

THE EFFECT OF SINUS NEMATODE INFECTION ON BRAINCASE VOLUME AND CRANIUM SHAPE IN THE MINK

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Mustelids, including American mink (*Neovison vison*), are definitive hosts for sinus nematodes of the genus *Skrjabinigylus*. Previous research has suggested that skrjabinigylus can cause a swelling of the frontal sinuses in mustelid hosts, leading to an inverse relationship between intensity of infection and braincase volume. We tested this hypothesis on 261 adult mink skulls collected in Ontario, Canada. Consistent with the hypothesis, we found a reduced slope in the relationship between skull size and braincase volume for male mink exhibiting lesions attributable to infection with *Skrjabinigylus*, compared to male mink with no lesions. However, we found no differences in slope for female mink. Male mink with lesions also had shorter postorbital lengths and mastoid breadths compared to males without lesions. Our results demonstrated that sinus nematodes may cause reduced braincase volume, but only in male mink. Infection may also have broader effects on skull shape than localized damage to the frontal bones and braincase roof. We suggest that parasitism of mink by *Skrjabinigylus* may be sex-biased because of the sexual size dimorphism of the species.

Key words: brain volume, mink, *Neovison vison*, Mustelidae, parasite, sex-biased mortality, sex-biased parasitism, sexual selection, sexual size dimorphism, *Skrjabinigylus*

Mustelids are definitive hosts for sinus nematodes of the genus *Skrjabinigylus* (Metastrongyloidea). Larval *Skrjabinigylus* are ingested by mustelids when foraging on terrestrial gastropods, which serve as intermediate hosts, or when foraging on a range of species that have been identified as paratenic hosts, such as mice, shrews, frogs, and snakes (Lankester and Anderson 1971). After ingestion, larvae penetrate the abdominal wall and molt into worms, which migrate through the abdomen to the spinal column and into the sinuses (Lankester and Anderson 1971).

A number of studies have described external cranial lesions in mustelids that result from infection with *Skrjabinigylus* (Addison et al. 1988; King 1977; Kirkland and Kirkland 1983; Lewis 1967). It has been suggested that in addition to these external lesions, internal swelling may occur on the roof of the braincase as a result of enlargement of the frontal sinuses (Lewis 1967; Maldonado and Kirkland 1986). Such swelling would reduce braincase volume and could cause deleterious effects, such as aberrant behavior, in affected individuals

because of pressure on the brain (Ewing and Hibbs 1966; Maldonado and Kirkland 1986). It is thought that the intensity of infection with *Skrjabinigylus* increases with age as a greater number of parasites are ingested (Addison et al. 1988; King 1991; Prigioni and Boria 1995). Therefore, the magnitude of internal swelling, if it occurs, should also increase with age. This hypothesis of a relatively smaller braincase in older, infected animals was supported for striped skunks (*Mephitis mephitis*) that were thought to have been infected with *S. chitwoodorum* (Maldonado and Kirkland 1986). There are no other published studies of the reduced braincase hypothesis.

The American mink (*Neovison vison*) is a common mustelid of North America. Prevalence of infection in mink by *S. nasicola* appears to be generally high (Dorney and Lauerman 1969; Kinsey and Langley 1963; Lankester 1970). Santi et al. (2006) found in Ontario that 80.5% of 630 mink were infected. External lesions on mink crania resulting from infection with *S. nasicola* have been described (Hansson 1968). Here, we test the hypothesis that infection with *Skrjabinigylus* causes internal swelling of the braincase in mink. We also carried out exploratory analyses for other effects of sinus nematode infection on skull shape, which have not been described. We hypothesized that skull features associated with the frontal bones and the cranium would be indirectly affected by nematode infections and would also change in shape as a result. In

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TABLE 1.—Dimensions measured from American mink (*Neovison vison*) skulls to test for effect of sinus nematode (*Skrjabinogylus nasicola*) infection on cranium shape.

Dimension ^a	Description	Acronym
Condylobasal length	Frontal nasale to foramen magnum	CBL
Brain basis length	Staphylion to base of foramen magnum	BBL
Palatal length	Staphylion to front of incisors	PAL
Toothrow length	Front of incisors to last molar	TRL
Postorbital length	Postorbital process to mastoid	POL
Nasal length	Frontal nasale to postorbital process	NAL
Interorbital constriction	From side to side	IOC
Postorbital constriction	From side to side	POC
Breadth over the canines	Greatest distance across canines	BRC
Mastoid breadth	From side to side	MAB
Cranial width	Greatest width of braincase	CRW
Zygomatic breadth	Greatest width of arches	ZB
Width of orbital constriction	From side to side	WOC
Width of foramen magnum	From side to side	WFM
Length of foramen magnum	From top to bottom	LFM
Caudal skull height	Basal to dorsal profile	CSH
Braincase height	Mastoid to dorsal profile	BCH
Braincase volume (cm ³)	Mass of lead pellets ÷ 6.653	VOL
Skull size (× 10 ⁻³ mm ³)	CBL × ZB × BCH × 10 ⁻³	SIZE

^a Units are in millimeters unless otherwise noted.

other words, we tested whether warping of the skull due to infection extends beyond localized damage to the frontal bones and roof of the braincase.

