

PATTERNS OF GASTROINTESTINAL PARASITISM AMONG FIVE SYMPATRIC PRAIRIE CARNIVORES: ARE MALES RESERVOIRS?

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ABSTRACT: Male vertebrates are believed to be disproportionately vulnerable to parasites, but empirical support for this contention is mixed. We tested the hypothesis of higher levels of parasitism in males with the use of counts of gastrointestinal helminths in 5 sympatric mammalian carnivores (American badgers, coyotes, red foxes, raccoons, striped skunks) from central Saskatchewan. Parasite burdens for females and males of each host species were compared with the use of prevalence (percentage of hosts infected), intensity (parasites per infected host), and overdispersion (proportion of heavily infected hosts that were male). Of 30 comparisons (13 each for prevalence and intensity, 4 for overdispersion), male bias was detected 8 times (27%), whereas female bias was detected only once (3%), adding some support to the notion that male mammals are more susceptible to parasitism. However, most of the statistical comparisons we undertook revealed no sexual bias ($n = 21$, 70%), suggesting that differential patterns of infection are not ubiquitous in mammals. Moreover, when detected, the magnitude and direction of bias varied among host species, helminth species, and metrics of infection. We conclude that sympatric and ecologically similar mammal species will not always share the tendency for males to be more susceptible to parasitism, and that studies incorporating multiple parasites and metrics of infection are more likely to detect sex bias.

Parasites tend to aggregate in particular hosts within species across a variety of taxa (Shaw and Dobson, 1995; Wilson et al., 1996; Shaw et al., 1998). Skewed parasite distributions within host populations are known to derive from individual differences in exposure and susceptibility (Wilson et al., 2002), but host traits consistently associated with heightened contact and vulnerability have been difficult to identify (Perkins et al., 2003). These traits are of wide interest, for parasite skew has important implications for the dynamics and stability of host populations, the responsiveness of host populations to parasite control measures, and the mechanisms of parasite transmission (Anderson and May, 1985; Bundy, 1988; Perkins et al., 2003).

In mammals, 1 trait often associated with vulnerability to parasitism is host sex (Poulin, 1996). Specifically, males have been hypothesized to be more prone to infection than females because: (1) their comparably large size and tendency to roam widely may render them easier and more accessible targets (Poulin, 1996; Arneberg, 2002; Moore and Wilson, 2002; Wilson et al., 2002), (2) testosterone allegedly suppresses immune function (Folstad and Karter, 1992), and/or (3) they should be expected to invest heavily in short-term mating success rather than longevity (Rolf, 2002). This hypothesis has received empirical support (Poulin, 1996; Schalk and Forbes, 1997). However, not all analyses have documented a male bias (e.g., Stien et al., 2002), and observed levels of bias often have been small (typically <5%), raising questions about biological significance (Wilson et al., 2002; Skorpington and Jensen, 2004). Thus, the notion that males in many mammal populations serve as reservoirs for parasites, i.e., tend to be more heavily burdened, remains contentious and, given that relevant data are scarce, merits further consideration.

We explored patterns of gastrointestinal parasitism in 5 sympatric prairie carnivore species, i.e., American badgers (*Taxidea*

taxus), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*). For each carnivore, helminth parasite communities in both sexes were quantified and compared to test the generality of the hypothesis that male mammals are more susceptible to parasitism than their female counterparts. In the absence of overall gender differences in parasite burdens, certain members of 1 sex may nevertheless act as reservoirs for parasites; thus, variance with respect to susceptibility may be greater in 1 sex than the other even if mean levels of infection are equivalent (Perkins et al., 2003; Ferrari et al., 2004; Skorpington and Jensen, 2004). Therefore, we addressed both mean parasite loads for males and females and the tendency of heavily infected individuals to belong to a particular sex. Importantly, particular parasites may possess ecological or life history attributes that typically lead them to burden (or preclude them from burdening) 1 sex more heavily irrespective of gender-specific patterns of susceptibility in their hosts (Reimchen and Nosil, 2001). By extension, such parasites should be expected to overburden the same sex (or to burden the sexes equally) in all potential host species that are ecologically similar, i.e., that occupy similar niches, in a given environment (Altizer et al., 2003). Therefore, we also hypothesized that, even if the male carnivores in our system are not inherently more vulnerable to parasitism, specific parasites sharing multiple host species should nevertheless manifest consistent distribution patterns, e.g., a consistent tendency to aggregate in males.

