Sex-biased parasitism in monogamous arctic foxes is driven by diet

Olwyn C. Friesen, James D. Roth,* and Lane C. Graham

Department of Biological Sciences, University of Manitoba, 50 Sifton Road, Winnipeg, Manitoba R3T 3E5, Canada

* Correspondent: *jim.roth@umanitoba.ca*

Male-biased parasite loads are common in vertebrates, particularly in species with intense sexual selection, yet few studies have examined sex-biased parasite loads in monogamous species with low sexual selection and no differential investment in ornaments or other sexually selected traits. The circumpolar arctic fox (*Vulpes lagopus*) is a socially monogamous predator with low sexual selection; both parents invest heavily in their young. To determine if parasite loads (abundance and intensity) in arctic foxes vary with sex, age, or diet, we identified and enumerated parasites in arctic fox carcasses collected in winter from local trappers at Churchill, Manitoba, Canada. We measured stable isotope ratios in muscle samples as a proxy for diet. Males had more cestodes, which are only transmitted through prey, but numbers of nematodes, which are acquired by direct transmission, did not differ between sexes. $\delta^{15}N$ values were lower in males, suggesting greater reliance on small mammals. Age did not affect diet or the number of cestodes, but the species of cestodes differed by age; for example, *Echinococcus multilocularis* was present only in subadults (< 1 year old). Nematodes were more abundant in subadults, likely because pups spend more time at dens in high densities, increasing exposure. Intraspecific differences in arctic fox parasites are best explained by variation in diet and foraging patterns, rather than hormone-mediated reduction in immunity. These results suggest that in monogamous species, males may not suffer compromised immunity as seen in species with strong sexual selection.

Key words: endoparasite, immunocompetence handicap hypothesis, sex-biased parasitism, sexual selection, *Vulpes lagopus*

Many species have evolved sex-based differences in diet, behavior (e.g., home range size), morphology (e.g., body size), and physiology (e.g., hormone concentrations) due to differences in reproductive strategies that may predispose 1 sex to greater parasite infection (Folstad and Karter 1992; Arneberg et al. 1998b; Wilson et al. 2002; Hillegass et al. 2008; Hosken and House 2011). Greater investment in reproduction by members of 1 sex may come at the expense of an increased vulnerability to parasites (Hillegass et al. 2008). Hosts may invest preferentially in sexually selected traits rather than immunity (Hillegass et al. 2008). Male-biased parasite loads are common in vertebrates, particularly in species where sexual selection is intense (Poulin 1996; Zuk and McKean 1996; Soliman and Marzouk 2001; Hillegass et al. 2008). Sex-biased parasite loads may also be a result of body size differences between sexes (Moore and Wilson 2002). Differences in home range size and interactions with conspecifics (such as in a polygynous mating system) could also increase male exposure to parasites compared to females (Nunn and Dokey 2006). The "immunocompetence handicap hypothesis" suggests a trade-off between immune function and testosterone (Folstad and Karter 1992). Testosterone suppresses the immune system, making males

with higher testosterone levels more vulnerable to infection or infestation by parasites (Folstad and Karter 1992).

Most studies on sex-biased parasitism in mammals have examined species with polygamous mating systems, where sexual selection is intense and males and females invest differently in reproduction (e.g., Soliman and Marzouk 2001; Morand et al. 2004; Krasnov et al. 2005; Hillegass et al. 2008; Harrison et al. 2010; Scantlebury et al. 2010). Few studies have examined sex-biased parasite loads in species with monogamous mating systems, and even fewer directly examined how diet, behavior, physiology (e.g., immunocompetence handicap hypothesis), and morphology relate to any sex-biased parasitism in these species (Porteous and Pankhurst 1998; Lutermann et al. 2012). In species with monogamous mating systems and low sexual selection, sexes may not invest differently in the development and maintenance of ornaments or other sexually selected traits. Therefore, males and females would be investing similar amounts of energy in reproduction, minimizing any differences in vulnerability to infection by parasites. Yet the relationships found between parasite load and sex have not been consistent in monogamous species. In the monogamous Patagonian mara (*Dolichotis patagonum*), females had

higher nematode parasite loads (Porteous and Pankhurst 1998), whereas in eastern rock sengis (*Elephantulus myurus*), adult males had the greatest larval parasite abundance (Lutermann et al. 2012).

