

**Spleen mass, body condition, and parasite load in male American mink (*Neovison vison*)**

Author(s): Albrecht I. Schulte-Hostedde and Sarah C. Elsasser

Source: Journal of Mammalogy, 92(1):221-226. 2011.

Published By: American Society of Mammalogists

URL: <http://www.bioone.org/doi/full/10.1644/10-MAMM-A-020.1>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is an electronic aggregator of bioscience research content, and the online home to over 160 journals and books published by not-for-profit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

## Spleen mass, body condition, and parasite load in male American mink (*Neovison vison*)

ALBRECHT I. SCHULTE-HOSTEDDE\* AND SARAH C. ELSASSER

Department of Biology, Laurentian University, Sudbury, Ontario P3E 2C6, Canada

\* Correspondent: [aschulte@hostedde@laurentian.ca](mailto:aschulte@hostedde@laurentian.ca)

One demand to which organisms must allocate energy for maintenance, growth, and reproduction is the immune system. Because the immune system is energetically costly, spleen size is expected to be condition-dependent. Parasites also can influence spleen size. Parasites draw resources from their host, with consequences for host body condition. Male American mink (*Neovison vison*) were examined for parasite prevalence, intensity, and richness to test several predictions: individuals in good condition have large spleens; heavily parasitized individuals have large spleens; and heavily parasitized individuals are in poorer condition than individuals with few parasites. Spleen mass was related positively to both body condition and parasite richness, but spleen mass was not associated with prevalence or intensity of individual parasites. Body condition was related weakly to the intensity of parasitism by the giant kidney worm and sinus worm, but otherwise parasite prevalence, intensity, or richness were not associated with body condition. These results are similar to those found in studies of birds, suggesting that comparable processes occur in mammals.

Key words: body size, condition dependence, immune system, parasite species richness

© 2011 American Society of Mammalogists

DOI: 10.1644/10-MAMM-A-020.1

Life-history theory argues that, in the face of finite resources, organisms must allocate energy to the various demands required for maintenance, growth, and reproduction (Roff 1992). These allocation decisions lead to trade-offs among demands. In recent years it has become increasingly apparent that the immune system and defense against pathogens are important and energetically demanding components of the life history of an organism (Martin et al. 2003, 2006; Sheldon and Verhulst 1996). A variety of experimental approaches have been used to assess immune function in natural populations of vertebrates, but using the size of immune system organs as an index of investment in the immune system is a common approach. Of particular interest has been the spleen, a relatively small but critical organ that is involved in the production of lymphocytes that are used to fight infection (John 1994).

The use of the size of the spleen as a proxy measure of immunological activity has been widespread, particularly in birds (Møller 1997; Møller et al. 1998; Shutler et al. 1999) and mammals (Cowan et al. 2009), under the assumption that a larger spleen produces and stores more lymphocytes than a smaller spleen (Nunn 2002). Because components of the immune system are presumed to be costly, individuals in good condition should be better able to invest in lymphocyte production or storage, or both. This pattern has been found in a

variety of contexts. For example, in a survey of 20 avian species Møller et al. (1998) found a positive relationship between body condition and spleen mass. Similarly, a kidney fat index was positively correlated with spleen mass in red deer (*Cervus elaphus*—Vicente et al. 2007), and abdominal fat was positively correlated with spleen mass in Natal mole-rats (*Cryptomys hottentotus natalensis*—Luttermann and Bennett 2008). Thus, in at least some species, individuals with relatively large spleens were in good physiological condition, consistent with the hypothesis that maintaining the immune system is energetically costly.

Alternatively, spleens can be enlarged in parasitized individuals, and thus spleen size is less affected by individual energetics and more by the presence of parasites. A comparative analysis of avian species found that the number of parasitic nematode species (species richness) was positively correlated with relative spleen mass (Morand and Poulin 2000). In an experiment with cliff swallows (*Petrochelidon pyrrhonota*) individuals from fumigated (and thus ectoparasite-free) colonies had smaller spleens than their parasitized counterparts (Brown and Brown 2002). In European eels



(*Anguilla anguilla*) relative spleen mass was highest in individuals heavily infected with the swimbladder nematode *Anguillicola crassus* (Lefebvre et al. 2004). In contrast, relative spleen size was negatively associated with nematode burdens in at least some age and sex classes of red deer, most notably adult males (Vicente et al. 2007). Although parasite loads are associated with relative spleen size, the direction of the relationship is apparently not universal.

