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The biology of the stoat (*Mustela erminea*) in the National Parks of New Zealand VI. Infestation with *Skrjabingylus nasicola*

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Abstract The natural distribution of the parasite *Skrjabingylus nasicola* was surveyed in 1492 stoats from New Zealand's National Parks. Infestation was rare in the young, so distribution was expressed as frequency of occurrence of skulls containing nematodes in samples of stoats more than 6 months old. Conservative estimates of incidence ranged from 0 to 37% in 27 local subsamples with at least 6 adults and subadults (mean 10%, n = 1005), sometimes varying substantially across short distances. Incidence was highest in beech forest and scrub/grassland habitats with annual rainfall less than 1600 mm. Subadult males (6–10 months old) were infested as frequently as adult males (older than 10 months), and there was no difference in incidence between the sexes. Worms recovered from 97 infested stoats occurred equally often in either side of the skull; were more often large (i.e., probably female) at all intensities of infestation; and numbered 1–73 per infested stoat (mean 12.9 in females, 14.2 in males; difference not significant). There was no evidence that infested stoats were smaller or lighter than uninfested onces.

Keywords *Mustela erminea*; New Zealand National Parks; trapping; *Skrjabingylus nasicola*; parasitology; host–parasite relationships.

INTRODUCTION

Skrjabingylus nasicola (Leuckart, 1842) is a parasitic nematode which inhabits the nasal and frontal sinuses of mustelids. The large, red worms may cause considerable distortion and damage to the skull, often resulting in pressure on the brain (illustrated for *Mustela nivalis* by King (1977)). In Russia, where the stoat is traditionally an important fur-bearer, Popov (1943) and Lavrov (1944) suggested that stoats heavily infested with *S. nasicola* were in poorer condition, less fertile, and died sooner than uninfested ones, and that in seasons following widespread infestation the fur harvest was reduced. In New Zealand *S. nasicola* has been identified only recently (King 1974), and its distribution and effects on stoats here have not been examined.

The morphology and taxonomy of *S. nasicola* are fairly well known (Lewis 1967, van Soest et al. 1972), but its life cycle in the wild has not been fully worked out. The first-stage larvae leave the definitive host with the faeces, and pass through an obligatory intermediate stage in a terrestrial mollusc (Théron 1975). When ingested by a mustelid, third-stage larvae migrate to the nasal sinuses along the spinal cord (Lankester & Anderson 1971); the route by which the larvae reach the mustelid from the mollusc is unknown. Hansson (1967) suggested shrews as a possible paratenic host. This could be so in Europe (van Soest et al. 1972), but not in New Zealand, where shrews are absent.

MATERIAL AND METHODS

A total of 1492 stoats from 14 collection areas in New Zealand, including all 10 National Parks, were searched for skrjabingylosis. The distribution of habitats, prey fauna, and material collected is summarised in King & Moody (1982a).

During autopsy the postorbital region of the skull of each stoat was scraped clear of superficial muscle and inspected for signs of damage by *S. nasicola* (illustrated for *erminea* by Hansson (1970)). If there were any swellings, dark patches, or perforations the skull was drilled open, and any worms found were extracted, counted, and stored in 75% ethanol. Skulls with no sign of infestation were not opened.

The incidence of infestation was measured as the percentage of individuals in a given sample in which worms were found. Not every skull that was opened contained worms, but this does not necessarily mean that some individuals recovered from skrjabingylosis. The signs of an early infestation are difficult to detect, especially in uncleaned skulls, and many of those which showed only a dark patch, and were found to contain no worms, were probably not

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Table 1 Correspondence between age classifications used by Hansson (1968) and in the present paper (male stoats from Craigieburn only).

New Zealand categories	No. of stoats per category of suture closure (Hansson 1968) I Open	II Coalescing	III Coalesced, visible	IV Coalesced, invisible
Young (Nov–Feb), ≤5 months	6	10	2	0
Subadult (Mar–Aug), 6–10 months	0	1†	14	0
Unclassified (Sep–Oct), >10 months	0	0	10	17
Adult (Nov–Aug), >12 months	0	0	2	22
Probable age at each category (months)	<6	<7	any	>10

†March

Table 2 Seasonal variation in the incidence of skrjabingylosis with age and sex of stoat host (sample sizes in parenthesis).