MATERIALS AND METHODS

Mink skulls used for this study were from a collection maintained by the Wildlife Research and Development Section of the Ontario Ministry of Natural Resources. The skulls originally were collected during 1961–1970 from fur harvesters in Ontario, Canada. The collection consisted of several hundred skulls from across the province, from which we selected a sample to analyze. We sought to avoid geographic variation in skull size to the extent possible, and so we used only skulls from central and northern Ontario (approximately within 45°–50° N and 77°–94° W). From this area, we randomly selected skulls to achieve as close to a balanced design as possible (equal numbers of lesioned and nonlesioned males and females). Because we wanted to avoid potentially spurious effects related to growth patterns, we sampled only adults. Some skulls had been aged during previous studies with cementum annuli counts, and many had been classified as juvenile or adult at the time of collection, so we used either this age information or assessment of bone sutures to ascertain age class (i.e., juvenile or adult—Johnston et al. 1987; Wiig 1985).

Similar to Maldonado and Kirkland (1986), skulls were identified as lesioned on the basis of external swelling, discoloration, or perforations to the frontal bones. We assumed that lesioned skulls had been infected with *S. nasicola* because other studies have shown that *S. nasicola* is prevalent in mink from Ontario (Lankester 1970; Santi et al. 2006). However, for

the purposes of our hypothesis test, knowledge of the particular species of *Skrjabinogylus* was not critical. Our method of identifying infected animals may have underestimated infection by 8–10% because some animals with low-intensity infections may not have lesions (Dougherty and Hall 1955; King 1977; Santi 2001). We obtained 261 skulls for analysis, including 81 lesioned and 78 nonlesioned skulls of adult males, and 70 lesioned and 32 nonlesioned skulls of adult females. There were more lesioned than nonlesioned skulls available for both sexes, and more males than females in the collection because of sex-biased harvest patterns (e.g., Buskirk and Lindstedt 1989). Thus, the nonlesioned skulls of adult females were the scarcest; we did not randomly sample this category but used the entire collection from the study area.

For testing the hypothesis of internal swelling in the braincase of infected mink, we followed the methods of Maldonado and Kirkland (1986). Their test of the hypothesis assumes that intensity of infection increases the swelling and also increases with age in mink (e.g., Addison et al. 1988; King 1991; Prigioni and Boria 1995). Intensity of infection is the parasitic burden, or number of worms per individual. Therefore, the slope of a regression between age and braincase volume should be less steep for infected animals, as a result of increased swelling in older, more intensely infected animals.

Braincase volume was estimated for each skull using the method of Eisenberg and Wilson (1978), described as follows. We poured number 6 lead shot into each skull through the foramen magnum, and repeatedly tapped the skull to ensure the pellets were completely settled. We then weighed the contents on a digital Acculab (Edgewood, New Jersey) pan scale (0.01-g accuracy). This process was repeated 3 times for each skull and the median value was then used for analysis. Masses (M) were converted to volumes (V) using the formula $V = M/6.653$, where 6.653 was a constant accounting for the density of lead.

The hypothesis test required that age be estimated for each animal. We had some individuals aged to year from cementum counts, but not the entire sample, so we used the same methods as Maldonado and Kirkland (1986) to infer age from skull size. Skull size was estimated as the product of 3 linear measures (CBL, BCH, and ZB; Table 1) divided by 10³. Linear dimensions were measured with a Mitutoyo (Mitutoyo Corporation, Kawasaki, Kanagawa, Japan) Digimatic caliper (0.01 mm accuracy). Each dimension was measured 3 times for each skull, and the median was used for analysis. Regressions for males and females separately were used to confirm the relationship between cementum estimates of age and skull size. For these regressions, skulls were sorted into known age classes of 1.5, 2.5, and ≥ 3.5 years. A variety of other linear skull dimensions also were measured in order to explore other potential differences in skull shape between lesioned and nonlesioned skulls (Table 1).