Parasites, by their very nature, derive resources from the host; thus body condition can be compromised by parasite burdens (Neuhaas 2003). Individuals in poor condition also might be unable to resist parasitic infection because of the energetic expense of mounting an immune defense (Martin et al. 2003). Alternatively, parasites might avoid infecting hosts in poor condition because of the relatively poor resources available in that host (Bize et al. 2008; Seppälä et al. 2008). Underlying these possibilities is the observation that host immunity is associated positively with body condition (Bize et al. 2008). Thus, host body condition and parasite load are interrelated in what could be a complex series of interactions.

The American mink (*Neovison vison*) is a semiaquatic member of Mustelidae that ranges across North America (Larivière 1999). American mink can be infected by a variety of parasites, including a sinus worm (*Skrjabingylus nasicola*) and a Guinea worm (*Dracunculus insignis*—Linscombe et al. 1982). The mammalian spleen plays a dual role, important in an immunological context and also functioning as a reservoir for red blood cells. Nonetheless, Corbin et al. (2008) concluded that spleen mass in red deer was an accurate measure of immune activity. We tested 2 predictions related to relative spleen mass in male American mink, under the assumption that relative spleen size reflects immune activity. First, we predicted that spleen mass was associated positively with body condition, reflecting the cost associated with maintaining an active immune system. Second, we predicted that spleen mass was related positively to parasite load, using parasite prevalence, intensity, and richness derived from a suite of internal parasites. Finally, we tested the prediction that body condition should decline with parasite prevalence, intensity, and richness.

## MATERIALS AND METHODS

**Samples.**—Mink carcasses were collected during the fur harvests (October to February) of 2005–2006, 2006–2007, and 2007–2008 from licensed Ontario fur trappers on registered trap lines in northeastern, southern, and southeastern Ontario, Canada, and frozen at  $-18^{\circ}\text{C}$  until dissection. Collection from trappers yielded individuals of both sexes, but the analysis was confined to males because of the paucity of females. Male-biased trapping does occur in Mustelidae, perhaps explaining our lack of females (Buskirk and Lindstedt 1989).

Prior to dissection specimens were thawed completely. Morphometric measurements then were taken and included total peltless mass ( $\pm 0.01$  g), total length (from nose to tip of tail,  $\pm 0.1$  cm), and tail length (base of tail to tip of tail,  $\pm$

0.1 cm). Animals were sexed by genital–gonadal examination and assigned to either a juvenile ( $<1$  year) or adult ( $>1$  year) age class based on the degree of temporal muscle coalescence (Poole et al. 1994). Only adults were used in subsequent analyses.

During dissection all external surfaces, intermuscular areas of the legs and feet, connective tissue beneath the latissimus dorsi and of the inguinal and axillary regions, and internal surfaces of the abdominal and pelvic cavities were examined for Guinea worm. Guinea worms were counted, sexed, measured with digital calipers ( $\pm 0.1$  mm), weighed ( $\pm 0.001$  g), and preserved in 70% ethanol. In addition, the frontal sinus cavities, nasal passages, gastrointestinal tract, liver, kidneys, lungs, bronchi, and trachea were inspected carefully for internal parasites with the aid of a stereomicroscope. Parasites were identified to the most precise taxa possible and preserved in 70% ethanol.

Spleens were removed from the mink, weighed ( $\pm 0.001$  g), and frozen ( $-18^{\circ}\text{C}$ ) in individual plastic bags. At a later date spleens were thawed, placed in individual aluminum containers, and freeze-dried (model 7754042; Lobconco, Kansas City, Missouri) for 7 days. Spleens then were weighed ( $\pm 0.001$  g). A separate study required a portion of tissue to be taken from a subsample (11) of spleens. In these cases the total fresh mass of the spleens was recorded, a portion of tissue removed and weighed, and the total freeze-dried mass was estimated from the percent of the total wet mass.