The age of a host often influences its parasite load; as the host may have continual exposure to parasites over time, parasite loads tend to increase with age (Wilson et al. 2002). The introduction of naive hosts during the reproductive season can affect patterns of parasite communities (Lutermann et al. 2012). In the absence of vertical transmission of the parasite, or reproduction of the parasite within the host, the host will continue to acquire parasites from the environment, increasing parasite loads over time (Hudson and Dobson 1995). If parasite mortality and acquisition remain constant, then the parasite load will only increase to an asymptote (Hudson and Dobson 1995). The parasite load of an older individual may also be higher if survival of younger individuals with high parasite loads is reduced in comparison to older individuals with similar loads (Soliman and Marzouk 2001). Nevertheless, if the host acquires immunity in response to exposure to parasites, its immune system should decrease parasite establishment, maturation, reproduction, and survival, and parasite loads should eventually decline after an initial increase (Hudson and Dobson 1995).

Arctic foxes (*Vulpes lagopus*) are monogamous predators that forage alone during most of the year (Angerbjörn et al. 2004). Unlike in polygamous mating systems where sexual selection is often high and sexes invest differently in reproduction, male and female arctic foxes invest similarly in reproduction, as their large litters (up to 25 pups—Audet et al. 2002) require biparental care. Although extrapair paternity does occur, it is not common, and the social father will still invest in the pups of its partner (Cameron et al. 2011). The lack of intense sexual selection on arctic foxes makes this species an interesting comparison to polygamous species for understanding differences in parasite load between sexes.

Differences in diet can affect the parasites to which an arctic fox is exposed (Meijer et al. 2011). As the interactions between predators and prey are key determinants of transmission intensity of many parasites, the consumption of different types of prey (e.g., birds versus mammals) will expose arctic foxes to different arrays of parasites (Raoul et al. 2010). However, no differences between male and female arctic foxes in diet, foraging patterns, or home range size have been documented (Angerbjörn et al. 2004; Eide et al. 2004), so no sex bias in parasite loads are predicted for monogamous arctic foxes. Yet age differences could exist based on their life history. For the 1st few months after birth, the pups are confined to their natal dens, where they remain while both parents forage for them (Audet et al. 2002). Age-related differences in diet may lead to intraspecific variation in parasite loads. Adult arctic foxes may cache eggs from the summer bird-breeding season for use in fall and winter (Samelius et al. 2007). As juveniles remain on the den during their 1st summer, they may not have access to cached bird eggs and may rely more heavily on lemmings and other rodents, which are important intermediate hosts for cestodes, such as *Echinococcus multilocularis*, *Taenia crassiceps*,

and *T. polyacantha arctica* (Rausch and Fay 1988; Loos-Frank 2000). The availability of eggs may reduce adult foxes' reliance on small mammalian prey and reduce their exposure to trophically transmitted parasites (e.g., cestodes). Therefore, if juveniles and adults differ in diet, the age class that relies more heavily on mammalian prey should have more cestodes. Furthermore, many ascarid nematodes can be transferred through indirect contamination of food or an area by infected feces (Okulewicz et al. 2012), and transmission increases with host density (Arneberg et al. 1998a). As arctic fox pups are confined to their natal dens for the 1st part of their lives, their exposure to nematodes may be high. The short life span (3–4 years on average—Audet et al. 2002) and large annual investment in reproduction made by arctic foxes also make these foxes interesting subjects to examine for effects of age on parasite load.

We examined intraspecific variation in parasite loads in arctic foxes to test the immunocompetence handicap hypothesis in a monogamous species. Male and female arctic foxes have no known differences in morphology, diet, or behavior and are socially monogamous with little difference in reproductive investment, suggesting they should have similar parasite loads. If testosterone suppresses the immune system, however, males should have higher parasite loads. Differences in diet between males and females would result in differences in cestode loads, but not in nematode loads. Assuming similar size and diet in subadults and adults, the development of immunity over time would decrease parasite loads in adults. If immunity does not develop over time, adults should have higher parasite loads due to increased exposure. Further, if diet differs between subadults and adults, with adults having more access to cached eggs, then subadults should have higher cestode loads.