	Percentage incidence (and n) Spring	Summer	Autumn	Winter
Female adults	9.3 (54)	11.8 (68)	7.1 (170)	8.6 (81)
young	0 (1)	0.6 (170)	—	—
χ^2	—	13.74	—	—
P	—	<0.001	—	—
Male adults	14.7(177)	10.1 (69)	7.5 (53)	11.2(89)
subadults	—	—	2.8 (106)	12.8 (39)
young	0(2)	1.3 (152)	—	—
χ^2	—	7.34	0.92	1.76
P	—	<0.01	>0.1	>0.1

Table 3 Geographical variation in incidence of skrjabingylosis in New Zealand stoats (seasons pooled, excluding young).

Sample number		Collection area or locality	n	Incidence (%)	Difference between localities χ^2	df	P
1.	UW	Urewera NP	16	13			
2.	TG	Tongariro NP	38	0			
3.	EG	Egmont NP	65	0			
4.	MB	Mount Bruce	22	5			
5.	AT	Abel Tasman NP	5	0			
6.	NL	Nelson Lakes NP	71	37			
	NLb	St Arnaud (beech)	39	28 }	11.5	1	<0.001
	NLv	St Arnaud (manuka)	12	83 }			
	NLr	L. Rotoroa	4	25			
	NLm	Mt Misery	8	0			
7.	AP	Arthurs Pass NP	73	14			
	APe	East side	45	16 }	1.78	1	>0.1
	APw	West side	10	0 }			
	APs	Summit	8	13			
8.	CB	Craigieburn FP	114	15			
		1097–1341 m	35	3 }	7.16	2	<0.05
		884–1097 m	45	24 }			
		792–884 m	26	15 }			
9.	MC	Mount Cook NP	115	7			
	MCb	Ball Hut Rd	86	7 }	—		
	MCv	Village	27	7 }			
10.	WL	Westland NP	98	0			
11.	MA	Mt Aspiring NP	17	0			
12.	TK	Takaro Lodge	49	29			
13.	FL	Fiordland NP	318	6			
	FLe	Eglinton Valley	155	7 }	8.09	3	<0.05
	FLh	Hollyford Valley	91	1 }			
	FLm	Milford	17	6 }			
	FLt	Te Anau	27	15 }			
14.	KK	Kaikoura	5	60			
			1005	**10**			

Difference between samples (excluding AT, KK): χ^2 = 113.3, 11 df, P <0.001

infested. On the other hand, a few infested skulls (0.3%) were not detected at autopsy, and were found to be damaged only after cleaning (see below). Our estimate of incidence is therefore a minimum.

The intensity of infestation was measured as the number of worms recovered from each infested host. In the weasel (*M. nivalis*) there is a close relationship between the number of worms carried and the extent of damage to the skull (Lewis 1978), but classification of the damage categories is not a completely objective process, and is unsuitable for use when more than one person is doing the autopsies. Categories of damage were therefore not separately recorded before suspect skulls were opened.

Both measures of infestation depend on the presence of worms that have grown to visible size and have discoloured or distorted the skull sufficiently to betray themselves. Very early infestations cannot be detected, and *S. nasicola* is not necessarily absent from collection areas where we have not recorded it.

The numbers of large and small worms were counted separately for either side of the skull. Large worms are all females and small ones mostly males, but since not all worms were sexed under the microscope we refer to them only as large or small. The specific identification was confirmed by Dr M. W. Lankester, of the University of Guelph, Ontario (King 1974).

The method of age classification used here is described by King & Moody (1982c). It differs from the method—based on closure of the nasal sutures—used by Hansson (1968, 1970), and it would be useful to have some comparison of the two. Table 1 shows the results of classifying a New Zealand sample both ways. Hansson's first 2 categories are passed by the age of about 6–7 months, and the fourth category contains only stoats over 10 months old.

RESULTS

Only 3 of 325 young stoats were found to be infested (Table 2). The difference in infestation between young and adults in summer is significant for both sexes, but by autumn the subadult males are not significantly less often infested than adults. Subsequent analyses therefore omit the young stoats.