**Statistical analyses.**—Fisher's exact tests, bootstrap *t*-tests, and confidence intervals of prevalence and mean intensities were performed using the software Quantitative Parasitology 3.0 (Reiczigel and Rózsa 2001). All other analyses were conducted using Statistica 8.0 (Statsoft Inc., Tulsa, Oklahoma). Statistical significance was accepted at  $\alpha = 0.05$ .

All morphological data, including spleen and body mass, were  $\log_{10}$ -transformed to improve the linearity of our analyses. Condition-dependence of spleen mass was assessed using multiple regression with body length and body mass as independent variables and spleen mass as the dependent variable. Partial correlation coefficients of body mass were interpreted as the relation between body condition and spleen mass because it is the independent effect of body mass corrected for size on the dependent variable. Using partial correlation coefficients for size-corrected mass (body condition) from a multiple regression is analogous to using residuals from a regression of body mass on structural body size but has the advantage of taking into account all of the degrees of freedom (Schulte-Hostedde et al. 2005). Male mink in good body condition were assumed to have had more energy reserves (fat or protein or both) than males in poor condition (Schulte-Hostedde et al. 2001).

Parasite richness was defined as the total number of species of parasites found in a host (male mink), and parasite intensity was defined as the total number of parasites for each of the 3 species of parasites that were quantified. Parasite prevalence was defined as the proportion of host individuals that were infected by a particular parasite (Bush et al. 1997). To assess

**TABLE 1.**—Summary statistics of morphological traits from 42 male American mink (*Neovison vison*).

|                     | $\bar{X}$ | Range       | SD    |
|---------------------|-----------|-------------|-------|
| Body mass (g)       | 683.2     | 452.7–895.2 | 111.3 |
| Body length (cm)    | 36.40     | 33.50–42.00 | 1.71  |
| Dry spleen mass (g) | 0.58      | 0.31–1.40   | 0.22  |
| Parasite richness   | 1.4       | 0–4         | 1.1   |

the relation between spleen mass and parasite richness we obtained residual spleen mass from the regression between spleen mass and body mass (Schulte-Hostedde et al. 2005) and regressed these residuals against parasite richness.

Parasite intensity was nonnormal, and so nonparametric (Spearman rank,  $r_s$ ) correlations between host body condition (calculated as residuals from a regression of body mass on body length—Schulte-Hostedde et al. 2005) and parasite intensity were generated. Separate correlation analyses were conducted for each of the 3 parasites for which intensity data were available (giant kidney worm, sinus worm, and Guinea worm).

To determine if body mass and spleen mass were correlated with the probability of infection by a specific parasite (prevalence) a generalized linear model with binomial distribution and logit-link function was used because parasite presence (0, absence of parasite; 1,  $\geq 1$  parasite) was the dependent variable. To determine if body condition was related to parasite prevalence and intensity we used a similar approach to that used with spleen mass. However, body mass and body length were included as independent variables in general linear models (binomial distribution, logit-link function), and we interpreted the partial correlation coefficient of body mass as the effect of body condition (mass corrected for body length) on spleen mass. To assess the relationship between body condition and parasite intensity rank correlations between intensity and residual body mass (body mass corrected for body length—Schulte-Hostedde et al. 2001) were used.

## RESULTS

Forty-three adult male mink were received from the fur trappers. One male was excluded from analysis because of a particularly small spleen ( $>3$  SDs from the mean); thus the morphological data from the remaining 42 males (Table 1) were used.

The dissections of male mink revealed a number of parasites, including Guinea worms (*D. insignis*), sinus worms (*S. nasicola*), lung worms (*Filaroides martis*), bronchus-tracheal worms (*Crenosoma* sp.), and giant kidney worms (*Diocotophyme renale*). In addition, we found in the gastrointestinal tract additional Nematoda, Trematoda, and Cestoda. The prevalence of all parasites and the intensity of giant kidney worm, sinus worm, and Guinea worm infections were determined (Table 2). The sinus worm had the highest prevalence and highest mean intensity of all parasites.

