

# A sex-biased effect of parasitism on skull morphology in river otters<sup>1</sup>

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**Abstract:** Parasitism is sex-biased in many animal species. In mammals, males often appear to be more severely affected, possibly as a result of costs associated with sexual selection. River otters (*Lontra canadensis*) and other members of the Mustelidae are definitive hosts for nematodes of the genus *Skrjabinogylus*, which have been found to cause lesions and deformation of the frontal bones of the skull. Infection has also been shown to reduce braincase volume in 2 mustelid species; thus, we hypothesized that a similar relationship exists in otters. Furthermore, we predicted that this effect of nematode parasitism would be biased toward males, which are the larger sex in otters. We used 130 male and female otter skulls collected throughout Ontario to test whether skulls with lesions attributable to nematode infection would show a male-biased reduction in braincase volume and other changes to skull morphology. We found that braincase volume was reduced in male otters with lesioned skulls and to a lesser extent in female otters with lesioned skulls. There was no detectable effect of age on braincase volume. We concluded that parasite-induced damage to otter skulls includes reduced braincase volume, and that this effect appears to be male-biased. This might affect behaviour of otters, reducing survival, and contributing to a pattern of sex-biased mortality.

**Keywords:** brain size, nematode, sex-biased parasitism, sexual selection, sexual size dimorphism, *Skrjabinogylus*.

**Résumé :** Chez plusieurs espèces animales, le parasitisme est biaisé en fonction du sexe. Chez les mammifères, les mâles semblent être plus souvent sévèrement affectés, probablement en raison des coûts associés à la sélection sexuelle. Les loutres de rivière (*Lontra canadensis*) et d'autres mustélidés sont des hôtes définitifs pour les nématodes du genre *Skrjabinogylus*, il a été démontré que ceux-ci sont responsables de lésions et de déformation des os frontaux du crâne. Il a aussi été démontré que l'infection réduit le volume crânien chez 2 espèces de mustélidés; ainsi, nous avons formulé l'hypothèse qu'une relation semblable existe chez les loutres. De plus, nous avons prédit que cet effet du parasitisme des nématodes serait biaisé vers les mâles, ceux-ci étant de plus grande taille chez les loutres. Nous avons utilisé 130 crânes de loutres mâles et femelles provenant de l'ensemble de l'Ontario afin d'évaluer si les crânes avec des lésions attribuables à l'infection de nématodes montraient une réduction du volume crânien biaisé vers les mâles ainsi que d'autres changements à la morphologie du crâne. Nous avons constaté que le volume crânien était réduit chez les loutres mâles ayant des lésions crâniennes et dans une moindre mesure chez les femelles avec lésions. Aucun effet de l'âge n'a été détecté sur le volume crânien. Nous avons conclu que les dommages causés par les parasites aux crânes des loutres, dont la réduction du volume crânien, sont un effet qui semble être biaisé vers les mâles. Cela pourrait influencer le comportement des loutres, réduisant leur survie et contribuant à un patron de mortalité biaisé en fonction du sexe.

**Mots-clés :** dimorphisme sexuel de taille, nématode, parasitisme biaisé en fonction du sexe, sélection sexuelle, *Skrjabinogylus*, taille du cerveau.

**Nomenclature:** Carreno, Reif & Nadler, 2005; Wilson & Reeder, 2005.

## Introduction

Parasites can have a wide range of effects on their hosts, including altered behaviour and morphology (Kirkland & Kirkland, 1983; Poulin, 1993; Cramer & Cameron, 2007) and reduced survival and productivity (Murray, Cary & Keith, 1997; Huber, 2008). Parasitism may often be sex biased and thus may affect the host sexes unequally (Moore & Wilson, 2002). This can lead to widely diverging effects of parasitism on the different sexes (e.g., Bize *et al.*, 2005; Perez-Orella & Schulte-Hostedde, 2005; Cowan *et al.*,

2007; Dare & Forbes, 2008), a phenomenon that likely has an underappreciated importance for species life histories.