We used least-squares regressions between skull size and braincase volume for lesioned and nonlesioned mink and tested for differences in slopes using a *t*-test (Zar 1999). Male and female mink were assessed separately because of the considerable sexual dimorphism of this species, in which males are larger (Ralls 1977). Maldonado and Kirkland (1986) combined sexes because skunks are not sexually dimorphic and no

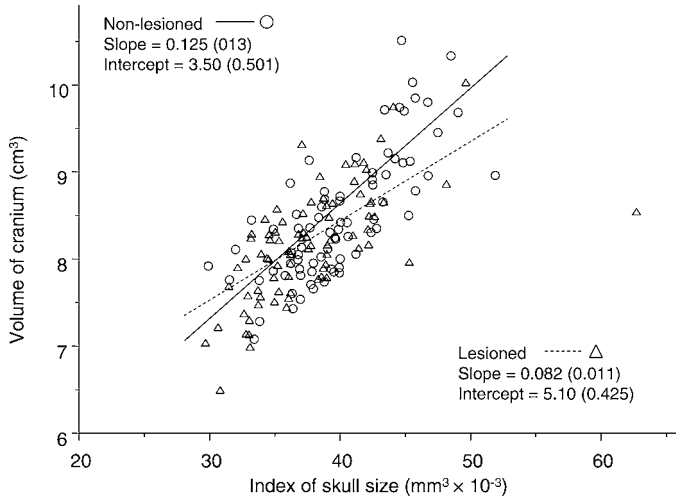


FIG. 1.—Least-squares regressions between skull size and cranium volume for adult male American mink (*Neovison vison*) exhibiting lesions ($n = 81$) attributable to infection with *Skrjabingylus* and those not exhibiting lesions ($n = 78$). Mink were collected from northern and central Ontario, Canada, during 1961–1970.

sex-related differences in infection or test consequence were anticipated. We also carried out analyses of variance to compare differences in volume and each linear dimension measured between lesioned and nonlesioned mink of each sex. We did this both to test for differences, and also to assess effect sizes where differences were present. For all analyses of variance, dependent variables were standardized by dividing each measure by the condylobasal length (CBL) for each respective skull. We used CBL instead of our index of skull size to minimize the effect of whole:part correlations that may result from using ratios. The index of skull size integrated 3 dimensions, whereas CBL represented only 1, and so the index was more likely to have whole:part correlations with other skull dimensions. Finally, we used logistic regressions and Akaike's information criterion (AIC) to rank multivariate models from the subset of CBL-standardized dimensions that were different between lesioned and nonlesioned individuals.

RESULTS

Linear regressions demonstrated that skull size was positively related to age for known-age male ($F = 4.66$, $d.f. = 1, 133$, $P = 0.032$) and female ($F = 4.32$, $d.f. = 1, 59$, $P = 0.041$) mink.

For male mink, there was a positive, linear relationship between skull size and braincase volume for both lesioned ($F = 53.24$, $d.f. = 1, 79$, $P < 0.001$, $R^2 = 0.40$) and nonlesioned ($F = 97.66$, $d.f. = 1, 76$, $P < 0.001$, $R^2 = 0.56$) skulls (Fig. 1). The slope of this relationship for nonlesioned skulls (0.125) was steeper than the slope for lesioned skulls (0.081; $t = 2.56$, $0.01 < P < 0.02$). Variance in braincase volume was not different between lesioned and nonlesioned males ($F = 1.33$, $d.f. = 77, 80$, $P = 0.203$).

Female mink also exhibited a positive, linear relationship between skull size and braincase volume for both lesioned ($F = 210.95$, $d.f. = 1, 68$, $P < 0.001$, $R^2 = 0.76$) and nonlesioned

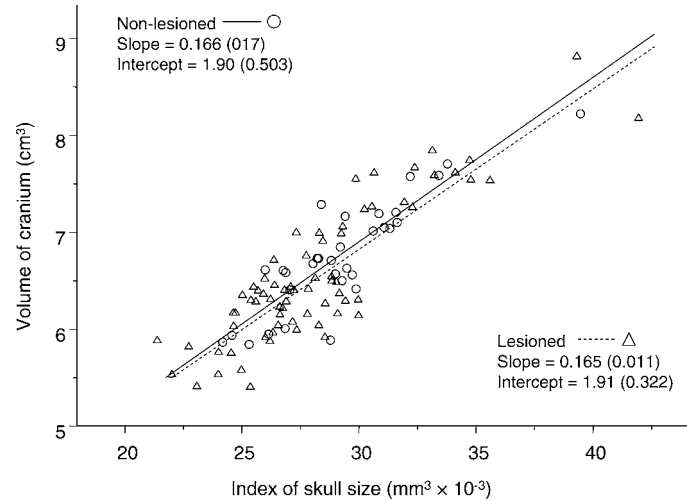


FIG. 2.—Least-squares regressions between skull size and cranium volume for female American mink (*Neovison vison*) exhibiting lesions ($n = 70$) attributable to infection with *Skrjabingylus* and those not exhibiting lesions ($n = 32$). Mink were collected from northern and central Ontario, Canada, during 1961–1970.