Body condition was positively related to spleen mass (overall model;  $F_{2,39} = 13.91$ ,  $P < 0.001$ ,  $r^2 = 0.42$ ; body

**TABLE 2.**—Summary statistics for parasitism of male American mink (*Neovison vison*), including host sample size ( $n$ ), parasite prevalence (proportion of hosts infected), and where available, intensity (number of parasites of each type per host), with associated 95% CIs. GI = gastrointestinal.

| Parasite          | $n$ | Prevalence | 95% CI       | Mean intensity | 95% CI     |
|-------------------|-----|------------|--------------|----------------|------------|
| Giant kidney worm | 42  | 0.119      | 0.0481–0.259 | 3.40           | 1.40–5.20  |
| Lung worm         | 40  | 0.375      | 0.235–0.538  | —              | —          |
| Trachea worm      | 40  | 0.025      | 0.001–0.13   | —              | —          |
| GI nematode       | 41  | 0.341      | 0.205–0.500  | —              | —          |
| GI cestode        | 41  | 0.049      | 0.009–0.167  | —              | —          |
| GI trematode      | 41  | 0.024      | 0.001–0.130  | —              | —          |
| Sinus worm        | 39  | 0.436      | 0.287–0.595  | 8.12           | 4.59–18.12 |
| Guinea worm       | 42  | 0.333      | 0.199–0.489  | 5.43           | 3.71–7.93  |

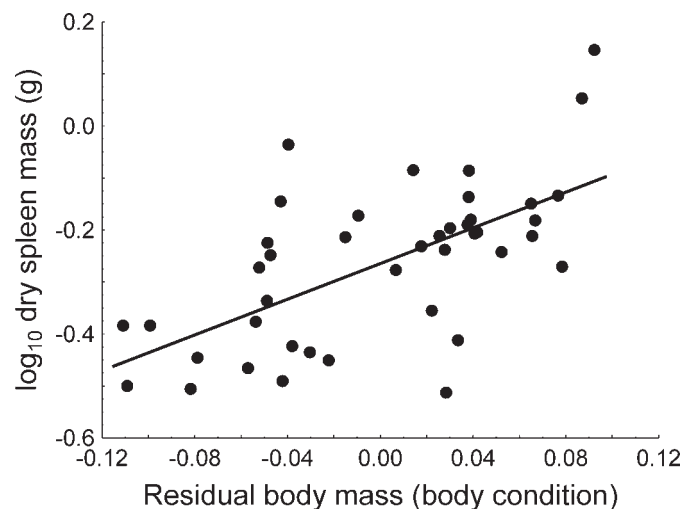
mass partial  $r = 0.638$ ,  $P < 0.001$ ; Fig. 1). Thus, male mink in good condition had relatively large spleens.

Relative spleen mass was not associated with parasite prevalence (Table 3) or intensity. Whether these correlations were conducted using all data, or excluded uninfected individuals, no significant relationships were detected ( $P > 0.15$ ,  $n = 42$  for all correlations).

We found little evidence of an effect of parasite prevalence on relative spleen mass. Spleen mass was not associated with parasite prevalence for any parasites except the sinus worm (Table 3). A negative marginally nonsignificant relationship was found between spleen size and prevalence of the sinus worm; male mink infected with sinus worms tended to have smaller spleens than male mink without sinus worms.

Spleen mass was positively related to parasite richness. Male mink with more types of parasites had relatively large spleens than male mink with fewer types of parasites ( $F_{1,36} = 12.55$ ,  $P = 0.001$ ,  $r^2 = 0.26$ ; Fig. 2).

Body condition was unrelated to parasite prevalence for all parasite types (Table 4), but some evidence suggested that

**FIG. 1.**—Semipartial correlation between residual body mass (body condition) and spleen mass of male American mink (*Neovison vison*).