In mammals, there is a tendency for parasitism to be male biased (Folstad & Karter, 1992; Schalk & Forbes, 1997; Moore & Wilson, 2002). Male-biased parasitism is thought to arise from sexual selection (Moore & Wilson, 2002), and more proximately from 1 of 2 hypothetical mechanisms. First, larger-bodied mammals, regardless of sex, may make an extra investment in growth and size at a cost of investing in the immune system (Sheldon & Verhulst, 1996). Sexual selection often leads to sexual size dimorphism (Isaac, 2005), so the larger sex of dimorphic species could become more susceptible to parasitism as a result. Second, males may have an immunocompetence

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handicap, owing to their use of testosterone in development of sexually selected traits (Folstad & Karter, 1992). Testosterone is immunosuppressive, and its increased use in males may make them more susceptible to parasitism than are females (Klein, 2000). Moore and Wilson (2002) found that the first of these hypotheses, related to body size *per se*, was sufficient to explain patterns of male-biased parasitism. This hypothesis predicts that in species with sexual size dimorphism, the larger of the sexes should exhibit increased rates of parasitism.

Metastrongyloid nematodes of the genus *Skrjabinogylus* are familiar parasites of the Mustelidae family that take refuge within the sinus cavities of the host skull (Kirkland & Kirkland, 1983; Maldonado & Kirkland, 1986). Six species are known from this genus (Carreno, Reif & Nadler, 2005). Larvae are ingested, develop into worms, and make their way from the gut to the frontal sinuses of the host, causing lesions and perforations of the frontal region of the cranium. Mustelid hosts become infected when they consume infected gastropods (generally snails and slugs), which are the intermediate host for the development of *Skrjabinogylus* larvae at their third stage, or by eating paratenic hosts, such as mice, rats, snakes, and frogs, which may also harbour the third-stage larvae (Lankester & Anderson, 1971).

Studies of 2 mustelid species, the striped skunk (*Mephitis mephitis*) and the American mink (*Neovison vison*), show that *Skrjabinogylus* infection of the sinuses can lead to a reduced braincase volume, presumably due to the swelling and warping of bones (Maldonado & Kirkland, 1986; Bowman & Tamlin, 2007). Swelling and pressure that would subsequently occur in the cranium can cause behavioural changes in hosts (e.g., Ewing & Hibbs, 1966) that could be detrimental to survival. Experiments have shown also that migration of *Skrjabinogylus* along the central nervous system to the sinuses can cause severe neurological damage (Lankester & Anderson, 1971).

The American mink is sexually dimorphic, with males being much larger than females. Male mink also appear to exhibit more severe morphological effects of *Skrjabinogylus* parasitism than do females. Bowman and Tamlin (2007) demonstrated a reduced braincase volume in males with lesions attributable to infection, but not in females. They also found changes to other characteristics of skull morphology. In particular, postorbital length and mastoid breadth were reduced in lesioned males.

In this study, we sought to determine if *Skrjabinogylus* parasitism causes similar male-biased changes in the cranial shape and braincase volume of another sexually dimorphic mustelid, the North American river otter (*Lontra canadensis*). Although many mustelids appear susceptible to *Skrjabinogylus*, larger species like *L. canadensis* have larger skulls with thicker bones than smaller species like the skunk and the mink. Thicker bones could potentially prevent swelling in the sinuses caused by heavy parasite loads that would otherwise cause the reduced braincase volume observed in smaller species (Maldonado & Kirkland, 1986; Addison *et al.*, 1988).