MATERIALS AND METHODS

Collection of specimens

Between April and June of 2000 and 2001, carnivores were collected roughly 75 km southwest of Weyburn, Saskatchewan, Canada (49°24'N, 104°39'W; see Azevedo et al., 2006, for study-area details) as part of a predator control program initiated by the Delta Waterfowl Foundation. Importantly, the carnivore species sampled are characterized by considerable dietary (see Azevedo et al., 2006) and spatial overlap (S. Larivière, unpubl. obs.) and are not known to exhibit marked gender differences with respect to diet (F. Azevedo, unpubl. obs.) in the study area. Thus, opportunities for shared parasites to infect both sexes of all of their hosts presumably were roughly comparable. Carnivores were harvested according to the protocol described by Azevedo et al. (2006); all predator removal procedures conformed to standard protocols and were approved by the University of Saskatchewan Animal Care Com-

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mittee (UCACS protocol No. 20010055), and no animals were killed specifically for the purposes of this investigation. The age (in years; based on patterns of tooth wear [Spinage, 1973]) and sex of each carnivore were determined following capture; stomachs and intestinal tracts were then extracted, massed, bagged, and frozen prior to laboratory analysis. Gravid females were excluded from analysis.

Laboratory analysis

Viscera from each carnivore sampled were thawed in the laboratory prior to examination. The contents and inner membrane of each stomach were flushed with water through sieves (3.35–0.60-mm mesh); intestinal tracts were sectioned (duodenum, ileum, jejunum), opened longitudinally, and flushed into sieves as well. Helminth parasites recovered in this manner were enumerated and identified to genus and, when possible, species.

Statistical analysis

For each carnivore examined, we calculated 2 sex-specific metrics of parasite infection, prevalence, and intensity. Prevalence was expressed as a binomial (infected or not), and intensity was expressed as the mean number of parasites per infected host (Poulin, 1996). These metrics were calculated with the use of both counts of individual parasite species, i.e., species-specific numerical abundance, and counts with all parasite species pooled, i.e., total numerical abundance (George-Nascimento et al., 2004). To address the possibility that cases of extreme infection in each carnivore species were confined to a particular sex, we also generated a third metric, overdispersion, which was expressed as the proportion of heavily infected hosts, i.e., those with intensity values falling within the top 20% of the distribution—parasites considered separately and pooled—that were male (Perkins et al., 2003; Ferrari et al., 2004; Skorpung and Jensen, 2004).

Binary measures of helminth prevalence for females and males of each carnivore species were evaluated against the null expectation of equality using logistic regression. Age (yr) and mass (g, stomach + intestinal tract) were included in the models as continuous covariates, because both variables may affect whether, and the degree to which, particular hosts are parasitized, e.g., age (Hudson and Dobson, 1995; Galvani, 2005) and mass (Poulin, 1997; Arneberg, 2002; George-Nascimento et al., 2004). Note, however, that age was not included as a covariate for coyotes, as information pertaining to this variable was not available. For all of the carnivores, neither age (all $P > 0.15$) nor gastrointestinal mass (all $P > 0.21$) differed between females and males. Although our statistical approach involved the use of multiple comparisons in some cases, i.e., when female and male prevalence values were compared across several parasite species, we elected not to apply Bonferroni corrections to avoid inflating the likelihood of Type II error (Perneger, 1998). Instead, to evaluate the possibility that significant results of particular tests were artifacts of multiple comparison, we compared each significant full model ($\alpha = 0.05$) to a simpler model based solely on age and mass using Akaike's Information Criteria (Burnham and Anderson, 1998); differences in AIC > 2 signified that the addition of the sex variable resulted in a substantially improved fit. Analyses of parasite distributions using generalized linear modeling approaches may produce spurious results in cases where sample sizes are particularly low (Wilson et al., 1996). Thus, predictive models of prevalence for particular parasite species were only built if both sexes were represented by at least 4 individuals (11 of 19 possible comparisons were censored). Measures of helminth parasite intensity were evaluated in similar fashion, save that predictive generalized linear models considered only infected individuals and a negative binomial error distribution served as the basis for statistical inference (Wilson et al., 1996; Wilson and Grenfell, 1997; Shaw et al., 1998; Dobson, 2002). Where reported, measures of intensity differing according to sex are accompanied by medians. Importantly, for both the prevalence and intensity metrics, effect sizes (differences in means) across the 5 carnivore species were not correlated with sample size (prevalence: linear regression, $t = 0.72$, $P = 0.49$; intensity: $t = -0.89$, $P = 0.39$; note that only the 13 comparisons meeting the minimum sample size criterion were assessed in both cases), minimizing the possibility of funnel effects (Palmer, 1999). Measures of parasite overdispersion were evaluated against the null expectation of equality across the sexes with the use of chi-square tests. Expected values for males were generated based on the number of females