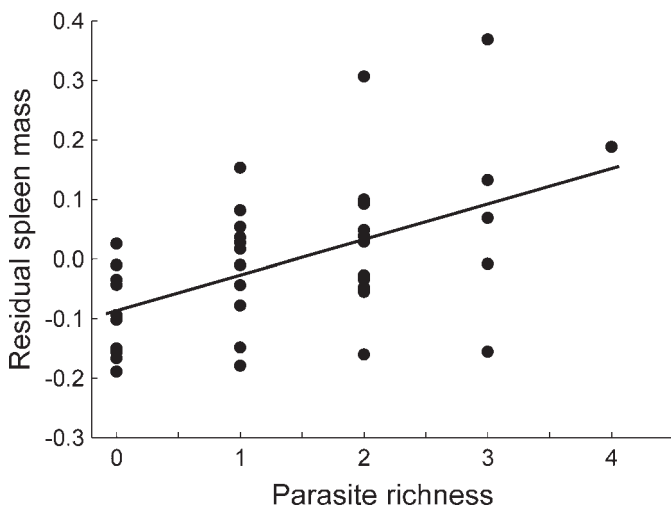
**TABLE 3.**—Generalized linear models with binomial distribution and logit-link function testing for effects of body mass and spleen mass on presence (coded 0 if uninfected, 1 if infected) of 8 parasites infecting male American mink (*Neovison vison*). GI = gastrointestinal.

| Parasite          | Effect      | Estimate | SE    | Wald statistic | P    |
|-------------------|-------------|----------|-------|----------------|------|
| Giant kidney worm | Body mass   | -19.55   | 12.24 | 2.55           | 0.11 |
|                   | Spleen mass | 0.23     | 4.70  | 0.002          | 0.96 |
| Lung worm         | Body mass   | 2.01     | 5.71  | 0.12           | 0.72 |
|                   | Spleen mass | -3.43    | 2.74  | 1.57           | 0.21 |
| Trachea worm      | Body mass   | -28.73   | 43.74 | 0.43           | 0.51 |
|                   | Spleen mass | 25.17    | 26.95 | 0.87           | 0.35 |
| GI nematode       | Body mass   | 10.32    | 6.04  | 2.92           | 0.09 |
|                   | Spleen mass | -2.26    | 2.68  | 0.71           | 0.40 |
| GI cestode        | Body mass   | 1.09     | 12.53 | 0.007          | 0.93 |
|                   | Spleen mass | -4.88    | 5.10  | 0.91           | 0.34 |
| GI trematode      | Body mass   | -24.05   | 26.98 | 0.79           | 0.37 |
|                   | Spleen mass | 3.51     | 11.24 | 0.10           | 0.76 |
| Sinus worm        | Body mass   | 0.39     | 5.94  | 0.004          | 0.95 |
|                   | Spleen mass | -5.34    | 3.12  | 2.92           | 0.09 |
| Guinea worm       | Body mass   | 2.51     | 5.62  | 0.20           | 0.65 |
|                   | Spleen mass | -3.05    | 2.72  | 1.26           | 0.26 |

**TABLE 4.**—Generalized linear models with binomial distribution and logit-link function testing for effects of body mass and body length on presence (coded 0 if uninfected, 1 if infected) of 8 parasites infecting male American mink (*Neovison vison*). Effect of body mass is corrected for body length to represent the effect of body condition on parasite presence. GI = gastrointestinal.

| Parasite          | Effect      | Estimate | SE    | Wald statistic | P    |
|-------------------|-------------|----------|-------|----------------|------|
| Giant kidney worm | Body mass   | -21.23   | 13.30 | 2.55           | 0.11 |
|                   | Body length | 8.62     | 32.42 | 0.07           | 0.79 |
| Lung worm         | Body mass   | -3.71    | 5.77  | 0.41           | 0.52 |
|                   | Body length | 9.30     | 20.57 | 0.20           | 0.65 |
| Trachea worm      | Body mass   | 11.02    | 17.63 | 0.46           | 0.50 |
|                   | Body length | -44.32   | 56.21 | 0.62           | 0.43 |
| GI nematode       | Body mass   | 4.76     | 6.05  | 0.62           | 0.43 |
|                   | Body length | 17.06    | 23.88 | 0.51           | 0.47 |
| GI cestode        | Body mass   | 4.72     | 14.17 | 0.11           | 0.74 |
|                   | Body length | -50.94   | 46.14 | 1.22           | 0.27 |
| GI trematode      | Body mass   | -2.99    | 26.94 | 0.01           | 0.91 |
|                   | Body length | -77.22   | 63.10 | 1.50           | 0.22 |
| Sinus worm        | Body mass   | -10.72   | 5.96  | 3.24           | 0.07 |
|                   | Body length | 27.89    | 21.41 | 1.70           | 0.19 |
| Guinea worm       | Body mass   | -3.08    | 5.71  | 0.29           | 0.59 |
|                   | Body length | 11.63    | 20.81 | 0.31           | 0.58 |