Our study is unique in that the age of each individual otter was known, so we could most directly test the hypothesis originally proposed by Maldonado and Kirkland (1986)

that braincase volumes decrease with age for both sexes in infected animals due to the accumulation of parasites. Previous tests of this hypotheses have had to infer a relationship between an index of skull size and age. In other words, relationships were tested between skull size (in lieu of age) and braincase volume (Maldonado & Kirkland, 1986; Bowman & Tamlin, 2007). We tested the hypothesis that braincase volumes of infected otters are reduced compared to uninfected otters of the same age, and that this effect is enhanced with age due to the accumulation of parasites. To further assess the effects of the parasites on skull shape, we also tested the hypotheses that other skull measurements, postorbital length and mastoid breadth, are reduced in infected otters, as found by Bowman and Tamlin (2007). This would suggest that *Skrjabinogylus* infection affects the overall morphology of the skull in addition to affecting braincase volume and causing localized damage to the frontal bones. Finally, we tested the prediction that these impacts of infection by sinus nematodes are more severe in males than in females owing to the sex-biased parasitism hypothesized to occur in sexually dimorphic species. Cranial damage associated with increased parasitism is one potential cost of larger body size in male otters, compared to females.

## Methods

A collection of otter skulls from the 1960s maintained by the Wildlife Research and Development Section of the Ontario Ministry of Natural Resources was used for this study. The skulls were collected by trappers from across Ontario during the 1960s and were the same skulls used in studies by Stephenson (1977) and Addison *et al.* (1988). Otters were aged by Stephenson (1977) using cementum annuli counts of canines. Skulls were examined for lesions typical of *Skrjabinogylus* parasites based on descriptions provided by Maldonado and Kirkland (1986) and Addison *et al.* (1988). Lesions included any discolouration, external swelling, or perforations of the frontal bones. Since we did not examine the parasites themselves, we assumed based on previous studies that lesions were attributable to infection by *Skrjabinogylus*, and most likely by *S. lutrae*, which is the only known parasite of this genus to infect North American river otters (Kimber & Kollias, 2000). Lankester and Crichton (1972) found *S. lutrae* to have a prevalence in otters of 8%, and the prevalence of frontal bone lesions in our collection of skulls was 13.4% (Addison *et al.*, 1988). Generally, the assumption that lesions are attributable to *Skrjabinogylus* parasites may result in an underestimate of infection prevalence, since 8-10% of individuals, usually those with a low-intensity infection, may not exhibit skull lesions (Dougherty & Hall, 1955; King, 1977). These estimates of under detection are based on other species, however, as such estimates have not been obtained for otters. We compared a sample of lesioned skulls to a similar-sized sample of unlesioned skulls. All age classes were sampled. In total, 58 female and 72 male otter skulls were used in this study. For female otters, age samples sizes were: < 1 y ( $n = 10$ ), 1 (8), 2 (12), 3 (8), 4 (9), 5 (5), 6 (4), and 7 (2). For males, age samples sizes were: < 1 y ( $n = 6$ ), 1 (11), 2 (14), 3 (15), 4 (6), 5 (5), 6 (3), 7 (5), 8 (1), 9 (3), 10 (2), and 12 (1).

We used methods similar to Maldonado and Kirkland (1986) and Bowman and Tamlin (2007) for skull mensuration. A digital caliper (0.01 mm accuracy; Mitutoyo Corporation, Kawasaki, Kanagawa, Japan) was used to measure each lesioned and unlesioned skull along 3 dimensions: condylobasal length (CBL), postorbital length (POL), and mastoid breadth (MAB). Each measurement was taken 3 times for each skull, and the median value was used for analysis. We measured the volume of 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 pan scale (0.01 g accuracy; Acculab, Edgewood, New Jersey, USA). 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.

We first sought to determine if a relationship existed between skull size (as indexed by CBL) and braincase volume. Since otter skulls do not vary in size predictably with age (Stephenson, 1977), we were interested in removing size-related variation in volume from our test of parasite effects. For each sex, we carried out bivariate linear regressions of the CBL–volume relationship, ignoring the presence of lesions. To remove potentially confounding effects of size on volume, we used the residuals of this relationship for each sex as a new volume variable (hereafter VOL). This variable described variation in braincase volume that was independent of skull size (Reist, 1985).

