

AGE-SPECIFIC PREVALENCE AND A POSSIBLE TRANSMISSION ROUTE FOR SKRJABINGYLOSIS IN NEW ZEALAND STOATS, *MUSTELA ERMINEA*

Summary: The prevalence of infestation of the skulls of stoats with the parasitic nematode *Skrjabingylus nasicola* was previously described in a national survey by King and Moody (1982). Since then, more samples from Craigieburn Forest Park and from the Eglinton Valley, Fiordland, have been collected, and a method of determining the actual ages of adult stoats has been developed. The extended samples are here examined for a relationship between infestation and age, which could not previously be tested. Prevalence generally increases with age, significantly so at Craigieburn. Stoats which had lived through one or more beech (*Nothofagus solandri*) mast years at Craigieburn were significantly more likely to be infested, when the effects of age were allowed for. The hypothesis is advanced that the paratenic host for *S. nasicola* in New Zealand is the feral house mouse, *Mus musculus*, which is more numerous after a heavy beech seed fall.

Keywords: Nematode; parasite; *Skrjabingylus nasicola*; prevalence; transmission; stoat; *Mustela erminea*; age structure; paratenic host; *Mus musculus*.

Introduction

The nematode parasite *Skrjabingylus nasicola* causes conspicuous lesions in the skulls of small mustelids. The bone in the post-orbital region may be distorted, swollen and thinned, or perforated with holes that may develop into large openings. The worms inside the affected area are large, bright red and easily dissected from fresh material; the damage they cause is often very frequent, and still visible in clean skulls. The prevalence of infestation in a population, and the extent of damage to the skulls, are both closely correlated with the worm burdens of individuals, as documented from fresh material by Lewis (1978), so the distribution of the disease can be surveyed from museum collections. These considerations make *skrjabingylus* a good subject for a parasitological study, and the northern hemisphere literature on it is large (summarised by King and Moody, 1982; King, 1989).

The stoat and the common weasel (*Mustela erminea* and *M. nivalis vulgaris*), two of the definitive hosts of *S. nasicola*, were introduced to New Zealand in considerable numbers from Britain late last century. *Skrjabingylus* is common in British stoats and weasels, so the colonising stock must have included many infested individuals. Other species of parasites that set out from Britain for New Zealand along with their hosts, such as the specific fleas of the rabbit (Gibb and Williams, 1990) and those of the hedgehog (Brockie, 1990), died out during the enforced quarantine on the long voyage under sail.

But individual worms of *S. nasicola* are long-lived; they survived the journey, at least in the same proportions as their hosts did, and are now established in the wild with them.

The distribution of *skrjabingylosis* in New Zealand was documented during an extensive survey of the biology of stoats collected, mostly from National Parks, between mid 1972 and March 1976 (King and Moody, 1982). There was very pronounced geographical variation in prevalence, ranging from 0 to 83% in 27 local subsamples with more than 6 stoats of 6 months old or older (mean 10%, total $n=1005$). In general, adults of the two sexes were equally often affected.

These data raised two interesting problems, concerning (1) the relationship between infestation and age, and (2) what determines the geographical distribution of the disease in New Zealand. Neither could be resolved from the information available at the time.

In two of the study areas included in the 1972-76 survey, sampling was extended from March 1976 to April 1978. They were Craigieburn Forest Park, Canterbury, where the mean prevalence in the 1972-76 sample was 15% ($n=114$); and the Eglinton Valley, Fiordland National Park (7%, $n=155$). In 1979-81, Grue and King (1984) collected a set of known-aged stoats from Fiordland, and confirmed from them that canine cementum annuli can be used to divide adult stoats into year classes. So canines from all adults in the two extended samples were sectioned, and population age structures constructed. These data

now provide a new opportunity to re-examine, at least in these localities, both the questions concerning skrjabinngylosis which could not be addressed by the previous national survey. A third extended sample with age structures was available from the Hollyford Valley, Fiordland, but the prevalence of skrjabinngylosis in that area is too low (1%, n=91) to analyse further.