male mink in good condition had higher intensity of parasites. When uninfected individuals were included, male mink in good condition had higher intensity of giant kidney worms ( $r_s = 0.306, n = 42, P = 0.048$ ) and sinus worms ( $r_s = 0.318, n = 39, P = 0.049$ ). The significant positive relationships between body condition and parasite intensity disappeared when uninfected individuals were excluded (maximum  $r_s = 0.089$ , maximum  $n = 17, P > 0.10$  for all parasites). No relationship between parasite intensity and body condition was detected for Guinea worms ( $r_s = 0.133, P = 0.41, n = 42$ ). Body condition was not related to parasite richness (overall model;  $F_{2,35} = 1.73, r^2 = 0.09, P = 0.19$ ; body mass partial  $r = 0.18, P = 0.28$ ).



**FIG. 2.**—Regression of residual spleen mass of male American mink (*Neovison vison*) on parasite richness (number of taxa).

### DISCUSSION

The energetic costs of immunity form the basis of the theory that the immune system is an important component of individual life history (Sheldon and Verhulst 1996). The spleen is an important organ that serves to produce and store lymphocytes (John 1994), so maintenance of such an important organ is hypothesized to be costly. Our results indicate that male mink in good body condition had relatively large spleens, a result consistent with a number of other studies spanning vertebrate taxa including birds (Møller et al. 1998) and mammals (Vicente et al. 2007). In contrast, little evidence existed for an effect of parasite burden on spleen mass, except that male mink with a high diversity of parasites had larger spleens than mink with a lower diversity of parasites. In general, the results are consistent with those of Møller et al. (1998), who found that spleen size in birds was associated with both body condition and disease status. As with Møller et al. (1998), the relationship between spleen mass and body condition in male mink was stronger than between spleen mass and parasite burden.

The role of parasites in determining individual spleen size has been explored in a number of taxa, with evidence indicating that parasite prevalence or intensity can predict spleen mass (Cowan et al. 2009). The results from this study were equivocal; we found little evidence for specific parasites influencing relative spleen mass. Nonetheless, parasite diversity (richness) was associated with relatively large spleens. This result mirrors the results of the comparative study by Morand and Poulin (2000) that found that parasitic nematode species richness was associated with large spleens among 24 species of birds. Parasite richness might be a better index of parasite burden than intensity and prevalence because these parameters often vary in time and space; parasite



intensity and prevalence vary geographically and temporally (Morand and Poulin (2000)). The samples from this study were collected across 3 years and a relatively large geographic area, and thus the use of parasite richness might be a more appropriate measure of parasite burden than other measures.

Parasites, by definition, acquire resources from their host, and thus individuals that are heavily parasitized are expected to carry reduced energy reserves relative to individuals that have few parasites. This expectation, while upheld in some studies (Fitze et al. 2004; Neuhaus 2003), is not universal (Khokhlova et al. 2002; Perez-Orella and Schulte-Hostedde 2005), and it seems that parasites might not always lead to immediate energetic costs for the host. Rather, the costs might be manifested in longer-term reductions in fitness (Willis and Poulin 1999). The results from our study indicate little evidence of a cost in terms of body condition and parasite burden. The only significant effects uncovered indicated that mink with higher parasite intensities were in better condition than those with lower intensities. One explanation may be that individuals in poor condition could be a poor choice of host because of the lack of resources that would be available to the parasite (Bize et al. 2008); thus parasites might be drawn to hosts in good condition. The poor nutritional state of the host can have a negative impact on parasite fitness (Bize et al. 2008; Seppälä et al. 2008), and thus a parasite-focused perspective might provide important insight into host–parasite interactions. Alternatively, and perhaps more likely in the case of the parasites assayed in this study, male mink in good condition are consuming more prey, thus increasing their encounter rate with parasites, leading to higher parasite intensities.