In studies of other mustelid species it appears that severity of *Skrjabinogylus* infection increases with age and that therefore skulls of older individuals are more damaged (Maldonado & Kirkland, 1986; Bowman & Tamlin, 2007; but see Santi *et al.*, 2006). Thus, we carried out an analysis that assessed the effects of both age and infection on VOL (the size-independent measurement of volume described above). For each sex, we used analysis of covariance to test for differences in volume due to lesions and covaried for age to test for an age effect on volume.

We followed the suggestion of Bowman and Tamlin (2007) and used the 2 additional measurements taken on each skull, POL and MAB, in an analysis of changes to these aspects of skull morphology associated with lesions. First, we removed through linear regression the effect of size (CBL) on each of these variables. Thus, we proceeded with subsequent analyses using the size-independent measures VOL, POL, and MAB. For each sex, we developed a set of candidate models based on the findings of Bowman and Tamlin (2007) for mink. We then carried out logistic regressions, testing for differences in these variables between lesioned and unlesioned skulls. We evaluated these candidate models using information-theoretic methods (Burnham & Anderson, 1998).

### Results

Otters exhibited a positive linear relationship between braincase volume and CBL (females  $F_{[1, 56]} = 31.84$ ,

$P < 0.0001$ ,  $R^2 = 0.36$ ; males  $F_{[1, 70]} = 14.29$ ,  $P < 0.0001$ ,  $R^2 = 0.17$ ) (Figure 1). For subsequent analyses of skull volume, we used the residuals from this relationship, which was a size-independent measure of braincase volume (VOL).

The mean (SE) VOL of lesioned male skulls was  $-1.03$  (0.44) and of unlesioned male skulls was  $0.98$  (0.56). The mean (SE) VOL of lesioned female skulls was  $-0.83$  (0.56) and of unlesioned female skulls was  $1.03$  (0.62). Neither sex exhibited an interaction between age and the presence of lesions with respect to VOL (females  $t = 0.66$ ,  $n = 58$ ,  $P = 0.23$ ; males  $t = 0.21$ ,  $n = 72$ ,  $P = 0.83$ ), suggesting that slopes were homogeneous between these treatments. Analysis of covariance demonstrated that for male skulls VOL was larger in unlesioned compared to lesioned skulls, whereas VOL did not vary with the covariate age (Table I). For females, however, there were no significant relationships between VOL and either the presence of lesions or the covariate age (Table I).

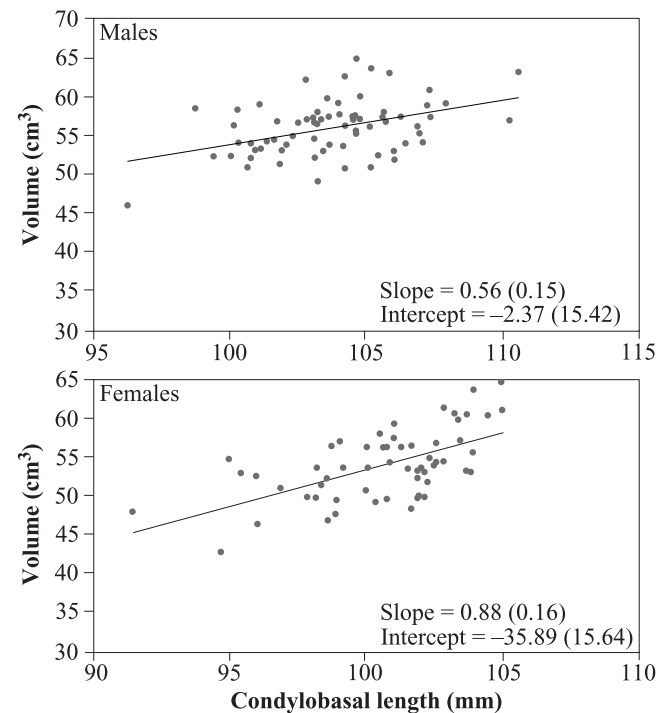


FIGURE 1. Relationships between condylobasal length and braincase volume for male and female river otters (*Lontra canadensis*) collected in Ontario, Canada during the 1960s. Least-squares regression slopes (SE) and intercepts (SE) are depicted.