and males being compared; to minimize bias, comparisons involving expected values < 5 for either sex were censored from the analysis (Zar, 1999).

RESULTS

Summary

Overall, we examined the helminth parasite communities occupying the gastrointestinal tracts of 332 carnivores. In total, 156 carnivores were harvested in 2000, whereas 176 were collected in 2001. Thirteen different helminth species (3 cestodes, 8 nematodes, 2 trematodes) were identified; 2 could only be assigned to genera. Two parasites (*Physaloptera maxillaris*, *Taenia crassiceps*) were found in 2 host species, and 2 others (*Physaloptera rara*, *Toxascaris leonina*) inhabited 3 hosts (Table I).

Badgers

We examined the gastrointestinal tracts of 48 American badgers, 18 of which were female and 30 of which were male. Five helminth species were recovered: 1 cestode (*Taenia taxidensis*), 3 nematodes (*Baylisascaris* sp., *Molinuev* sp., *Physaloptera maxillaris*), and 1 trematode (*Euparyphium melis*). All tracts examined contained parasites (range: 3–1,341), meaning that females and males were equally likely to be parasitized by at least 1 helminth species. Prevalence measures for particular helminth parasites ranged from 2 to 96%, being greatest for *P. maxillaris*; the tendency of individuals to be parasitized never differed between females and males after accounting for age and gastrointestinal mass (2 cases, all P for sex variable in models ≥ 0.13 ; Table I). Among infected badgers, intensity values for the 5 helminths ranged from 1 to 1,341, again being highest for *P. maxillaris*. With all parasite species combined, females tended to be more heavily burdened than males (Fig. 1a), but this disparity was not significant after accounting for age and mass ($\beta = -0.36 \pm 0.65$ [95% CI]; $P = 0.209$). Where comparisons were possible (2 of 5 parasites), female and male burdens were statistically equivalent for 1 helminth species (*P. maxillaris*, $\beta = -0.50 \pm 0.67$, $P = 0.257$), while male burdens were significantly higher for the other (*T. taxidensis*: females = 1.5, males = 3.0; $\beta = 1.52 \pm 1.40$, $P = 0.05$) (Fig. 1c, d). With all helminth parasites combined, heavily infected badgers ($n = 10$) were equally likely to be male (5) and female (5) ($P = 1$); individual helminth species could not be analyzed in this fashion.

Coyotes

In exploring the gastrointestinal tracts of 25 coyotes (11 females, 14 males), we recovered 4 parasite species: 1 cestode (*T. crassiceps*) and 3 nematodes (*P. rara*, *T. leonina*, *Uncinaria stenocephala*). All tracts contained parasites (range: 2–102); prevalence measures for particular helminth species ranged from 12 to 100%, being highest for *T. leonina*. Where comparison was possible (1 case), the tendency of females and males to be parasitized by particular helminths did not differ ($P = 0.39$; Table I). Among infected coyotes, intensity measures for particular parasites ranged from 1 to 101, being highest for *U. stenocephala*. With parasites pooled, the extent of infection in males (27.0) exceeded that in females (6.0) significantly ($\beta = -0.98 \pm 0.74$, $P = 0.015$; Fig. 2a), and the full model was superior to a simpler competitor incorporating only