Materials and Methods

Study area.—We obtained carcasses of arctic foxes harvested by local trappers from the Churchill registered trapline district on the west coast of Hudson Bay (58°N, 94°W). This region is the southernmost edge of the arctic tundra, near the transitional zone between tundra and boreal forest. The climate of this area is strongly influenced by Hudson Bay, which remains frozen for 7–8 months every year (Rouse 1991). Collared lemmings (*Dicrostonyx richardsonii*) are important prey for arctic foxes year-round; alternative prey availability fluctuates seasonally, as many migratory birds, including lesser snow geese (*Chen caerulescens caerulescens*), Canada geese (*Branta canadensis interior*), and many species of shorebirds, are important prey during summer, and ringed seals (*Pusa hispida*) can serve as important food sources in winter (Roth 2002, 2003). Previous research on this arctic fox population found an even sex ratio and no differences in diet based on sex or age (Roth 2002, 2003).

Endoparasite sampling.—Our sample included foxes harvested in December 2010–February 2011 and December 2011–February 2012. We handled carcasses as approved by the University of Manitoba Animal Care Committee and in accordance with the guidelines for animal care and use published

by the American Society of Mammalogists (Sikes et al. 2011). We determined the endoparasite community through standard necropsy techniques (Munson 2000). We x-rayed canine teeth to distinguish adults from subadults based on the size of the pulp cavity (Grue and Jensen 1976) and sent teeth with small pulp cavities to Matson's Laboratory (Milltown, Montana) for age estimation using counts of cementum annuli (Fancy 1980). Foxes born the previous spring (< 1 year old) were considered subadults because they had reached full adult size but had not yet become reproductive (Roth 2003), but they do reach sexual maturity and can breed their 1st year (Audet et al. 2002). We measured spine length (to 0.5 cm) and mass (to 0.1 kg, Pesola spring scale) and used the residuals of a regression of body mass on spine length as a measure of body condition for each individual (Schulte-Hostedde et al. 2001). We collected intestines, lungs, liver, kidneys, spleen, stomach, and heart from each individual to examine for parasites or other pathology.

Each intestine was split longitudinally and scraped to remove all parasites and then examined under a dissecting microscope to ensure removal of all parasites. We used sedimentation and counting to examine the scraped residue (Eckert 2003). Stomachs were examined and split to look for any parasites. Nematodes found in nodules on the surface of the stomach wall were carefully removed. All the other organs (lungs, liver, kidneys, spleen, stomach, and heart) were also examined and dissected to look for any other macroparasite infections.

All parasites were identified to species (when possible), weighed (dry mass, 0.1 g), and preserved in 70% ethanol. Prior to fixation, the scolex of each cestode was removed and squashed between a cover slip and glass slide. We used scolex squashes to identify species using a compound microscope (based on the number, shape, and size of rostellar hooks following Abuladze 1964, Rausch and Fay 1988, and Loos-Frank 2000). Nematodes were identified following Georgi (1974) and Anderson (1992). *Echinococcus* sp. was identified by characteristic morphology (see Thompson 1995). *E. multilocularis* is a very small cestode that was abundant in infected foxes, but specimens were in poor condition (broken into pieces), making their abundance difficult to quantify, and only rough estimates could be made. *E. multilocularis* intensity was estimated using dilution counts (Thompson et al. 2006). Due to their disproportionately large numbers (some with over 10,000), this species was analyzed separately from *Taenia* spp. intensity and abundance but included in prevalence measurements. We dried and weighed each individual *Taenia* spp. The biomass of *E. multilocularis* was estimated by taking the mean dry mass of 10 individuals and multiplying this mass by the number of individuals estimated in each individual fox. We added the total mass of *E. multilocularis* to the total mass of *Taenia* spp. to obtain the total mass of cestodes in each arctic fox. Parasite taxa were quantified using 3 measurements: prevalence (presence or absence of parasite in a fox), intensity (number of parasites per infected fox, excluding any individual foxes with no parasites), and abundance (number of parasites per fox—Rozsa et al. 2000). The number of parasites represents a count of individual parasites of each taxon examined.

Diet analysis.—We used stable isotope ratios of muscle samples to compare the diets of different sexes and ages of arctic foxes (Roth 2003). Differences in stable isotope ratios of the prey were transferred to the consumer, so the stable isotope ratios of the arctic foxes reflect their diet (Kelly 2000). For example, an arctic fox that has consumed terrestrial food sources will have lower $^{13}C/^{12}C$ ratios compared to those that consume purely marine sources (Chisholm et al. 1982), and foxes that consumed a mixed diet would have an intermediate signature. Nitrogen stable isotope ratios ($^{15}N/^{14}N$) also differ between marine and terrestrial sources and vary geographically and with trophic level (Schoeninger et al. 1983; Roth et al. 2007).