Relationship between prevalence and age

When the 1972-76 material was analysed, we (King and Moody, 1982) had no satisfactory method of classifying stoats into year classes. The age determination technique we used could accurately identify young of both sexes up to 4 months old, and young males of 5 to 10 months old, but all other animals were classed together as adults. In British common weasels, prevalence certainly increases with age (King, 1977), but we could not check on the reasonable assumption that skrjabinngylus is probably also more frequent, or causes more damage, in older stoats in New Zealand. We were also aware that some of the oddities we observed in the patterns of prevalence with sex, year, and locality might have been due to hidden errors introduced by variation in the proportion of older stoats, but we could not eliminate them.

Transmission and geographical variation in prevalence

The 1972-76 survey apparently showed that the geographical variation in prevalence of skrjabinngylosis in New Zealand was inversely correlated with rainfall. All the local subsamples with the highest rates of infestation (15-83%) were collected from areas with mean annual rainfall of less than 1600 mm yr⁻¹, whereas all the subsamples with rates of 0 to 13% came from areas with mean annual rainfall of 2000 to more than 6000 mm yr⁻¹. This pattern was far too strong to be dismissed as sampling error, and yet the opposite, positive correlation was expected. The obligatory intermediate hosts of the parasite are terrestrial molluscs, which in the Northern Hemisphere are generally more common and more active in damper climates. Furthermore, the larvae of the parasite leave the mustelid host in the scats and are susceptible to dessication whilst seeking a mollusc to invade; hence their success rate should also be higher in damper climates. Over very large areas of North America and USSR, prevalence is higher in wetter climates (Lavrov, 1944; Dougherty and Hall, 1955), and in different districts of Sweden and Britain, prevalence and/or damage increases with the number of rainy days a year (Hansson, 1970; King, 1977).

The unexpected pattern found in New Zealand was completely inexplicable, especially as it was clear

from other observations that the apparent general correlation between rainfall and prevalence could not be causal. For example, there were significant differences in prevalence between localities within sample areas, sometimes only a few kilometres apart. At Craigieburn, prevalence was significantly higher in stoats caught near the centre of the forest (24% of 45) than in those caught at its margins less than 2 km away near the treeline (3% of 35) or adjacent to lower altitude sheep pastures (15% of 26); at St. Arnaud (Nelson), prevalence was more than twice as high in stoats collected from manuka scrub near the village (83% of 12) than in those from the beech forest less than 1 km away (28% of 39); at Arthurs Pass, 30% of 20 stoats collected from traps near Klondyke Corner, a popular picnic shelter, were infested as against 4% of 25 stoats caught within 5 km elsewhere on the eastern side of the pass (for statistics and full details see King and Moody, 1982). Such small-scale local variation could hardly be controlled by climate. The obvious alternative explanation, that it was due to local variation in the distribution of an intermediate host, could not be examined because the life cycle of the parasite in New Zealand was then (and still is) unknown.

Mustelids must pick up the invasive larvae in their food. In Europe, the biology of the parasite has been well studied in the laboratory, but the normal route by which the larvae travel from the mollusc to the mustelid was unknown until recently. Mustelids seldom eat molluscs directly, and the only other small mammals implicated by previous studies as paratenic hosts, the shrews, are usually avoided except as an alternative to starvation. However, in Switzerland Weber and Mermod (1983; 1985) detected encysted third-stage larvae in wood mice (*Apodemus* sp.) and bank voles (*Clethrionomys* sp.), and experimentally infested laboratory-bred ferrets by feeding them wood mice and bank voles inoculated with invasive (third-stage) larvae. The life cycle was seen to have been completed when a new generation of invasive larvae appeared in the scats of the ferrets which had eaten infected rodents. The latent period between ingestion of the larvae and the successful establishment of adult breeding worms ranged from 24 to 30 days.