Variation in incidence with location and sex

Table 3 gives the proportions of adult and subadult stoats with skrjabingylosis for each of the 14 collection areas (mapped in Fig. 1) and, where appropriate, separately for each locality within the collection area. There is no significant difference between the sexes in overall incidence (males 11.1% of 611, females 8.1% of 394: $\chi^2 = 2.40$, 1 df, $P > 0.1$) or between localities (2-tailed signs test, $P = 0.30$). However, there are large differences between collection areas in incidence in both sexes pooled ($\chi^2 = 113.3$, 11 df, $P < 0.001$, testing only the 12 collection areas with $n > 5$). For 3 of these areas there are also significant differences between localities within the collection area. At St Arnaud, incidence is more than twice as high in the sample from the manuka scrub around the village as in that from the beech forest less than 1 km away; at Craigieburn, incidence is higher in samples from the centre of the forest than in those from its margins less than 2 km in either direction; in Fiordland, incidence is higher in samples from the east side of the Main Divide (Eglinton, Te Anau) than in those from the west, 20–30 km away. The stoats from Takaro Lodge are more than 4 times as often infested as those from the Eglinton Valley about 40 km to the north. At Arthur's Pass too incidence is apparently higher on the east side of the Divide (though not significantly so), but unevenly distributed; 30% of the 20 stoats caught at Klondyke Corner, on the edge of the broad gravel bed of the Waimakariri River, were found to be infested as against 4% of the 25 stoats caught within 5 km elsewhere on the eastern side ($P = 0.04$).

In general, incidence is higher in samples from the eastern beech forest/grassland habitats and lower in those from the western podocarp/mixed forests. At least in the South Island rainfall is higher in the west, and it is noticeable that the highest incidences are found only in areas with annual rainfall of less than about 1600 mm (Fig. 2). However, this is not necessarily a causal correlation, and where there are large local variations in incidence it could not be.

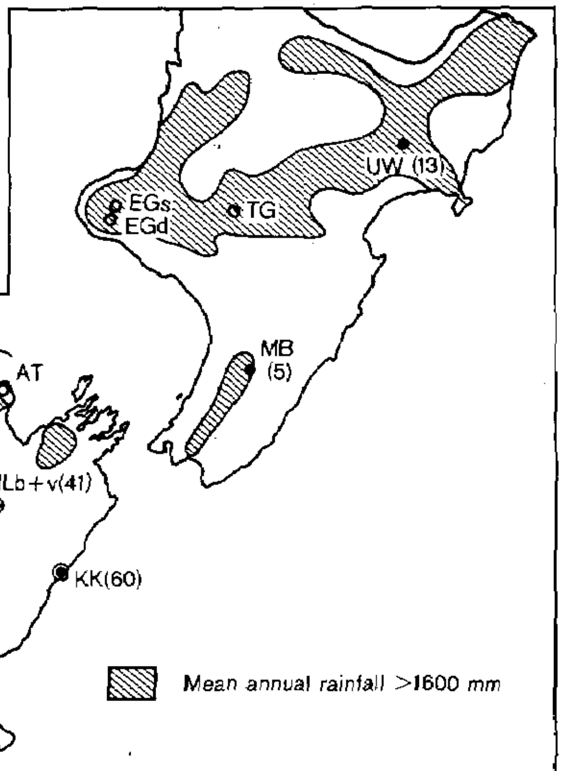
Checks on incidence

Early lesions are sometimes difficult to see in fresh material, especially if the skull is damaged or rotten, so all the cleaned skulls were checked again for signs of skrjabingylosis that might have been missed previously. A total of 5 skulls (1 each from Urewera, Craigieburn, the Eglinton and Hollyford valleys, and Westland) show signs of minor deformation in the postorbital region which may be due to *S. nasicola*. The Westland skull is the only one indicating that skrjabingylosis might be present in that area. Since worms were not recovered from any of the 5 skulls, these records do not appear in Table 3.

Having determined the pattern of geographic variation, it is possible to check more rigorously the differences in incidence with age and sex suggested by the pooled samples in Table 2. The 6 largest samples ($n > 39$) with at least moderate incidence

Table 4 Distribution of large and small *Skrjabingylus nasicola* on the left and right sides of 97 New Zealand stoat skulls.