Our samples were collected during December–February and represent the early winter diet, as muscle reflects the 1–2 months prior to death (Hobson and Clark 1992; Dalerum and Angerbjörn 2005). Muscle samples were freeze-dried and powdered, and lipids were removed using a soxhlet apparatus (Roth 2003) due to lipid variation affecting measurements of $\delta^{13}C$ (Rau et al. 1992). Stable isotope ratios for all samples were measured using a continuous flow isotope ratio mass spectrometer at the University of Windsor. Stable isotope values are presented in parts per thousand (‰) relative to Pee Dee Belemnite (carbon) and atmospheric N_2 (nitrogen) standards as follows:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}} - 1 \right) \right] \times 10^3$$

where X is ^{13}C or ^{15}N and R is the ratio of the heavy isotopes to light isotopes (e.g., $^{13}C/^{12}C$ or $^{15}N/^{14}N$).

Statistical analysis.—We compared morphological differences (i.e., body mass and spine length) between males and females as well as between subadults and adults using analysis of variance (ANOVA). We log-transformed body mass and parasite data to improve normality. Differences in parasite intensity and abundance between sex and age were compared using 2-way ANOVA. As none of the log-transformed cestode species data was normally distributed, we used Fisher's exact test to compare differences in individual species prevalence, intensity, and abundance between sex and age classes, due to a low sample size when cestode prevalence was split into cestode species. We used multinomial logistic regression to compare differences in prevalence between sex and age classes. We used multivariate analysis of variance (MANOVA) and 2-way ANOVA to compare differences in stable isotope ratios between sexes and ages to detect differences in diet (Hummel and Sligo 1971). Cestode abundance followed a negative binomial distribution, so negative binomial regression was used to examine relationships between individual arctic fox diet and cestode abundance. Transformed nematode abundance was normally distributed, so we used linear regression to examine relationships between individual arctic fox diet and nematode abundance. We performed statistical analyses in JMP 10 (SAS Institute Inc. 2012) and R statistical software (R Development Core Team 2012).

RESULTS

We necropsied 3 arctic foxes in 2011 and 55 foxes in 2012, but 6 arctic foxes from 2012 were excluded from analysis because the gastrointestinal tracts were damaged by scavengers. The sex ratio (31 males:21 females) was slightly male biased but within published ranges (Macpherson 1969), and the greater number of subadults ($n = 32$) than adults ($n = 20$) was consistent with previous studies of age structure (Macpherson 1969). Condition residuals ranged from −7.8 to 6.1, which is a larger range than previously documented (Prestrud and Pond 2003), suggesting we obtained a range of animals from very poor to great condition with no bias toward trapping starving foxes. The similarity between the age structure and sex ratio of our sample to previously published studies and the large range in body condition suggests a lack of trapper bias toward any 1 sex, age class, or condition type. Males and females did not differ in spine length ($\bar{X} \pm SD$—males: 410 ± 4.8 mm and females: 405 ± 5.9 mm; ANOVA, $F_{1,51} = 0.94$, $P = 0.34$), body mass (males: 2.6 ± 0.7 kg and females: 2.5 ± 1.1 kg; $F_{1,51} = 1.01$, $P = 0.32$), or body condition (males: 0.20 ± 0.40 and females: -0.09 ± 0.49; $F_{1,50} = 0.15$, $P = 0.69$). Likewise, subadults and adults did not differ in spine length (subadults: 407 ± 5.3 mm and adults: 410 ± 4.8 mm; $F_{1,50} = 0.23$, $P = 0.64$), body mass (subadults: 2.5 ± 0.1 kg and adults: 2.6 ± 0.1 kg; $F_{1,50} = 0.042$, $P = 0.84$), or body condition (subadults: -0.09 ± 0.49 and adults: 0.20 ± 0.40; $F_{1,50} = 0.17$, $P = 0.68$). All adult arctic foxes in our sample were 1 year old.