($F = 94.37$, $d.f. = 1, 30$, $P < 0.001$, $R^2 = 0.76$) skulls (Fig. 2). The slope of this relationship for nonlesioned skulls (0.166) was no different than the slope for lesioned skulls (0.165; $t = 0.07$, $P > 0.9$). Variance in braincase volume was not different between lesioned and nonlesioned females ($F = 0.67$, $d.f. = 31, 69$, $P = 0.228$).

Braincase volumes (VOL) were smaller in lesioned males than in nonlesioned males when compared using analyses of variance of volumes standardized by CBL ($F = 4.88$, $d.f. = 1, 157$, $P = 0.029$, $R^2 = 0.030$; Table 2). The only other differences between groups from the list of dimensions measured (Table 1) were mastoid breadth (MAB; $F = 5.28$, $d.f. = 1, 157$, $P = 0.023$, $R^2 = 0.033$) and postorbital length (POL; $F = 4.79$, $d.f. = 1, 157$, $P = 0.030$, $R^2 = 0.029$), which were both larger in nonlesioned males (Table 2). We explored this curious finding further to determine if it was related to the changes in braincase volume. For nonlesioned skulls, there was no relationship between the CBL-standardized dimensions MAB and POL ($r = 0.10$, $d.f. = 1, 76$, $P = 0.334$), between MAB or VOL ($r = 0.08$, $d.f. = 1, 76$, $P = 0.505$), or between VOL and POL ($r = -0.04$, $d.f. = 1, 76$, $P = 0.710$). For lesioned skulls, however, there was a stronger, positive relationship between POL and MAB ($r = 0.22$, $d.f. = 1, 79$, $P = 0.050$). There was no relationship between VOL and POL ($r = 0.08$, $d.f. = 1, 79$, $P = 0.459$) or VOL and MAB ($r = 0.15$, $d.f. = 1, 79$, $P = 0.180$). Logistic regressions of combinations of POL, MAB, and VOL demonstrated that the best model to discriminate between lesioned and nonlesioned male skulls was one that contained VOL and an interaction between MAB and POL ($\chi^2 = 11.98$, $n = 159$, $P = 0.003$, McFadden's $\rho^2 = 0.054$; Table 3).

There were no differences between the braincase volumes of lesioned and nonlesioned females when volumes were standardized by CBL ($F = 2.21$, $d.f. = 1, 100$, $P = 0.140$,

TABLE 2.—Some dimensions measured from male and female American mink (*Neovison vison*) skulls categorized according to presence or absence of lesions attributable to infection with *Skrjabinigylus nasicola*. All dimensions are standardized according to condylobasal length. Mink skulls were collected in Ontario, Canada. The 95% lower and upper confidence intervals for the mean are shown as *LCL* and *UCL*, respectively.

Dimension	Group ^a	<i>n</i>	\bar{X}^b	<i>LCL</i>	<i>UCL</i>
Braincase volume ^c	NLM	78	0.132	0.130	0.134
	LM	81	0.129	0.127	0.131
	NLF	32	0.116	0.113	0.118
	LF	70	0.113	0.111	0.115
Postorbital length ^d	NLM	78	0.666	0.664	0.669
	LM	81	0.662	0.659	0.665
Mastoid breadth ^d	NLM	78	0.517	0.514	0.519
	LM	81	0.513	0.510	0.515

^a Nonlesioned males (NLM), lesioned males (LM), nonlesioned females (NLF), and lesioned females (LF).

^b All comparisons $0.01 < P < 0.05$, except for NLF versus LF braincase volumes ($P = 0.140$).

^c cm^3/mm .

^d mm/mm .

$R^2 = 0.022$; Table 2). Sexual dimorphism in braincase volume was evident, because the mean volume per CBL (lesioned and nonlesioned combined) was $0.114 \text{ cm}^3/\text{mm}$ for females ($0.113\text{--}0.116 \text{ cm}^3/\text{mm}$; 95% confidence interval) compared to $0.130 \text{ cm}^3/\text{mm}$ for males ($0.129\text{--}0.132 \text{ cm}^3/\text{mm}$).