	Large worms Left	Large worms Right		Small worms Left	Small worms Right	
Total worms	394	396	**790**	257	288	**545**
Mean per host	4.06	4.08	**8.14**	2.65	2.97	**5.62**



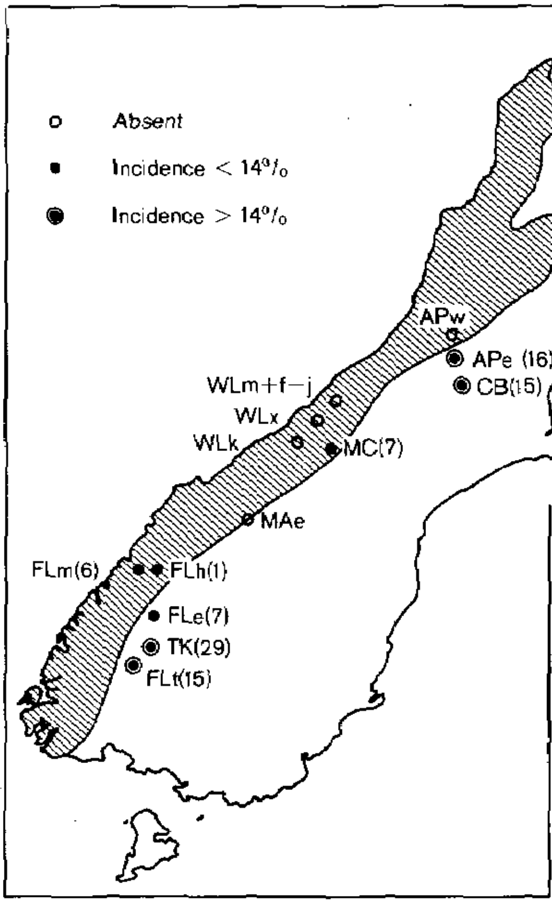


Fig. 1 Distribution of *Skrjabingylus nasicola* in stoats collected for this study. Numbers in parentheses are actual rates of incidence (%). Abbreviations explained in Table 3.

(>7%) were therefore re-analysed by age, sex, and season. To obtain large enough samples the 6 areas were grouped as 3 pairs of similar incidence. The St Arnaud beech forest sample and the Takaro sample (28% and 29% incidence) represented relatively heavily infested populations, Arthur's Pass (east side) and Craigieburn (16% and 15%) moderately infested populations, and Mount Cook and the Eglinton Valley (both 7%) lightly infested populations. Comparisons made using the 2-tailed signs

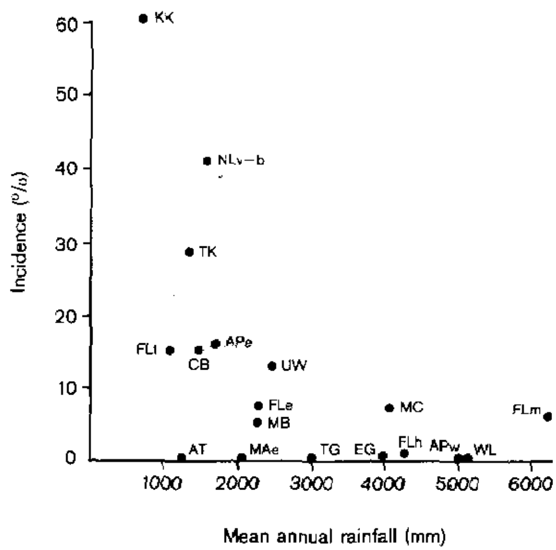


Fig. 2 Incidence of *Skrjabingylus nasicola* in relation to mean annual rainfall. Abbreviations explained in Table 3.

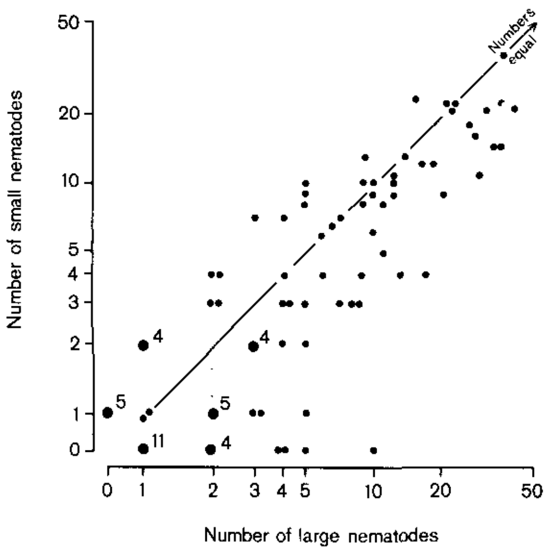


Fig. 3 Relationship between the numbers of large and small *Skrjabingylus nasicola* found in individual stoats; *n* (stoats) = 97. Note that although a log–log plot separates the points at the lower end of the scale, and allows all the points to be plotted in a single figure, it disguises the reduction in correlation among the higher values.