We found 4 species of cestodes; *Taenia polyacantha arctica* was the most prevalent (76.9%), with *T. crassiceps* (29.0%), *E. multilocularis* (19.2%), and *T. multiceps* (17.3%) also present (Fig. 1; see Supporting Information S1). Most individuals only hosted 1 species of cestode (53.8%), with 2 species in some (34.6%), and a small number having 3 or more cestode species (7.7%). Ascarid nematodes were present in all arctic foxes (100% prevalence). A spirurid nematode, *Spirocerca lupi*, was found in cysts on the external wall of the stomach in 55.8% of the arctic foxes. One 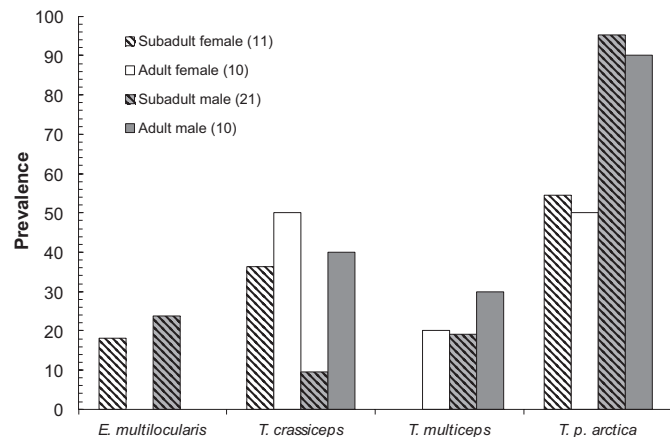cyst was found in the mesentery near the stomach. No macroparasites were found in the lungs, livers, kidneys, spleens, or hearts.

Cestode abundance was higher in males than in females (2-way ANOVA, intensity: $F_{1,46} = 3.65$, $P = 0.062$; abundance: $F_{1,48} = 6.34$, $P = 0.015$; Fig. 2) but did not differ based on age (intensity: $F_{1,46} = 0.037$, $P = 0.85$; abundance: $F_{1,48} = 0.061$, $P = 0.81$; Fig. 2), with no interaction effect (intensity: $F_{3,46} = 0.661$, $P = 0.420$; abundance: $F_{3,48} = 0.244$, $P = 0.473$; Fig. 2). Cestode prevalence did not differ between sex and age (multinomial logistic regression: whole model $R^2 = 0.22$, $\chi^2 = 7.7 \times 10^{-7}$, $P = 1.0$; sex: $\chi^2 = 3.64$, $P = 0.057$; age: $\chi^2 = 0.0050$, $P = 0.94$). *T. polyacantha arctica* was more prevalent in males (Fisher's exact test, $P = 0.008$), but *T. crassiceps* tended to be more prevalent in females ($P = 0.0645$). Prevalence of *T. multiceps* (Fisher's exact test, $P = 0.29$) did not differ in males and females (Fig. 1). *T. crassiceps* was found more often in adults than subadults (Fisher's exact test, $P = 0.044$; Fig. 1). *E. multilocularis* was only present in subadults (Fig. 1; see Supporting Information S1).

Subadults had more gastrointestinal nematodes than adults (intensity and abundance: $F_{1,48} = 4.93$, $P = 0.031$; Fig. 2), but males and females did not differ (intensity and abundance: $F_{1,48} = 0.11$, $P = 0.74$; Fig. 2) and no interaction was present (intensity and abundance: $F_{1,48} = 0.59$, $P = 0.45$). *S. lupi* tended
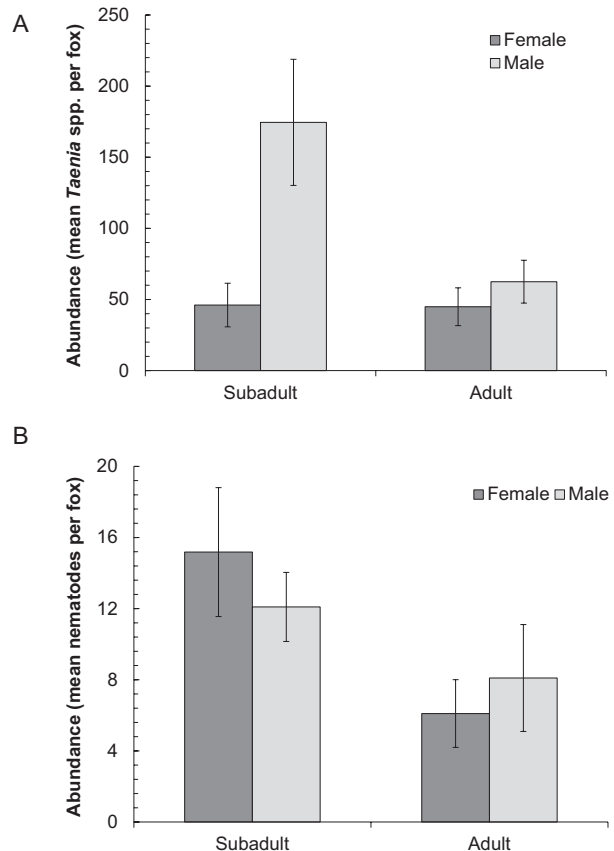