TABLE I. Gastrointestinal parasite prevalence, i.e., the number of hosts infected out of the total sample (in parentheses), and species richness for 5 sympatric prairie carnivores. Note that, for each carnivore species, parasite information is presented for males and females separately, and that each parasite has been designated as a cestode,¹ nematode,² or trematode.³ Sex-specific differences in prevalence deviating significantly from parity after accounting for subject age and gastrointestinal mass (identified with the use of generalized linear models with binomial error distributions) are presented in bold; statistical comparisons were undertaken only when both sexes were represented by at least 4 individuals.

Parasite	Badgers		Coyotes		Foxes		Raccoons		Skunks	
	M (30)	F (18)	M (14)	F (11)	M (23)	F (16)	M (35)	F (12)	M (117)	F (55)
<i>Alaria arisaemoides</i> ³					1	0				
<i>Atrioaenia procyonis</i> ¹							6	0		
<i>Baylisascaris columnaris</i> ²									57	8
<i>Baylisascaris procyonis</i> ²							6	1		
<i>Baylisascaris</i> sp. ²	3	5								
<i>Euparyphium melis</i> ³	1	0								
<i>Molineus</i> sp. ²	3	0								
<i>Physaloptera maxillaris</i> ²	29	17							113	54
<i>Physaloptera rara</i> ²			2	1	6	6	18	7		
<i>Taenia crassiceps</i> ¹			3	2	5	2				
<i>Taenia taxidensis</i> ¹	7	4								
<i>Toxascaris leonina</i> ²			14	11	22	14	7	2		
<i>Uncinaria stenocephala</i> ²			6	1						
All	30	18	14	11	23	16	30	10	115	55

age and mass (Δ AIC differential = 3.73). Where comparison was possible (1 case), male and female parasite burdens did not differ significantly (*T. leonina*: $\beta = -0.56 \pm 0.78$, $P = 0.09$; Fig. 2c). The dispersion parameter could not be calculated for coyotes, as too few individuals were examined.

Foxes

The gastrointestinal tracts of 39 red foxes were explored (16 females, 23 males). Four parasites were recovered: 1 cestode (*T. crassiceps*), 2 nematodes (*P. rara*, *T. leonina*), and 1 trematode (*Alaria arisaemoides*). Every tract was parasitized (range: 3–336). Prevalence for individual helminth species ranged from 3 to 92%, being highest for *T. leonina*, and never differed between females and males (2 comparisons, all $P > 0.46$; Table I). Among parasitized individuals, infection intensity for specific parasites ranged from 1 to 312, again being highest for *T. leonina*. With helminths pooled, infection intensity in females was qualitatively higher than in males (Fig. 3a), but this difference was only marginally significant ($\beta = 0.93 \pm 1.23$, $P = 0.065$), and support for the full model over a simpler version incorporating only age and mass was not strong (Δ AIC = 1.40). Where species-specific comparisons were possible (2 of 4 cases), females were more heavily parasitized by *T. leonina* (females = 18.5, males = 15.0; $\beta = 0.81 \pm 0.59$, $P = 0.009$; Δ AIC = 4.82; Fig. 3c), whereas sex differences were not detected for *P. rara* ($\beta = 1.32 \pm 1.67$, $P = 0.128$; Fig. 3b). Patterns of overdispersion were not evaluated because too few foxes were collected.