Small rodents are a favourite prey of stoats throughout their range (King, 1989). In New Zealand, there are no wood mice or bank voles, but there are feral house mice (*Mus musculus*). Normally, these mice are relatively scarce, and those that can be found are eaten more frequently by female stoats than by males. But the beech (*Nothofagus* sp.) forests of Craigieburn and Fiordland display periodic masting, and for about a year after a good seedfall, mice become temporarily very numerous (King, 1982, 1983). Stoats react with a strong functional and numerical response

to the increase in these favoured prey, as documented by King (1983). During a post-seedfall irruption of mice, individual stoats of all ages and both sexes eat many more mice per head than normal, and the breeding success of female stoats is strongly linked to the density of mice in spring and summer. The survival of embryonic and nestling stoats born in a post-seedfall spring is much higher than usual, and in the summer after the seedfall the local population of stoats is temporarily increased by the dispersal of an exceptionally large cohort of newly independent young. In the intervening years, the breeding success and survival of the stoats, and the proportion of mice in their diet, return to their more usual lower levels.

A mustelid, once infested, is apparently not able either to evict the parasites or to repair the damage. Multiple infestations are possible, which must increase the damage with time. Evidence of infestation should therefore accumulate throughout the life of an individual stoat, and can be recorded by examination of its skull after death. If mice carry the invasive larvae, then stoats born in or living through a period when mice are numerous, i.e., in seedfall years, should have a greater chance of picking up the parasite than stoats that have lived only in non-seedfall years. Since the chances of becoming infested or re-infested increase with the number of mice eaten, then prevalence should be higher in older stoats and/or in those which have lived through one or more seed years. Now that it is possible to reconstruct the life spans of individual stoats, this prediction can be tested by comparing the pattern of infestation against the life histories of the stoats examined and the detailed records of beech seedfall available from Craigieburn Forest.

Methods

Stoats were collected in Fenn traps, stored frozen, and examined in the laboratory by routine procedures described by King and Moody (1982). During dissection of the carcasses, the heads were skinned, scraped clear of muscle and carefully inspected. Any skulls showing a hint of a dark stain or damage in the post-orbital region were opened with a small drill, and the worms extracted. Apparently undamaged skulls were not opened, so it is not possible to say whether any individuals harboured worms without being damaged. To minimise the risk that very early lesions had been overlooked in the fresh material, the clean skulls were all checked again for signs of distortion. Of 1005 skulls examined, only 5 showed signs of previously undetected deformation that could have been due to skrajbingylosis. Worms were not

recovered from these specimens, so they were not counted as positive records.

The prevalence of infestation (called "incidence" by King and Moody, 1982) was defined as the percentage frequency of positive records (at least one worm recovered) in a given sample. The term "infestation" is preferred to "infection", since the latter implies inclusion of the latent period between entry of the larvae and the development of visible adult worms. That period is, however, quite short, potentially only a matter of weeks. This conclusion was implied by the experimental work of Weber and Mermod (1985), and confirmed in the 1972-76 material; males of 5-10 months old were already infested as frequently (though generally less severely) as older males. Even so, estimates of prevalence derived by these methods are probably somewhat conservative. Infestation was rare in young stoats less than 5 months old, so they were omitted from the samples.

Populations of mice were monitored at Craigieburn every three months from February 1974 to May 1976. The same trap line was later operated once more, and an additional density index for February 1977 calculated, by E.B. Spurr (*pers. comm.*). In Fiordland, mouse trapping began in November 1973 in the Eglinton Valley and terminated after February 1978. The methods used to trap the mice and to calculate the density indices, plus the full results, are summarised by King (1983). Mice were not examined for larvae, because the possible connection between mice and skrajbingylus was not realised at the time.