TABLE I. Analysis of covariance for size-adjusted braincase volume of river otter (*Lontra canadensis*) skulls collected during the 1960s in Ontario, Canada. Skulls were of known ages and either had lesions attributable to *Skrjabinogylus* infection ( $n = 32$  for females;  $n = 35$  for males) or not ( $n = 26$  for females;  $n = 37$  for males).

Sex	Variable	F	P
Female	Lesion	2.86	0.096
	Age	2.71	0.105
Male	Lesion	7.33	0.009
	Age	1.52	0.222

For males, all models that included the VOL term were better than the model that included only the constant. Moreover, the model with only the VOL term was the highest ranked of the candidate model set (Table II). Models with POL were generally higher ranked than those with MAB but lower ranked than those with VOL. For females, once again the VOL-only model was the highest ranked, and models with VOL were generally higher ranked than other models (Table III). Models with POL were higher ranked than models with MAB. The constant-only model had  $\Delta\text{AIC}$  of just over 2.0 for the female set, however, suggesting that it was nearly as likely as the top-ranked model to be the best model in the candidate set (Richards, 2005). This suggests that the highest-ranked candidate models for the female data set were only weakly supported.

## Discussion

Our data were consistent with the hypothesis of Maldonado and Kirkland (1986) that infection with sinus

TABLE II. Model selection results of logistic regression analyses carried out to discriminate between male river otter (*Lontra canadensis*) skulls from Ontario, Canada presumed to be infected ( $n = 35$ ) or not infected ( $n = 37$ ) by *Skrjabinigylus* nematodes. Skull dimensions were size-independent residuals of linear regressions between brain case volume (VOL), postorbital length (POL), or mastoid breadth (MAB) and condylobasal length (as an index of skull size). Model selection criteria were log-likelihood (LL), number of parameters (K), and Akaike's Information Criterion (AIC).

Model	LL	K	AIC	$\Delta\text{AIC}$
VOL	-46.01	2	96.02	0.00
VOL + POL	-45.61	3	97.22	1.20
VOL + MAB	-45.96	3	97.92	1.90
VOL + MAB * POL	-46.00	3	98.00	1.98
VOL + MAB + POL	-45.60	4	99.20	3.18
POL	-47.98	2	99.96	3.94
Constant	-49.88	1	101.76	5.74
MAB + POL	-47.97	3	101.94	5.92
MAB	-49.63	2	103.26	7.24
MAB * POL	-49.84	2	103.68	7.66

TABLE III. Model selection results of logistic regression analyses carried out to discriminate between female river otter (*Lontra canadensis*) skulls from Ontario, Canada presumed to be infected ( $n = 32$ ) or not infected ( $n = 26$ ) by *Skrjabinigylus* nematodes. Skull dimensions were size-independent residuals of linear regressions between brain case volume (VOL), postorbital length (POL), or mastoid breadth (MAB) and condylobasal length (as an index of skull size). Model selection criteria were log-likelihood (LL), number of parameters (K), and Akaike's Information Criterion (AIC).