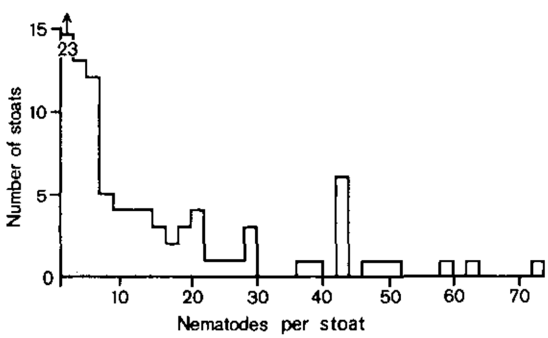


Fig. 4 Frequency distribution of *Skrjabingylus nasicola* per infested stoat.

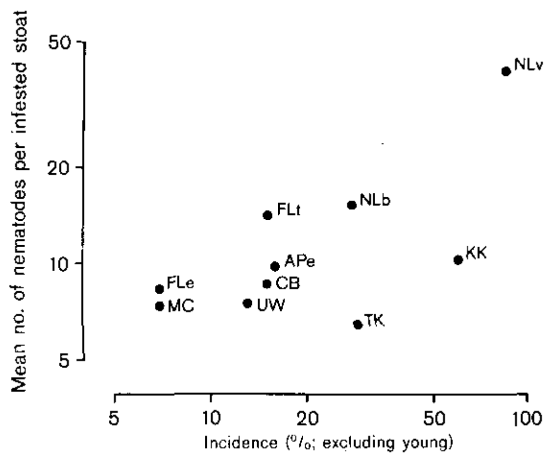


Fig. 5 Relationship between incidence of *Skrjabingylus nasicola* and intensity of infestation. Abbreviations explained in Table 3.

test confirm the lower incidence in the young (P = 0.022) and the insignificant difference between sexes (P = 0.146).

For some areas there is variation from year to year in incidence. At present we cannot tell whether this is due to real variation in rates of infestation or to hidden sampling error, e.g., variation in the proportion of older stoats. If there were significant annual variation in infestation it could affect the geographic pattern described above.

Distribution of *Skrjabingylus* worms

The numbers of large and small worms taken from 97 infested stoats were recorded separately for either side of the skull, as shown in Table 4. There is no difference between left and right in the total number of worms recovered (651 and 684 respectively; χ^2 = 0.82, 1 df, $P > 0.1$).

Most stoats (73%) were found to carry more large worms than small ones. The mean number of large worms per stoat is 8.14, and of small ones 5.62 (Table 4). The excess of large worms is significant ($P < 0.01$, 2-tailed signs test) but independent of the number of worms present (Fig. 3). Hence, it is reasonable to sum the counts of large and small worms and consider the total number present.

The frequency distribution of worms per stoat is irregular (Fig. 4). Half the infested stoats carried 6 or fewer worms, but a substantial proportion (14%) carried more than 30 worms. This variability cannot be reduced by plotting distribution from heavily infested areas separately, as the highest counts are not confined to areas with the highest incidence. Counts of 30 or more were recorded 10 times from St Arnaud (beech and village areas together, combined incidence 41%), but also once from the summit of Arthur's Pass (13%), once from the Te Anau district (15%), and once from the Eglinton Valley (7%). As this implies, a relationship between incidence and number of worms exists but is not strong. Excluding 3 samples for which intensity of infestation was calculated from only a single stoat, the correlation is significant (r = 0.79, 9 df, $P <$ 0.01), but largely because of the position of a single point, that for the St Arnaud village area (Fig. 5).

Table 5 Numbers of *Skrjabingylus nasicola* per infested stoat (including three young); abbreviations as in Table 3.