The diet of the stoats collected was deduced by gut analysis, according to the methods described by King and Moody (1982). The frequency of occurrence of any given item, e.g., mice, was calculated as the percentage of guts containing mice among all the guts containing food. The relationships between seedfall, mouse populations and the diet of stoats in all three extended samples were described by King (1983).

Summary seedfall data collected from the Cline at Craigieburn (the nearest to the stoat and mouse traplines) since 1965 are given by Allen and Platt (1990), and further details were supplied for this analysis by R.B. Allen (*pers. comm.*).

Results

Prevalence in relation to sex

In the previous national survey, males tended to be infested more frequently than females (males 11.1 % of 611, females 8.1% of 394) but the difference was not

significant ($X^2 = 2.40$, $P > 0.1$). In the extended samples from Craigieburn and the Eglinton, the differences tended in the same direction but were still not significant. At Craigieburn, where prevalence was generally higher than the national average, prevalence in males was 23.9% of 71, females 15.2% of 66 ($X^2 = 1.67$, $P = 0.20$); in the Eglinton, where prevalence is relatively low, the figure for males was 8.5% of 118, and for females 3.7% of 81 ($X^2 = 1.79$, $P = 0.18$).

Prevalence in relation to age

Table 1 shows the frequency distributions of skulls with and without *skrijabingylus* by sex and age class. As before, the first age class starts at 5 months of age in both sexes. Because the number of adults drops rapidly in the older year classes, and the tendency for greater prevalence in males is not significant, for the purposes of statistical testing the frequencies were pooled as shown. In the Eglinton sample, prevalence was relatively constant with age (5.4% at 0.5-1.0 yr, 8.2% at 3+ yr) but at Craigieburn, prevalence was already 10.4% at 0.5-1.0 yr and rose to 35.3% at 3+ yr. Chi-squared tests showed that the increase in incidence with age at Craigieburn was significant ($P < 0.01$).

A different way of looking at these data would be to calculate the actual mean ages of individuals with and without signs of damage. These figures confirm that, at Craigieburn, infested individuals were, on average, significantly older (23.3 months) than uninfested ones (16.1 months: Mann Whitney U-test significant at $P < 0.01$). For the Eglinton, the figures were 26.7 months and 24.3 months, respectively ($P = 0.68$).

Unfortunately, the pooling of data from both sexes for these tests introduces a potential confusion. At Craigieburn, though not in the Eglinton, females lived shorter lives on average compared with males (mean age in this sample, which excludes individuals less than 5 months old, was 22.0 months in males, and 12.6 months in females, $P < 0.01$). In the Eglinton, males also lived slightly longer than females, though not significantly so (males 26.7 months, females 21.1, $P = 0.09$).

Although the tendency for increased prevalence in males is not significant, it is quite consistent; and when combined with the greater average age at death of males, it could explain the apparently general increase in infestation with age. Clearly it is necessary to determine the effect of age on infestation rate independently of sex. However, first it is necessary to identify other potential causes of disturbance to a simple age-sex relationship. For example, if there is any significant variation between years in the chances of a stoat encountering invasive larvae, then a test of the age-sex relationship must be controlled for the degree of exposure to risk of infestation.

Table 1: Distribution of stoats with and without *skrijabingylus* in relation to age and sex. Positive: skull damaged, worms recovered. Negative: no sign of any damage. skull not opened. Ages are given in years beginning at 1 October, the assumed average date of birth, except the first year class, which includes only stoats killed between 1 March and 30 September of their first year of life.