Raccoons

In examining 47 gastrointestinal tracts from raccoons (12 females, 35 males), we encountered 4 parasites: 1 cestode (*Atrioaenia procyonis*) and 3 nematodes (*Baylisascaris procyonis*, *P. rara*, *T. leonina*). Of the tracts examined, 85% contained helminths (range: 1–227); females and males were equally likely to be parasitized ($P = 0.823$). Prevalence for particular hel-

minth species fell between 13 and 53%, being highest for *P. rara*, and never differed between females and males (1 comparison, $P = 0.170$; Table I). Among infected individuals, infection intensity for specific parasites ranged from 1 to 227, being greatest for *T. leonina*. With parasites combined, male burdens (3.0) significantly exceeded those of females (1.0) ($\beta = -2.21 \pm 1.15$, $P = 0.002$; Fig. 4a); support for the full model

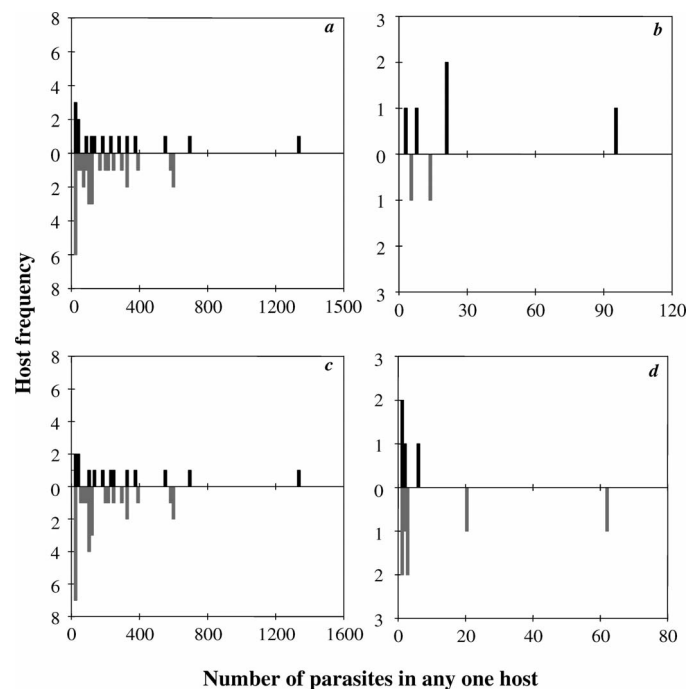


FIGURE 1. Frequency distributions of gastrointestinal parasites recovered from 48 American badgers: (a) all parasites, (b) *Baylisascaris* sp., (c) *Physaloptera maxillaris*, (d) *Taenia taxidensis*. Parasite distributions in females ($n = 18$) appear in black; those for males ($n = 30$) are shaded gray.

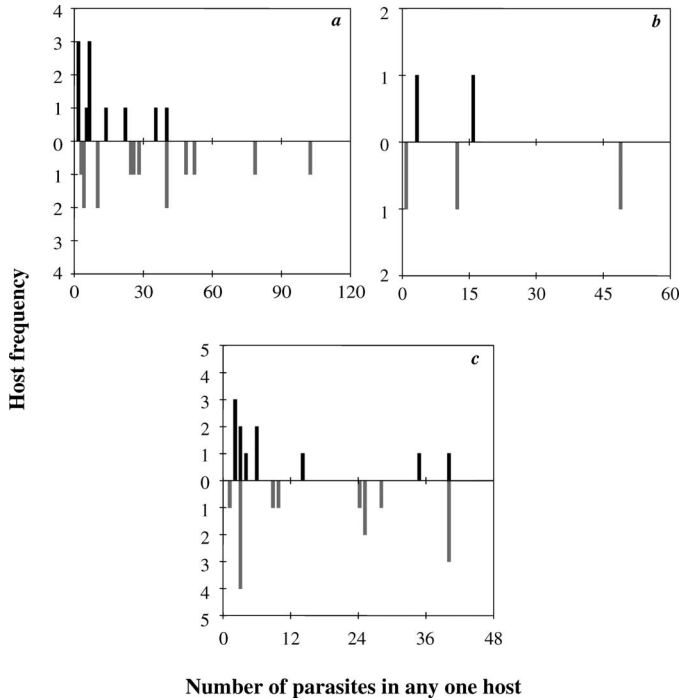


FIGURE 2. Frequency distributions of gastrointestinal parasites recovered from 25 coyotes: (a) all parasites, (b) *Taenia crassiceps*, (c) *Toxascaris leonina*. Parasite distributions in females ($n = 11$) appear in black; those for males ($n = 14$) are shaded gray.

incorporating sex was strong ($\Delta AIC = 7.72$). For the parasite that could be analyzed independently (*P. rara*), female and male burdens did not differ significantly ($\beta = 0.41 \pm 0.64$, $P = 0.211$; Fig. 4b). The dispersion parameter was not analyzed due to low sample size.