Sample number		Collection area or locality	Parasite burden (mean)	*n*
1.	UW		7.5	2
	NL	Total	25.9	27
2.		St Arnaud (beech)	16.6	13
3.		St Arnaud (manuka)	40.6	10
4.		L. Rotoroa	19.0	1
5.	AP	Total	11.7	10
		East side	9.9	7
		Summit	44.0	1
6.	CB		8.4	18
7.	MC	Total	7.4	8
		Ball Hut Rd	7.2	6
		Village	8.0	2
8.	TK		6.5	12
	FL	Total	10.8	17
9.		Eglinton	8.3	11
10.		Hollyford	22.0	1
11.		Te Anau	14.25	4
12.	KK		10.3	3

Kruskal-Wallis one-way analysis of variance: H = 26.8, 11 df, $0.01 < P < 0.001$ (localities treated separately if possible, hence total of 12 samples tested, numbered as in column 1). Totals for a collection area may also include stoats from outside the localities specified.

Table 6 Mean body size of stoats with and without skrjabingylosis (excluding young); abbreviations as in Table 3.

	Males Skrj.	*n*	None	*n*	Females Skrj.	*n*	None	*n*	P†
BODY WEIGHT (g)									
NLb	292.7	7	313.3	12					
CB	359.3	12	352.5	33	216.5	4	222.9	43	
MCb	345.5	4	334.0	23					1.0
TK	303.0	5	301.7	13	178.6	7	194.0	11	
FLe	335.8	8	328.3	65					
HEAD-AND-BODY LENGTH (mm)									
NLb	283.0	7	285.7	17					
CB	292.3	13	289.4	35	265.8	4	260.8	44	
MCb	286.2	5	290.0	28					0.10
TK	285.0	6	284.7	14	255.4	7	255.3	15	
FLe	286.0	8	286.6	72					
CONDYLOBASAL LENGTH (mm)									
NLb	50.33	6	50.49	13					
CB	50.84	8	50.18	35	46.28	4	46.08	41	
MCb	49.62	4	49.39	27					0.46
TK	50.56	5	50.59	14	45.77	6	45.75	14	
FLe	51.15	4	50.14	68					

†Significance of difference in 7 sex/area comparisons (2-tailed signs text)

The 3 counts for young lie well within the range fo. older stoats from the same populations.

The mean number of worms carried by female stoats is slightly lower (12.9±16.22 SD) than the mean number carried by males (14.2±15.84 SD), but the difference is not significant (U = 988 (z = 0.15) in a Mann-Whitney U-test, $P > 0.05$; young included).

There is no seasonal variation in the number of worms per stoat, even in the youngest subadults (Fig. 6). One subadult male caught at the beginning of March (i.e., about 6 months old) already carried over 40 worms. However, the intensity of infestation differs significantly between localities (Table 5).

Infestation and body size of hosts

Table 6 compares body and skull measurements of infested subadult and adult stoats with those of uninfested ones, considering only pairs of local samples (because of considerable geographical variation in size; see King & Moody (1982c)) with at least 4 stoats each. In 3 of 7 sex/area comparisons, infested stoats weigh less; in all 3 they have smaller bodies, and in 2 they have smaller skulls. None of these differences is significant (all $P > 0.4$, 2-tailed signs tests). Similar results are obtained even if the more numerous smaller samples (one of the pair with $n < 4$) are included. Nor are infested animals obviously less fat, so far as can be ascertained from the rough indicator of fatness used by King (1977) ($P = 0.72$ in a 2-tailed signs test.)

DISCUSSION

The estimates of the incidence and intensity of infestation obtained from this study are somewhat conservative when compared with previous studies based only on assessment of damage in cleaned skulls. In the latter kind of survey the proportion of skulls showing lesions but which did not contain worms at death is not known; and in this survey lesions were not recorded separately. However, the difference should not be great, as Hansson (1968) found that all *erminea* skulls classified as damaged contained parasites, and in the present material a negligible number of damaged skulls were not opened.

