—favours the possibility of a latitudinal shift in breeding season, and late delay does not explain the status of the 6 October females mentioned above.

Fertile males were certainly present at all middle and northerly latitudes by September, and in fact probably by August (Fig. 7). There would have been plenty of time for the 'failed' females to be newly fertilised by the time they were caught.

Total resorption cannot be demonstrated because it cannot be reliably distinguished from post-mortem decay, but one pregnancy was observed in which 7 of the 8 embryos were resorbing (Table 2). Three captive females examined by Gulamhusein were

carrying palpable embryos but subsequently failed to litter (Rowlands 1974).

A possible explanation for the distribution of 'failed' females is discussed, with additional data, by King (1981). Most of them were collected in beech forests during or after population declines of mice (*Mus musculus*) (Fitzgerald 1978).

#### Disorders of the gonads

Some abnormalities of the gonads were noted. Four ovaries showed signs of cysts, though some were still producing corpora lutea. In 9 males one testis was larger than the other, and in a further 3 males one of the pair appeared to contain a cyst. The only one of all these abnormalities to be diagnosed was the largest of the ovarian tumours, which came from a female collected at Mount Cook on 10 April 1974. Dr R. A. Archibald, consultant pathologist at the Santa Clara Medical Centre, California, diagnosed it as a teratoma of predominantly solid type, though whether malignant or benign could not be determined. The other ovary of the same female was normal, and contained 5 corpora lutea of delay.

#### DISCUSSION

The annual cycle in stoats is made especially difficult to work out by the inconvenient scarcity of females at the critical period (Table 1), a problem common to most collections (Deanesly 1935, Watzka 1940, Fitzgerald 1964, Stubbe 1969, van Soest & van Bree 1970, Danilov & Tumanov 1975). Müller (1970) noted that even tame female stoats in captivity became shy and retiring about 2 months before producing their young. If wild females spend more time in their nests at this season they will be less likely to be caught. Conversely, males become more active in spring, especially the young ones (Erlinge 1977).

In general features the annual cycle in stoats from New Zealand (Fitzgerald 1964; this study) is consistent with that described for stoats in Britain (Deanesly 1935, Gulamhusein & Tam 1974), but displaced by about 6 months. Occasional disagreements—(e.g., higher minimum weight of fertile testes (Deanesly 1935, Danilov & Tumanov 1972) and an earlier peak in testis weight (Fitzgerald 1964)—can largely be explained by differences in technique or in sample sizes.

The literature on the reproductive cycle in the stoat has been complicated by 2 unsupported but persistent ideas. The first, put forward by Deanesly (1935) but later (1943) corrected by her, interpreted the corpora lutea of delay as products of repeated spontaneous ovulation throughout the autumn and winter. Unfortunately the correction is a short note, easily missed, and Deanesly's original interpretation

continued to be repeated for years in reference books, including 2 published as late as 1964. The second idea, advanced by Watzka (1940) and more lately by Kopein (1965), suggests that female stoats not fertilised during the main breeding season in summer are able to mate in spring and produce a litter without delayed implantation. Watzka's evidence was histological, but insufficient at the critical season; Kopein based his conclusion on the timing of the appearance of the young and the age structure of his trapped samples. Even if Kopein's method of age determination were perfectly accurate, without histological evidence his data can be taken to show only an unusually extended period of births, not a second oestrus period and undelayed gestation. Wright (1963) and Müller (1970) found no behavioural evidence for an early spring mating period in *erminea* in the U.S.A. and Germany respectively. Furthermore, Wright (1942a) pointed out that in *frenata* the males are not fertile until late March, so that young from a spring mating could not appear until late May at the earliest, which does not correspond with field records. In the present material there is no evidence of oestrus in early spring, but consideration of the 'failed' females does suggest an alternative interpretation of at least Watzka's material. Possibly females which were not mated or which lost their litter could be fertilised for the next cycle as soon as the males are ready, which would be 6–8 weeks before the successful females come into post-partum oestrus; this could give the impression of an early and a late oestrus season. Wright (1948) noted that female *frenata* which had not been mated the previous season, or had not suckled their litter, came on heat somewhat earlier than the others. Two of his 3 captive females mated early produced young in the following season, after an even longer gestation period than usual.

The monthly distribution of stoats in active reproductive condition observed in this material is consistent with the hypothesis that the cycle in both sexes is controlled by daylength. Experimental work has shown that implantation can be induced out of season only by manipulation of perceived daylength (Pearson & Enders 1944), and not, for example, by injection of hormones (Gulamhusein & Thawley 1974). In our material, enlargement of the testes and of the corpora lutea of delay begin soon after the winter solstice. By August the difference in timing between northern and southern animals in testis weights and in estimated implantation dates corresponded in extent and direction with the difference in daylength at that season (Fig. 6 and 7). The difference is fine, but is also apparent in another process affected by daylength, the initiation of the spring moult (King & Moody 1982c), as previously observed by Wright (1942b). Russian observers have also noted a latitudinal displacement in

breeding activity, in both stoats (Aspsov & Popov 1940, Danilov & Tumanov 1972, 1975) and polecats (*M. putorius*) (Danilov & Rusakov 1969). However, the initiation of the autumn moult is also earlier in the south, whereas the autumn regression of the testes is not (Fig. 7). This suggests that the end of the breeding season for males is a rather passive decline not controlled by daylength, in contrast with the more active processes of preparation for breeding and for both seasonal moults.

The remarkable scarcity of oestrous females caught suggests either that the oestrus period in stoats is quite short or that oestrous females are especially elusive. In the present material pre-oestrus stages were observed in only 5 adults, and full oestrus in only 1 adult and no young; all 6 were collected in September or October ( $n = 46$  for the 2 months). B. M. Fitzgerald (pers. comm.) found no oestrous females among 9 collected in September and October. Peaks in the cycles of testis weight and ovary weight coincided in October. Most parous adults were in a new cycle of delay by the end of November, and all young females but one had already ovulated by that time. In contrast, the males remained fertile at least until the end of January.

Gulamhusein stated firmly that "the stoat is an induced ovulator and, consequently, corpora lutea were not found in the ovaries until after mating had taken place" (Rowlands 1972). Wright (1963) stated categorically that "at the end of the breeding season the ovaries of unmated female *frenata* are without corpora." Three New Zealand females kept in captivity for a year, isolated from males, contained no corpora lutea when autopsied at least 3 months after the normal mating season (C.M.K. pers. obs.). Yet in the present material, only 2 of 451 females collected between December and July inclusive had no corpora. If oestrus is brief and synchronised by daylength, and ovulation is induced, the efficiency of male stoats at finding receptive females is remarkable. The proverbial English description of a particularly persistent human suitor as 'a bit of a stoat' is clearly no mean compliment.

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