Skunks

We examined the gastrointestinal tracts of 173 skunks (58 females, 115 males). Two nematodes were encountered, i.e., *B. columnaris* and *P. maxillaris*. Parasites (range: 1–3,247) occurred in 99% of the tracts explored, meaning that females and males were equally likely to be infected. Prevalence values for the 2 helminth species were 62% (*B. columnaris*) and 97% (*P. maxillaris*) (Table I). Females and males were equally likely to be infected by *P. maxillaris* ($P = 0.76$), whereas males were more likely to play host to *B. columnaris* ($\beta = -1.39 \pm 0.76$, $P < 0.001$); support for the full model in the latter case was strong ($\Delta AIC = 12.6$). Among infected individuals, infection intensity for particular parasites ranged from 1 to 3,243, being greatest for *P. maxillaris*. With helminths pooled, female and male burdens did not differ ($\beta = -0.26 \pm 0.34$, $P = 0.118$; Fig. 5a). When analyzed on a species-specific basis, male burdens exceeded those of females for *B. columnaris* (females = 3.0, males = 6.0; $\beta = -1.32 \pm 0.78$, $P = 0.001$, $\Delta AIC = 6.65$; Fig. 5b), whereas no difference was detected for *P. maxillaris* ($\beta = -0.23 \pm 0.35$, $P = 0.729$; Fig. 5c). With all helminths combined, heavily infected skunks ($n = 35$) were more likely to be male (26) than female (9) ($P = 0.004$); a similar trend was detected for each parasite species (*B. columnaris*: n

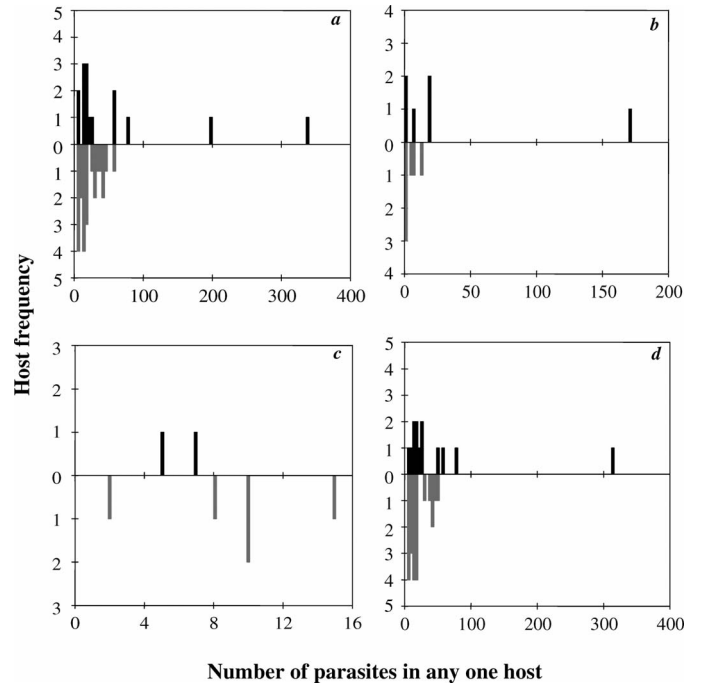


FIGURE 3. Frequency distributions of gastrointestinal parasites recovered from 39 red foxes: (a) all parasites, (b) *Physaloptera rara*, (c) *Taenia crassiceps*, (d) *Toxascaris leonina*. Parasite distributions in females ($n = 16$) appear in black; those for males ($n = 23$) are shaded gray.