The natural incidence of skrjabingylosis in New Zealand stoats varies greatly from place to place. Lavrov (1944), Dougherty & Hall (1955), Hansson (1970), and van Soest et al. (1972) also found marked geographic variation in the incidence of this disease in stoats from Russia, North America, Scandinavia, and Holland respectively. Regional variation in incidence is to be expected, but it is surprising to find it on so local a scale as in some of the New Zealand samples. Although several of the differences in incidence between localities less than 5 km apart are statistically significant and not due to any obvious sampling bias, nevertheless their biological significance remains unclear. Stoats are certainly capable of movement, or even home range

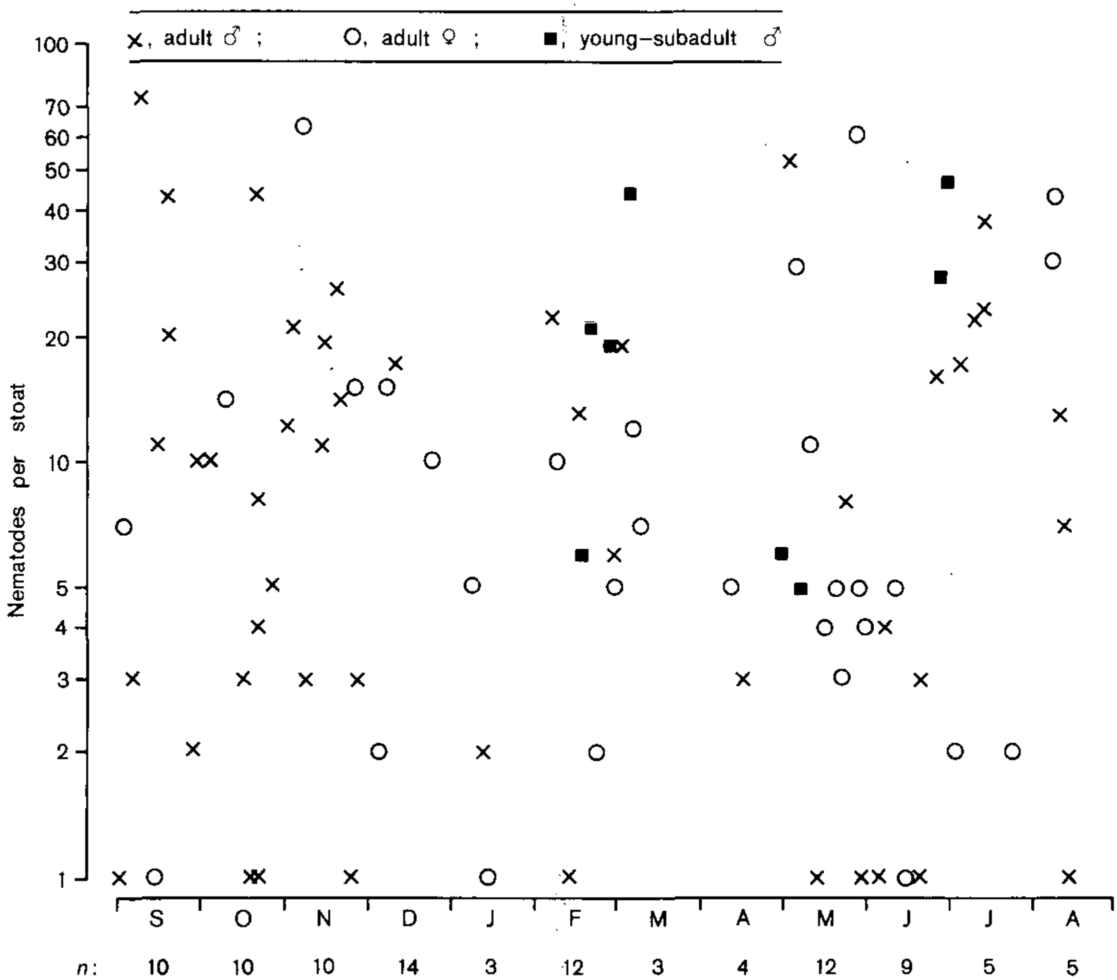


Fig. 6 Seasonal distribution of numbers of *Skrjabingylus nasicola* per infested stoat.

tenure, across greater distances than those separating the groups of traps at St Arnaud, Craigieburn, and eastern Arthur's Pass, which produced such different results.

The average incidence in these samples, 10%, is low by comparison with the averages for many parts of Europe and Russia, generally 20–70% (Popov 1943, Lavrov 1944, Hansson 1970, Vershinin 1972, van Soest et al. 1972), and for North America, frequently 100% (Dougherty & Hall 1955). Such averages conceal extensive local variation, and in some places in New Zealand stoats may be at least as frequently infested as some of their Northern Hemisphere relatives.