EGLINTON VALLEY, FIORDLAND NATIONAL PARK				
Age (yr)	Males		Females	
	Positive	Negative	Positive	Negative
0.5-1	2	34	2	36
1-2	4	21	0	14
2-3	1	21	0	15
3-4	2	16	1	6
4-5	0	9	0	3
5-6	0	3	0	3
6-7	0	3	0	1
1-8	1	1	0	0
Totals	10	108	3	78

Age	Sexes pooled		% infested
	Positive	Negative	
0.5-1	4	70	5.4
1-3	5	71	6.6
3+	4	45	8.2
Total	199		

$X^2 = 0.3317$, $df = 2$, $P > 0.05$

CRAIGIEBURN FOREST PARK, CANTERBURY				
Age (yr)	Males		Females	
	Positive	Negative	Positive	Negative
0.5-1	4	29	4	40
1-2	7	9	2	10
2-3	2	7	2	4
3-4	0	2	0	1
4-5	2	2	0	1
5-6	1	2	1	0
6-7	1	1	0	0
1-8	0	1	0	0
8-9	0	1	0	0
9+	0	0	1	0
Totals	17	54	10	56

Age	Sexes pooled		% infested
	Positive	Negative	
0.5-1	8	69	10.4
1-3	13	30	30.2
3+	6	11	35.3
Total	137		

$X^2 = 9.845$, $df = 2$, $P < 0.001$

There was substantial annual variation in prevalence at Craigieburn (Table 2). But it did not vary in the direction expected. If prevalence increases with age, one would predict that the annual samples in which prevalence was highest would be the ones having the greatest proportion of older animals, but this is not the case (Table 2). The Spearman rank correlation coefficient, r_s , is 0.72 ($P>0.05$). Clearly there must be some other variable involved, which is strong enough to over-ride the effect of age established above.

Prevalence in relation to diet

If mice are the paratenic hosts from which stoats pick up skrajbingylosis, then one would expect to find an increase in prevalence in years in which mice are abundant. The pronounced annual variation in the proportion of mice in the diet at Craigieburn is indeed correlated with the annual variation in prevalence of skrajbingylosis ($r_s = 0.89, P < 0.05$; Table 2).

Table 2: Annual variation at Craigieburn Forest Park in the prevalence of skrajbingylosis (sexes pooled), the proportion of adults in the population, and the proportion of mice in the diet. Years begin at October 1, the assumed average date of birth of young stoats. Figures for mouse density cover the year from implantation of the annual crop of stoat embryos in August, through to the following winter, and are expressed as the total number of mice collected per 100 trap nights (TN) over the four sample periods (August, November, February, May) following the end of the seedfall. For seedfall data, see Allen and Platt (1990); for further details on age structures, see King and Grue. in prep.

Spearman rank correlation coefficients:

Prevalence with age structure, $r_s=0.72, P>0.05$;

Prevalence with proportion of mice eaten, $r_s=0.89,$

$P<0.05$

* beech seed years.

¹February and May, 1974 only.

²February 1977 only.

Year	Prevalence		% >1 yr old	% mice in diet	Mice/ 100TN		
	Pos.	Neg.					
1972-3	2	14	13	16	81	19	-
1973-4	4	24	14	28	50	12	(4.3) ¹
1974-5	7	34	17	41	32	33*	44.5
1975-6	1	10	9	11	73	6	1.0
1976-7	11	23	32	34	21	49*	(23.4) ²
1977-R	2	5	29	7	71	20	-
Totals				137			

Table 3: Effect of year of birth (affecting the diet of young) on prevalence of skrajbingylosis and the age structure of stoats. Stoats of both sexes from Craigieburn and Eglinton Valley areas are pooled. Seed year cohorts are those born in 1971 and 1976 in the Eglinton, and 1969, 1971, 1974 and 1976 at Craigieburn; young born in these years eat many more mice than those born in other years. $X^2=2.55, df=2, P>0.25$

Age	Born in a seed year		Born in a non-seed year	
	Positive	Negative	Positive	Negative
0.5-1 yr	7	78	4	54
1-3 yr	6	59	12	38
3+ yr	3	9	4	29
Totals	16	146	20	121

The temporary increase in abundance of mice after a seedfall easily spans the period between the birth of the young stoats in early October and their dispersal as independent hunters in late December and January. Young stoats that are born in a seedfall year can therefore be presumed to eat mice (either supplied by their mother or as their own early kills) more often than those born in other years, and thereby be at greater risk of contracting skrajbingylosus. Table 3 shows the prevalence of skrajbingylosus in the cohorts born in seed and in non-seed years separately. The numbers of animals in the positive cells of the table are small, and the age-frequency distributions of infested stoats born in seed and non-seed years are not different.