Fig. 2.—Abundance ($\bar{X} \pm SE$) of A) *Taenia* spp. cestodes and B) nematodes in arctic foxes (*Vulpes lagopus*) based on sex and age (subadult females: $n = 11$, adult females: $n = 10$, subadult males: $n = 21$, and adult males: $n = 10$). Foxes were collected near Churchill, Manitoba, in December 2010–February 2011 and December 2011–February 2012.

Fig. 1.—Prevalence (percentage of foxes infected) of cestode species (*Echinococcus multilocularis*, *Taenia crassiceps*, *Taenia multiceps*, and *Taenia polyacantha arctica*) in arctic foxes (*Vulpes lagopus*) from Churchill, Manitoba, in winter 2011 and 2012. Sample sizes listed in the legend.

to be more prevalent in adults (Fisher's exact test, $P = 0.088$), although there was no sex difference ($P = 0.67$), but no difference in abundance was observed between sexes and age (sex: Wilcoxon Rank Sum Test, $Z = -0.12$, $P = 0.91$; age: $Z = 0.81$, $P = 0.42$), nor in intensity (sex: $Z = -0.49$, $P = 0.62$; age: $Z = -1.4$, $P = 0.16$) of *S. lupi*.

Arctic fox males and females differed in muscle stable isotope ratios (MANOVA, $F_{2,47} = 4.03$, $P = 0.042$) and there was an interaction between sex and age ($F_{2,47} = 5.12$, $P = 0.0097$) although no main effect of age was detected ($F_{2,47} = 0.41$, $P = 0.67$). Females had higher $\delta^{13}C$ values ($F_{1,48} = 4.48$, $P = 0.040$; Fig. 3), and although there was no main effect of age on $\delta^{13}C$ ($F_{1,48} = 0.47$, $P = 0.50$), we found a significant interaction between sex and age ($F_{1,48} = 7.0$, $P = 0.011$). Females also had higher $\delta^{15}N$ values ($F_{1,48} = 7.6$, $P = 0.0082$; Fig. 3), but we found no effect of age ($F_{1,48} = 0.75$, $P = 0.39$) nor an interaction between sex and age ($F_{1,48} = 0.051$, $P = 0.82$).

Taenia spp. abundance was negatively related to $\delta^{15}N$ from arctic fox muscle (negative binomial regression, $z = -2.34$, $P = 0.020$; Fig. 4), with a significant interaction between $\delta^{15}N$ and $\delta^{13}C$ ($z = -2.44$, $P = 0.015$) but no main effect of $\delta^{13}C$ ($z = 0.62$, $P = 0.14$). Overall cestode biomass was not related to either $\delta^{15}N$ (negative binomial regression, $z = -0.93$, $P = 0.35$) or $\delta^{13}C$ ($z = 1.54$, $P = 0.120$) from arctic fox muscle. Nematode abundance was not related to $\delta^{13}C$ (linear regression, $R^2 = 0.030$, $F_{1,50} = 1.58$, $P = 0.21$) nor $\delta^{15}N$ values ($R^2 = 0.0019$, $F_{1,50} = 0.094$, $P = 0.76$).

DISCUSSION

Sex-biased parasitism was present in monogamous arctic foxes and these differences were linked to variation in the diet between males and females. More specifically, cestodes were more abundant in male arctic foxes, particularly subadult males, although nematode loads did not differ between sexes. As male and female arctic foxes have no differences in home range size, morphology, or body condition, the sex difference in parasite load is likely due to either differences in diet, which was not expected, or physiology, as proposed by the immunocompetence handicap hypothesis.