Most studies find first-year mustelids to be less often infested than adults, but comparisons are difficult. Hansson's categories of age are only indirectly comparable with ours (Table 1); Popov's age categories were not defined, and though he found a year-to-year variation of 21–45% he did not state that he had controlled for this in the age comparisons. But we can at least agree with Hansson (1968) that infestation builds up rapidly; very few young (less than 5 months old) are infested, but in subadult males (6–10 months old) incidence is already similar to that in adults. In the smaller skulls of weasels skrjabingylosis can be detected at an even earlier age: skulls of British weasels less than 3 months old were damaged much more frequently than those of stoats under 5 months old in New Zealand (King 1977).

The mean number of worms per infested host in New Zealand (12.9 for females, 14.2 for males) is higher than the corresponding figures from Sweden

(9.7 and 9.4 respectively; Hansson 1968). In both studies the frequency distributions of worms per stoat are positively skewed, and most infested stoats carried less than 10 worms each. An excess of large (mostly female) worms seems to be typical of *S. nasicola* (Lewis 1978). These figures, like those for incidence, suggest that skrjabingylosis is at least as well developed in some of the New Zealand localities—where it has established, with its host, within the past 100 years—as it is in Sweden, where it has presumably been present for very much longer.

We are unable to show any detrimental effect of infestation on stoats. In contrast to Popov (1943) and van Soest et al. (1972) we have found no consistent difference in body size between infested and uninfested individuals, and our data are insufficient to allow the relationship between infestation and mortality rates to be examined. For both tests a more precise method of age determination is required, as well as rather more information on the population dynamics of stoats than we at present possess. However, studies claiming to demonstrate the detrimental effects of skrjabingylosis have not provided very rigorous proof. Popov (1943), Lavrov (1944), and van Soest et al. (1972) gave no evidence of having tested their data or of having eliminated various possible sources of bias. Kogteva & Morosov (1970) also stated—again, without quoting significance tests—that pine martens (*Martes martes*) infested with skrjabingylosis weighed less and were in poorer condition than uninfested ones, but commented that there were some very heavy and well fed specimens among the badly infested martens. Popov (1943) and Kogteva & Morosov (1970) showed a decline in incidence of skrjabingylosis in the higher age classes of stoats and martens, and Popov explicitly attributed this to differential mortality of infested individuals, but without considering sampling error or other possible explanations. The claimed detrimental effect may very well exist, and indeed, looking at the extent of distortion of infested skulls, it is easy to believe; but the data so far presented have not yet proved it, even for the smaller, easily damaged, and very frequently infested skulls of weasels in Britain (King 1977). If infestation is not disadvantageous, the supposed causal link between heavy infestation and subsequent population declines of stoats in Russia (Popov 1943, Lavrov 1944) should be regarded as unproven.

The most surprising feature of the distribution of skrjabingylosis in New Zealand is the apparently negative correlation with rainfall (Fig. 1 and 2). Over very large areas in North America and Russia incidence increased in wetter climates (Lavrov 1944, Dougherty & Hall 1955), and in different districts of Sweden and Britain frequencies of infestation and/or damage increased with the number of rainy days per year (Hansson 1970, King 1977). In New Zealand *S. nasicola* is least common in wetter podocarp and mixed forests (Egmont, Westland, Hollyford Valley) and most common in open country or in drier beech forests with extensive open country nearby (St Arnaud, Craigieburn, eastern Arthur's Pass, Takaro, Te Anau). Possible explanations include the following. (1) There is some feature of the ecology of open country or drier forest in New Zealand which favours the transmission of the disease, for example a higher density of a paratenic host which avoids wet forest. This could explain some of the otherwise mysterious local variations in incidence observed. The paratenic host must presumably be one of the prey species of stoats described by King & Moody (1982b). (2) The annual rainfall in most of the New Zealand localities sampled is relatively high (all but one averaged between 1100 mm and 6300 mm), whereas in all 7 British localities sampled by King (1977) annual rainfall was less than 1200 mm. The New Zealand and British data could represent the 2 sides of a unimodal distribution, with the mode of infestation at 1100–1200 mm per annum. The seasonal and daily pattern of rainfall could also affect the abundance of molluscs and the survival of the free larvae, which are very susceptible to desiccation and to freezing in water (Hansson 1974).

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