However, stoats of any age can pick up the infestation, so perhaps a more relevant variable to examine might be the number of seed years that an individual has lived through. For example, stoats that have experienced, at any age, one or more seed years should have had a greater chance of picking up the infestation than those whose lives spanned the interval between two seed years. The use of seed data requires the assumption that the three-step connection postulated between seeds, mice and stoats is real and relevant, and this has not yet been proven. But on the other hand, this approach has the advantage that the supposed connection can be pursued further back in time than the existing records for mouse density at Craigieburn, which started only in February 1974 (Table 2). The earliest seed years experienced by the oldest stoats can then be taken into account. The seeding data from Craigieburn run from 1965, and the oldest stoat examined was born in 1964. When the life spans of all the Craigieburn specimens were matched with the seeding data (Table 4), it became clear that the infested individuals had indeed lived through more seed years than the uninfested ones.

Table 4: Effect of the number of seed years through which an individual has lived, regardless of year of birth, on prevalence of *skrjabingylus* in stoats at Craigieburn. Stoats can pick up the invasive larvae at any age.

	Number of seed years lived through		
	Male	Female	Sexes pooled
Infested	1.29	1.60	1.41
Not infested	1.15	0.80	0.97
Totals	71	66	137
P	>0.05	<0.01	<0.05

The difficulty with this simple comparison is that there is an obvious logical association between the number of seed years experienced and age; and in the Craigieburn data there is also an association between age and sex. So no correlation with seed years can be claimed unless these confounding variables can be eliminated.

An ANOVA test with age in months as the fixed co-variable is the appropriate method of testing for the relationships between sex and infestation rate in relation to the number of seed years, whilst correcting for age. The results showed that (1) males do live through more seed years than females ($P < 0.05$); (2) Craigieburn stoats are significantly more likely to pick up *skrjabingylus* the more seed years they live through ($P < 0.05$); the influence of seed years alone is significant in the females ($P < 0.01$), but not in the males.

The same tests could not be applied to the Eglinton data, because the seeding records collected by King (1983) spanned only the period when trapping was in progress (1974-79), so the seed falls in the earlier years lived by the oldest stoats were unrecorded. Seeding data were available from the Takitimu Range, about 75 km south of the Eglinton Valley, but the beeches there are a different species (*N. menziesii*), and their seeding was not synchronous with that of the *N. fusca* of the Eglinton. Moreover, the prevalence of *skrjabingylus* in the Eglinton was probably too low for any variation due to age, sex or year to be detectable from these samples.

Discussion

Since the damage caused to the skull of a stoat by *skrjabingylus* is permanent, the expected increase in prevalence with years of age, confirmed in the Craigieburn sample, is not surprising. However, rather little error will be introduced into a study if the ages of the adults are not known, since the number of stoats in the higher year-classes is small (Table 1). Pooled data for adults, e.g., those presented by King and Moody (1982), are therefore probably still valid.