The immunocompetence handicap hypothesis suggests that the immune system is suppressed by testosterone, increasing the individuals' vulnerability to parasitic infection or infestation (Zuk 1990; Zuk and McKean 1996). Although male arctic foxes had more cestodes than females, we found no differences in the presence of nematode parasites between males and females. If differences in immunity were causing a male bias in vulnerability to parasite infection, there should be differences in both cestodes and nematodes (Hepworth et al. 2010; Jacobs and Zuk 2012). Testosterone has been shown to inhibit multiple parts of the immune response and should affect both nematodes and cestodes (Hepworth et al. 2010; Jacobs and Zuk 2012). The lack of a consistent relationship between parasite loads and sex in our study strongly suggests that the difference in parasite loads between males and females was due to factors other than hormones, like diet.

Differences in diet between male and female arctic foxes were reflected in their stable isotope ratios, with consistently higher $\delta^{15}N$ values in females. As small mammals in our study area have much lower $\delta^{15}N$ values than birds (McDonald 2013), these results suggest males consumed more small mammals, which are important intermediate hosts for cestodes (Loos-Frank 2000). Thus, a diet with higher proportion of these prey should expose an arctic fox to more larval stages and would explain higher cestode intensity and abundance (Meijer et al. 2011). Differences in diet should only affect cestodes, not ascarid nematodes. Further, stable isotope ratios were related to *Taenia* spp. abundance, which increased with decreasing $\delta^{15}N$ values, suggesting a diet high in small mammals was linked to a higher *Taenia* spp. abundance. Although overall cestode biomass was not related to $\delta^{15}N$ or $\delta^{13}C$, competition in the gastrointestinal tract affects cestode biomass (Holmes 1961), and individual cestode biomass shifts over
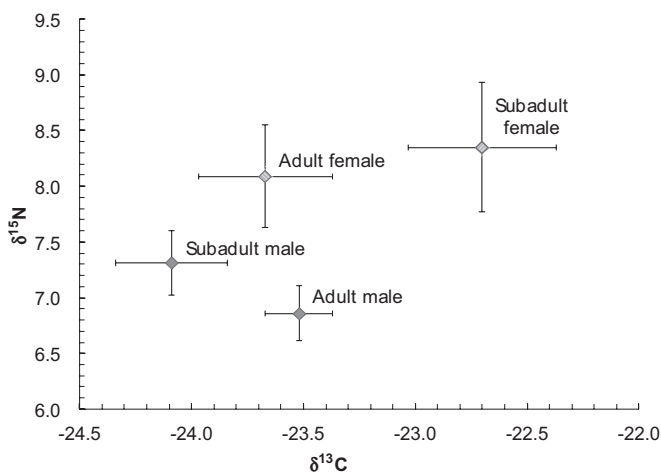

Fig. 3.—Stable isotope ratios ($\overline{X} \pm SE$) of arctic fox (*Vulpes lagopus*) muscle tissue, separated by sex and age, from Churchill, Manitoba, Canada. Arctic foxes were sampled in December 2010–February 2011 and December 2011–February 2012.
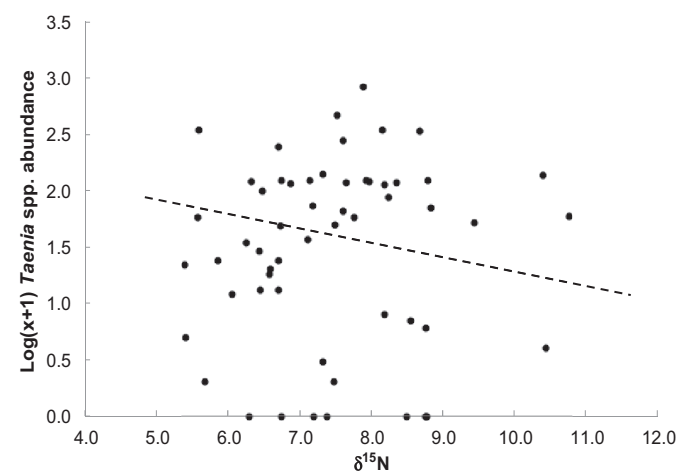

Fig. 4.—Relationship between *Taenia* spp. abundance (log $x + 1$ number of cestodes per fox) and $\delta^{15}N$ value of muscle from arctic foxes (*Vulpes lagopus*; $n = 52$) harvested in 2011 and 2012 in Churchill, Manitoba, Canada. Dashed line represents direction of relationship.

time (e.g., growth) leading to potential disconnects between cestode abundance and biomass. Higher mean δ¹⁵N values in females, despite variation between subadults and adults, support the idea that males' diets included more small mammals than females'. This observed difference in diet is counter to our expectation that there should be no difference in diet between males and females. The relationship between *Taenia* spp. and diet further suggests that diet, not compromised immunity, leads to the differences in cestodes between male and female arctic foxes.