Several additional research directions are intimated by the results of our study. The need to assess sex differences in immunocompetence (Stoehr and Kokko 2006) by examining sexual dimorphism in organs related to immunity such as the spleen is the next logical step. In addition, the condition-dependence of spleen mass observed here is correlative in nature, and thus an experimental approach involving supplemental feeding would help establish any causality between body condition (energy reserves) and immune function. The use of alternative measures of immune activity (e.g., white blood cell counts) also should be considered when testing for the effects of parasites and energy reserves on immune function.

#### ACKNOWLEDGMENTS

Foremost, we thank the various trapping councils and their members for providing the samples used in this study. T. Johnston generously allowed us access to the freeze dryer. The manuscript was improved by comments from J. Bowman, D. Edwards, K. Gooderham, and D. Shutler. Financial support was provided by a Natural Sciences and Engineering Research Council Discovery grant to AIS-H.

#### LITERATURE CITED

- BIZE, P., C. JEANNERET, A. KLOPFENSTEIN, AND A. ROULIN. 2008. What makes a host profitable? Parasites balance host nutritive resources against immunity. *American Naturalist* 171:107–118.
- BROWN, C. R., AND M. B. BROWN. 2002. Spleen volume varies with colony size and parasite load in a colonial bird. *Proceedings of the Royal Society of London, B. Biological Sciences* 269:1367–1373.
- BUSH, A. O., K. D. LAFFERTY, J. M. LOTZ, AND A. W. SHOSTAK. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* 83:575–583.
- BUSKIRK, S. W., AND S. L. LINDSTEDT. 1989. Sex biases in trapped samples of Mustelidae. *Journal of Mammalogy* 70:88–97.
- CORBIN, E., J. VICENTE, M. P. MARTIN-HERNANDO, P. ACEVEDO, L. PEREZ-RODRIGUEZ, AND C. GORTAZAR. 2008. Spleen mass as a measure of immune strength in mammals. *Mammal Review* 38:108–115.
- COWAN, K. M., D. SHUTLER, T. B. HERMAN, AND D. T. STEWART. 2009. Splenic mass of masked shrews, *Sorex cinereus*, in relation to body mass, sex, age, day of the year, and bladder nematode, *Liniscus* (= *Capillaria*) *maseri*, infection. *Journal of Parasitology* 95:228–230.
- FITZE, P. S., B. TSCHIRREN, AND H. RICHNER. 2004. Life history and fitness consequences of ectoparasites. *Ecology* 73:216–226.
- JOHN, J. L. 1994. The avian spleen: a neglected organ. *Quarterly Review Biology* 69:327–351.
- KHOKHLOVA, I. S., B. R. KRASNOV, M. KAM, N. I. BURDELOVA, AND A. A. DEGEN. 2002. Energy costs of ectoparasitism: the flea *Xenopsylla ramensis* on the desert gerbil *Gerbillus dasyurus*. *Journal of Zoology (London)* 256:349–354.
- LARIVIERE, S. 1999. *Mustela vison*. *Mammalian Species* 608:1–9.
- LEFEBVRE, F., B. MOUNAIX, G. POIZAT, AND A. J. CRIVELLI. 2004. Impacts of the swimbladder nematode *Anguillicola crassus* on *Anguilla anguilla*: variation in liver and spleen masses. *Journal of Fish Biology* 64:435–447.
- LINSCOMBE, G., N. KINLER, AND R. J. AUERLICH. 1982. Mink. Pp. 629–643 in *Wild mammals of North America: biology, management and economics* (J. A. Chapman and G. A. Feldhamer, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- LUTTERMANN, H., AND N. C. BENNETT. 2008. Strong immune function: a benefit promoting the evolution of sociality? *Journal of Zoology (London)* 275:26–32.
- MARTIN, L. B., II, A. SCHEURLEIN, AND M. WIKELSKI. 2003. Immune activity elevates energy expenditure of house sparrows: a link between direct and indirect costs? *Proceedings of the Royal Society of London, B. Biological Sciences* 270:153–158.
- MARTIN, L. B., II, Z. M. WEIL, J. R. KUHLMAN, AND R. J. NELSON. 2006. Trade-offs within the immune systems of female white-footed mice, *Peromyscus leucopus*. *Functional Ecology* 20:630–636.
- MØLLER, A. P. 1997. Immune defence, extra-pair paternity, and sexual selection in birds. *Proceedings of the Royal Society of London, B. Biological Sciences* 264:561–566.
- MØLLER, A. P., P. CHRISTE, J. ERRITZØE, AND J. MAVAREZ. 1998. Condition, disease and immune defence. *Oikos* 83:301–306.
- MORAND, S., AND R. POULIN. 2000. Nematode parasite species richness and the evolution of spleen size in birds. *Canadian Journal of Zoology* 78:1356–1360.
- NEUHAUS, P. 2003. Parasite removal and its impact on litter size and body condition in Columbian ground squirrels (*Spermophilus columbianus*). *Biology Letters* 270:213–215.
- NUNN, C. L. 2002. Spleen size, disease risk and sexual selection: a comparative study in primates. *Evolutionary Ecology Research* 4:91–107.
- PEREZ-ORELLA, C., AND A. I. SCHULTE-HOSTEDDE. 2005. Effects of sex and body size on ectoparasite load in the northern flying squirrel. *Canadian Journal of Zoology* 83:1381–1385.