The observation that mustelids can pick up *skrjabingylus* from small rodents was originally the result of Weber and Mermod's (1983, 1985) experimental work on European species (*Apodemus*, *Clethrionomys*, and domestic ferrets) in the laboratory. Extrapolation of this idea to a hypothesis that feral house mice can transmit *skrjabingylus* to wild stoats in New Zealand, a totally different environment, cannot be proven from these data. The link between prevalence and diet suggested here does not by any means qualify as a rigorous test of that hypothesis, but it certainly provides grounds for interest in further work on the transmission of *skrjabingylus* in beech forests. If feral house mice do contribute to the transmission cycle of the parasites in New Zealand, then the variation in their density with habitat could counteract the influence of climate and explain several curious observations on the distribution of the disease in New Zealand. For example: (1) the effect of exposure to seed years would be expected to be greater in the females, which eat mice more often than do males (King and Moody, 1982); (2) the unexpected rarity of *skrjabingylus* in high rainfall areas is consistent with the general distribution of mice in relation to habitat. Feral house mice are generally less common (0-5 mice per 100 trapnights) in wetter mixed podocarp-broadleaf forests, and more common in the drier beech forests (often 0-25, rarely to more than 70 per 100 trapnights: published records summarised by Murphy and Pickard, 1990); (3) mice are more likely to have been eaten by those individual stoats that were collected during the 1972-76 survey from the interior of Craigieburn Forest, from near St. Arnaud village and from the Klondyke picnic shelter, that were found to be more often infested, than other stoats collected from places nearby (King and Moody, 1982).

If this hypothesis is correct, it implies yet another difference between the biology of *skrjabingylus* in New Zealand and in the northern hemisphere. In Europe and Asia several studies have shown that the incidence of *skrjabingylus* increases in the year after the density of stoats has declined; Popov (1943) and Lavrov (1944) attributed the decline to the detrimental effects of infestation on the hosts. However, Debrot and Mermod (1981) suggested that the relationship actually works the other way round. All three of these studies were done in areas where water voles (*Arvicola terrestris*) are the favoured prey of stoats. These voles are strictly herbivorous, and not at all implicated in the transmission of *skrjabingylus*. Their populations are also very unstable. In the years that water voles are common, stoats feed mainly on them and *skrjabingylus* is rare. After a decline in voles, the stoats have to turn to other food, including wood mice, the most likely of the possible alternative prey to be carrying invasive larvae, and incidence increases.

In Debrot's (1981) study area, incidence rose from 4% when stoats were feeding only on water voles, to 50% after the forced change in diet. This situation contrasts with the one in New Zealand beech forests, where the favoured rodents are the ones that are suspected of carrying the disease, and the incidence drops, not rises, when stoats have to find alternative food.

The natural incidence of skrjabingylosis at Craigieburn is certainly too low to have any effect on the population dynamics of the local stoats. Even in the oldest individuals, prevalence never reached 100%, and the damage was never severe. In the 1972-76 analysis, comparisons of matched samples showed that infested individuals were no smaller, lighter or leaner than uninfested ones, so there is no evidence that afflicted individuals were seriously disadvantaged (King and Moody, 1982); similar tests on samples of British common weasels, in which both incidence and damage were often far higher than generally observed in New Zealand stoats, led to the same conclusion (King, 1977). Neither did affected individuals die sooner - rather the opposite, in fact (Table 4). It could be argued that the worst-affected individuals were already dead; but if a condition that develops slowly and persists over many years were actually fatal, one would expect to find a borderline class of almost-dead individuals showing signs of severe debilitation, as well as evidence that those affected even more severely had already left the population. The mortality rate of first year stoats at Craigieburn in the years we sampled was very high (King and Grue, *in prep.*), but not, at that age, at all influenced by skrjabingylosis. There are no comparable age-specific data from the few areas where the incidence of the parasite is higher; only two of 27 local subsamples recorded a prevalence exceeding 30%. Regrettably, this study confirms our previous conclusion (King and Moody, 1982) that the possibility of enlisting the help of *S. nasicola* at natural densities to control stoats in protected natural areas seems remote indeed.

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References

- Allen, R.B.; Platt, K.H. 1990. Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, New Zealand. *Oikos* 57: 199-206.