Increased availability of new naive hosts during the breeding season may contribute to parasite community patterns (Lutermann et al. 2012). Consistent with this idea, subadult arctic foxes carried more nematodes than adults although all our arctic foxes were infected with nematodes. As arctic foxes have large litters and pups are confined to the den for the 1st few months of their lives, the high densities of pups feeding at dens where feces concentrate may explain this higher nematode abundance in subadults (Macpherson 1969). Previous studies found increased nematode prevalence in younger animals (Saeed and Kapel 2006; Stien et al. 2010), but all our foxes were infected with nematodes. As *S. lupi* is a trophically transmitted nematode, its higher prevalence in adults is likely due to continual exposure over time.

The cestode *E. multilocularis* was prevalent in subadults but absent in adults, suggesting the development of acquired immunity (Hofer et al. 2000). The development of immunity is controversial, as many studies have shown a lack of acquired immunity to *E. multilocularis* (Budke et al. 2005; Stien et al. 2010). As we found no differences in diet that would explain this difference in *E. multilocularis* prevalence, our results strongly support the idea that arctic foxes acquire immunity over time.

Further, the prevalence of *E. multilocularis* is low in our area in comparison with previous studies of other regions in Canada (Gesy 2012). Although increased interactions with sympatric red fox (*Vulpes vulpes*) could increase prevalence of *E. multilocularis* in this region, we did not find high prevalence in arctic foxes, and *E. multilocularis* is completely absent from red foxes in this area (Friesen 2013). As *E. multilocularis* is a parasite of human health concern, with the ability to cause death in human hosts (Romig et al. 2006), its low prevalence is a positive for the local community, particularly the trappers who interact directly with these foxes.

Taenia polyacantha arctica was the most prevalent cestode found and was more prevalent in males, likely leading to the overall male bias in cestodes. Previous research found other *Taenia* species to be more dominant in arctic foxes, specifically *T. crassiceps* in the Northwest Territories of Canada (Eaton and Secord 1979) and *T. ovis krabbei* in Greenland (Kapel and Nansen 1996). Kapel and Nansen (1996) demonstrated that geographic region is an important factor in species composition of helminths (cestodes, nematodes, and trematodes), suggesting that these differences are likely due to disparities in the prevalence of *Taenia* species between different regions.

Intraspecific variation in parasite loads in this arctic fox population can best be explained by diet and feeding behavior, which creates differential exposure between different ages and sexes. Previous studies have not documented differences in the diet of male and female arctic foxes, so the explanation for this difference will need further study. Social monogamy apparently reduced sex differences in immunity predicted by the immunocompetence handicap hypothesis, as males and females differed in cestodes but not nematodes. These results suggest that males in other monogamous species also may not suffer compromised immunity to the same extent as seen in species with strong sexual selection.

Arctic fox populations are cyclic, with periods of high and low abundance (Macpherson 1969), reflecting cyclic population dynamics exhibited by lemmings, which affect the use of alternative food sources by foxes (Chesemore 1968; Roth 2002). Lemming population cycles are dampening, however, likely due to changing snow conditions related to climate change, reducing an important intermediate host for both *T. crassiceps* and *T. polyacantha arctica* (Loos-Frank 2000; Ims et al. 2008). Changes in age structure and prey availability over time with population cyclicity will likely affect the population's parasites. As subadult foxes seem to be important hosts for nematodes, lower pup survival due to declining lemming populations could impact parasite populations over time, decreasing nematode loads in the population. Furthermore, reduced arctic fox densities may lower parasite prevalence throughout the region. Undoubtedly, further studies to compare parasite communities in arctic fox at periods of high abundance and low abundance would be useful. Although current evidence has not demonstrated a relationship between body condition and parasite load in these foxes (Friesen 2013), further research into the impact of high parasite loads, particularly nematodes, will help predict the effects of changing prey availability and resulting parasite densities on the population dynamics of this arctic predator.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Prevalence, intensity, and abundance of cestode species and nematode groups in arctic foxes (*Vulpes lagopus*) from Churchill, Manitoba, Canada.

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