Model	LL	K	AIC	$\Delta\text{AIC}$
VOL	-37.49	2	78.98	0.00
VOL + MAB * POL	-36.83	3	79.66	0.68
VOL + POL	-37.15	3	80.30	1.32
POL	-38.35	2	80.70	1.72
VOL + MAB	-37.49	3	80.98	2.00
Constant	-39.89	1	81.78	2.80
VOL + MAB + POL	-37.15	4	82.30	3.32
MAB * POL	-39.21	2	82.42	3.44
MAB + POL	-38.31	3	82.62	3.64
MAB	-39.64	2	83.28	4.30

nematodes can reduce the braincase volume of mustelids, including in this case the river otter. This effect has previously been demonstrated in the striped skunk and the American mink (Maldonado & Kirkland, 1986; Bowman & Tamlin, 2007), both of which are smaller, with thinner bones, than otters. A reduction in braincase volume due to a parasitic infection could potentially lead to reduced survival in otters, since neurological damage is a possible consequence of both the infection and the associated cranial swelling (Ewing & Hibbs, 1966; Lankester & Anderson, 1971).

The reduction in braincase volume associated with lesions was more pronounced in males than in females, a result that was consistent with the hypothesis that effects of parasitism should be male-biased in otters, owing to their sexual size dimorphism (Moore & Wilson, 2002). Generally, in polygynous mating systems such as the otter's, larger males are selected by females (Blundell, Ben-David & Bowers, 2002). Therefore, sexual selection requires males to invest in growth and large size, potentially at the cost of increased parasitism and reduced survival compared to smaller females (Owen-Smith, 1993; Moore & Wilson, 2002; Isaac, 2005). The sexual size dimorphism hypothesis suggests that in such mating systems, parasitism should be biased toward males. It is also possible, however, that our results could be attributed to an immunocompetence handicap associated with the effects of testosterone in males (*e.g.*, Perez-Orella & Schulte-Hostedde, 2005).

The Ontario otter skulls did not exhibit any variation in prevalence of lesions between sexes (Addison *et al.*, 1988), but the intensity of infection has not been studied. Given the observed braincase volume effect, the intensity of infection may have been greater in males. However, establishing this link will require further study. For now, we can only conclude that either infected males accumulate more parasites than infected females or males are more damaged than females by an equivalent load of parasites.

Otter skulls do not appear to increase in size with age beyond their first few months (Stephenson, 1977). Similarly, we did not detect a relationship between age and braincase volume. There was also no relationship detected between age and the prevalence of lesions in the Ontario otter skulls (Addison *et al.*, 1988). Previous studies have suggested that intensity of *Skrjabinigylus* infection should increase with age as host mustelids accumulate parasites, testing this hypothesis by comparing size and volume regressions between lesioned and unlesioned skulls (Maldonado & Kirkland, 1986; Bowman & Tamlin, 2007). This method uses size as a proxy for age. We made no such assumption of such a relationship, since all of our skulls were aged. We were unable to detect a relationship between age and braincase volume. Instead, it appeared that braincase volumes could be reduced in infected male otters of any age.

We did not find strong support for our hypothesis that in addition to braincase volume, postorbital length and mastoid breadth were also reduced in infected otters. This hypothesis was based on a study of mink skulls (Bowman & Tamlin, 2007), where a model including both braincase volume and an interaction between mastoid breadth and postorbital length was the highest ranked. Bowman and Tamlin (2007) interpreted this as an indication that overall

skull morphology was affected by sinus nematode infection. For the otter skulls, models including braincase volume were the highest ranked and the postorbital length and mastoid breadth terms were generally only weakly supported. For males, 3 models including braincase volume and some combination of mastoid breadth or postorbital length terms were considered equivalent to one including only braincase volume (Table II). Thus, there was some support for these morphological effects, but they were not as pronounced as in mink.

We conclude that river otters exhibit sex-biased effects of sinus nematode parasitism. The most pronounced of these effects we observed was a reduction in braincase volume in lesioned compared to unlesioned otter skulls, greater in males than in females. Such a reduction might affect behaviour in otters, as has been observed in other species infected by sinus nematodes. It would be interesting in subsequent studies to test whether *Skrjabinogylus* infection can actually lead to reduced survival in otters and in other mustelids. This could contribute to the pattern of male-biased mortality commonly observed in mustelids (e.g., Gehrt, 2005; Koen, Bowman & Findlay, 2007).

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