- Brockie, R.B. 1990. European hedgehog. In: C.M. King (Editor), *The handbook of New Zealand mammals*, pp. 99-113. Oxford University Press, Auckland, N.Z. 600 pp.
- Debrot, S. 1981. Trophic relations between the stoat (*Mustela erminea* L.) and its prey, mainly the water vole (*Arvicola terrestris* Scherman). In: J.A. Chapman and D. Pursley (Editors), *World Furbearer Conference Proceedings*, pp. 1259-1289. Frostburg, Maryland, U.S.A. 2056 pp.
- Debrot, S.; Mermod, C. 1981. Cranial helminth parasites of the stoat and other mustelids in Switzerland. In: J.A. Chapman and D. Pursley (Editors), *World Furbearer Conference Proceedings*, pp. 690-705. Frostburg, Maryland, U.S.A. 2056 p.
- Dougherty, E.C.; Hall, E.R. 1955. The biological relationships between American weasels (genus *Mustela*) and nematodes of the genus *Skrjabingylus* Petrov 1927 (Nematoda: Metastrongylidae), the causative organisms of certain lesions in weasel skulls. *Revista Iberica de Parasitologia, Granada (España), Tomo Extraordinario*, March 1955.
- Gibb, J.A.; Williams, J.M. 1990. European rabbit. In: C.M. King (Editor), *The handbook of New Zealand mammals*, pp. 138-160. Oxford University Press, Auckland, N.Z. 600 pp.
- Grue, H.E.; King, C.M. 1984. Evaluation of age criteria in New Zealand stoats (*Mustela erminea*) of known age. *New Zealand Journal of Zoology* 11: 437-443.
- Hansson, I. 1970. Cranial helminth parasites in species of Mustelidae: II. Regional frequencies of damage in preserved crania from Denmark, Finland, Sweden, Greenland and the northeast of Canada compared with the helminth invasion in fresh mustelid skulls from Sweden. *Arkiv foer Zoologi* 22: 571-594.
- King, C.M. 1977. The effects of the nematode parasite *Skrjabingylus nasicola* on British weasels (*Mustela nivalis*). *Journal of Zoology (London)* 182: 225-249.
- King, C.M. 1982. Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*), in relation to seedfall of southern beech. *New Zealand Journal of Zoology* 9: 467-480.
- King, C.M. 1983. The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology* 52: 141-166.
- King, C.M. 1989. *The natural history of weasels and stoats*. Christopher Helm. London, U.K. 253 pp.
- King, C.M.; Moody, J.E. 1982. The biology of the stoat (*Mustela erminea*) in the National Parks of

- New Zealand. *New Zealand Journal of Zoology* 9: 49-144.
- Lavrov, N.P. 1944. Effect of helminth invasions and infectious diseases on variations in numbers of the ermine, *Mustela erminea* L. In: King, C.M. (Editor), *Biology of mustelids: some soviet research* (1975), pp. 170-187. British Library, Boston Spa, U.K. 266 pp.
- Lewis, J.W. 1978. A population study of the metastrongylid nematode *Skrjabinigylus nasicola* in the weasel, *Mustela nivalis*. *Journal of Zoology (London)* 184: 225-229.
- Murphy, E.C.; Pickard, C.R. 1990. House mouse. In: King, C.M. (Editor), *The handbook of New Zealand mammals*, pp. 225-242. Oxford University Press, Auckland, N.Z. 600 p.
- Popov, V.A. 1943. Numerosity of *Mustela erminea* Pall. as affected by *Skrjabinigylus* invasion. *Comptes Rendus de l'Academie des Sciences* 39: 160-162.
- Weber, J.-M.; Mermod, C. 1983. Experimental transmission of *Skrjabinigylus nasicola*, parasitic nematode of mustelids. *Acta Zoologica Fennica* 174: 237-238.
- Weber, J.-M.; Mermod, C. 1985. Quantitative aspects of the life cycle of *Skrjabinigylus nasicola*, a parasitic nematode of the frontal sinuses of mustelids. *Zeitschrifte fur Parasitenkunde* 71: 631-638.