DISCUSSION

Our data were consistent with the hypothesis that *Skrjabinigylus* infection causes reduced braincase volume in older male mink due to swelling of the frontal sinuses, and associated down-warping of the braincase roof. However, we did not support this hypothesis for female mink. For males, the effect was a small one, because the presence of lesions presumably caused by *S. nasicola* explained about 3% of the variation in adult braincase volume.

As Maldonado and Kirkland (1986) suggested, it appears possible that infections with *Skrjabinigylus* could become intense enough in mink to reduce braincase volume, putting pressure on the brain that subsequently affects behavior. We know of no reported cases of aberrant behavior in wild mink attributable to infection with *Skrjabinigylus*. It appears from the few descriptions of such behavior in other species (e.g., Ewing and Hibbs 1966) that symptoms would be rather similar to mercury poisoning, which has been reported for mink (Wobeser 1976). This underscores the need for careful postmortem examination where cause of death is to be determined.

The lack of an apparent effect of *Skrjabinigylus* on brain volumes of female mink may be related to the high degree of sexual dimorphism of this species. Male mink are 1.6–1.9 times larger than females (Ralls 1977). Recent studies suggest that sexual size dimorphism results in male-biased parasitism and mortality (Moore and Wilson 2002; Wilson et al. 2003). According to this hypothesis, polygynous males of sexually dimorphic species invest in growth and reproduction and are therefore more susceptible than females to parasitism.

TABLE 3.—Model selection results of logistic regression analyses carried out to discriminate between adult male American mink (*Neovison vison*) skulls from Ontario presumed to be infected ($n = 81$) or not infected ($n = 78$) by *Skrjabinigylus* nematodes. Skull dimensions were standardized by condylobasal length and included braincase volume (VOL), mastoid breadth (MAB), and postorbital length (POL). Model selection criteria were log-likelihood (LL), number of parameters (*K*), and Akaike's information criterion (AIC).

Variable	LL	<i>K</i>	AIC	ΔAIC
VOL + MAB × POL	−104.19	3	214.39	0
MAB × POL	−105.97	2	215.95	1.56
VOL + MAB + POL	−104.14	4	216.28	1.89
POL + VOL	−105.54	3	217.07	2.68
VOL + MAB	−105.71	3	217.42	3.03
MAB + POL	−105.94	3	217.88	3.49
MAB	−107.56	2	219.12	4.73
VOL	−107.75	2	219.50	5.11
POL	−107.80	2	219.60	5.21
Constant	−110.18	1	222.36	7.97

Mortality associated with parasitism is therefore sex-biased. It seems reasonable that this mechanism would result in higher intensity of infection in male mink. Very few studies have assessed intensity of infection with *Skrjabinigylus* in sexually dimorphic mustelids. Santi et al. (2006) found that the intensity of infection was highest in juvenile male mink from Ontario, compared to juvenile females and adults. Skulls of male least weasels (*Mustela nivalis*) were more severely damaged than skulls of females in England (King 1977), and similarly, male long-tailed weasels (*Mustela frenata*) were more severely damaged than females in Manitoba (Gamble and Riewe 1982).

An alternative explanation for the lack of an apparent effect of *Skrjabinigylus* on brain volumes of female mink is that it may simply be that because the female mink skulls were much smaller than the male skulls ($28.5 \times 10^{-3} \text{ mm}^3$ versus $38.8 \times 10^{-3} \text{ mm}^3$, respectively), there was a small effect that occurred but was within our measurement and instrument error. This possibility is consistent with the hypothesis that effects of *Skrjabinigylus* on mink crania are not sex biased.

It appears that there are broader effects on the skull of infection by *Skrjabinigylus* than just reduced braincase volume. We found that postorbital length and mastoid breadth were both reduced in lesioned males. Further, these 2 dimensions were positively correlated in lesioned male mink but not in nonlesioned males (i.e., there was an interaction between POL and MAB that was due to infection). We interpret this as support for our hypothesis that sinus nematode infection can indirectly influence skull shape along dimensions associated with the frontal bones and the cranium, such as the postorbital length and mastoid breadth. It appears that warping of the skull due to infection can extend beyond the localized damage to the frontal bones and roof of the braincase.

To date, the few studies of skull damage in mustelids attributable to infection with *Skrjabinigylus* have tended to focus on braincase volume and damage to the frontal bones. We suggest that future studies should be undertaken using morphometric methods of broader skull characteristics to test

for links between infection and skull shape. We also encourage additional studies of infection with *Skrjablingylus* in sexually dimorphic mustelids to determine if there are consistent patterns of sex-biased parasitism and mortality.

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