- POOLE, K. G., G. M. MATSON, M. A. STRICKLAND, A. J. MAGOUN, R. P. GRAF, AND L. M. DIX. 1994. Age and sex determination for American martens and fishers. Pp. 204–223 in *Martens, sables, and fishers: biology and conservation* (S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, eds.). Cornell University Press, Ithaca, New York.
- REICZIGEL, J., AND L. RÓZSA. 2001. Quantitative parasitology 3.0. <http://www.zoologia.hu/qp/qp.html>. Accessed 26 July 2010.
- ROFF, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman & Hall, New York.
- SCHULTE-HOSTEDDE, A. I., J. S. MILLAR, AND G. J. HICKLING. 2001. Evaluating body condition in small mammals. *Canadian Journal of Zoology* 79:1021–1029.
- SCHULTE-HOSTEDDE, A. I., B. ZINNER, J. S. MILLAR, AND G. J. HICKLING. 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology* 86:155–163.
- SEPPÄLÄ, O., K. LILJEROOS, A. KARVONEN, AND J. JOKELA. 2008. Host condition as a constraint for parasite reproduction. *Oikos* 117:749–753.
- SHELDON, B. C., AND S. VERHULST. 1996. Ecological immunology: costly parasite defenses and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution* 11:317–321.
- SHUTLER, D., R. T. ALISAUSKAS, AND J. D. McLAUGHLIN. 1999. Mass dynamics of the spleen and other organs in geese: measures of immune relationships to helminths? *Canadian Journal of Zoology* 77:351–359.
- STOEHR, A. M., AND H. KOKKO. 2006. Sexual dimorphism in immunocompetence: what does life-history theory predict? *Behavioral Ecology* 17:751–756.
- VICENTE, J., L. PEREZ-RODRIGUEZ, AND C. GORTAZAR. 2007. Sex, age, spleen size, and kidney fat of red deer relative to infection intensities of the lungworm *Elaphostrongylus cervi*. *Naturwissenschaften* 94:581–587.
- WILLIS, C., AND R. POULIN. 1999. Effects of the tapeworm *Hymenolepis diminuta* on maternal investment in rats. *Canadian Journal of Zoology* 77:1001–1005.

*Submitted 19 January 2010. Accepted 7 September 2010.*

*Associate Editor was Christian C. Voigt.*