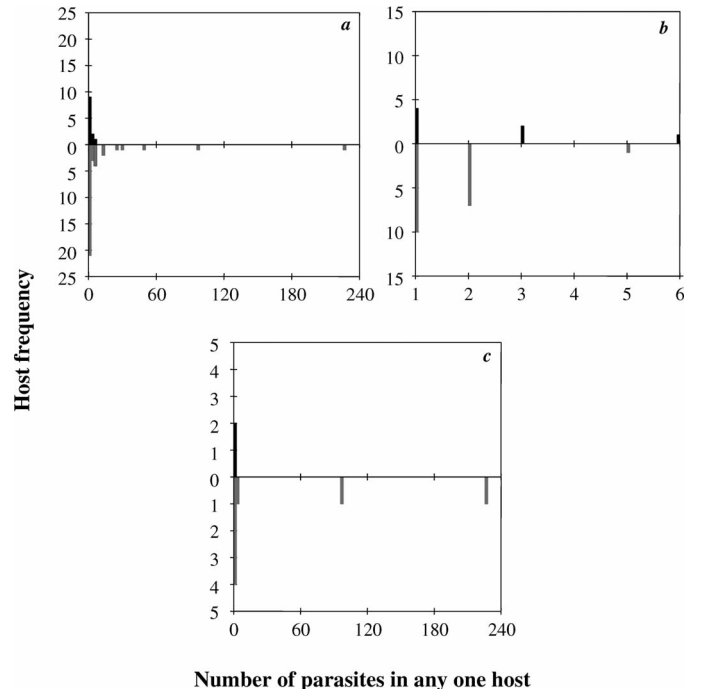


FIGURE 4. Frequency distributions of gastrointestinal parasites recovered from 47 raccoons: (a) all parasites, (b) *Physaloptera rara*, (c) *Toxascaris leonina*. Parasite distributions in females ($n = 12$) appear in black; those for males ($n = 35$) are shaded gray.

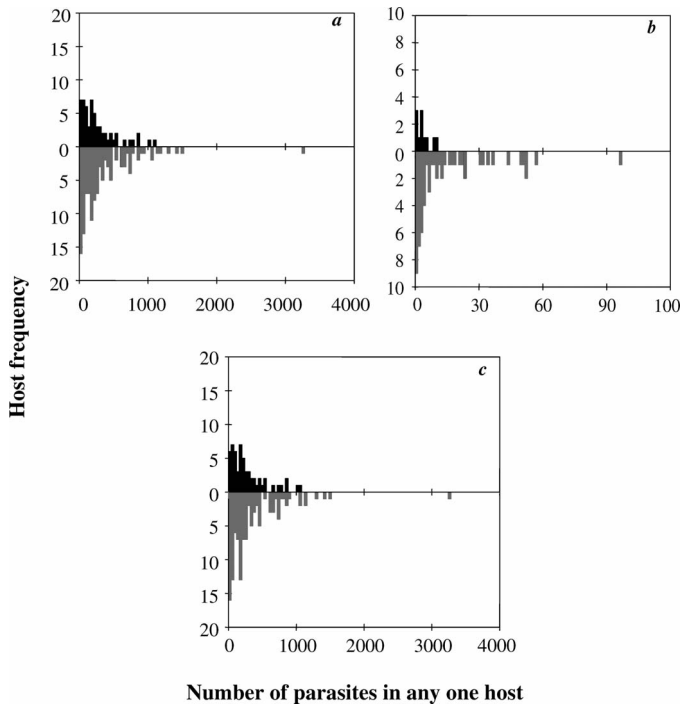


FIGURE 5. Frequency distributions of gastrointestinal parasites recovered from 173 striped skunks: (a) all parasites, (b) *Baylisascaris columnaris*, (c) *Physaloptera maxillaris*. Parasite distributions in females ($n = 58$) appear in black; those for males ($n = 115$) are shaded gray.

$= 14$, 0 females, 14 males, $P < 0.001$; *P. maxillaris*: $n = 34$, 9 females, 25 males, $P = 0.006$).

Shared parasites

Of the 4 parasites that infected multiple host species, only 1 manifested a consistent distribution pattern in females and males; thus, *P. rara* showed no bias in foxes and raccoons (note that metrics of infection for this species could not be assessed statistically in coyotes). Two parasites differed in their tendency to infect males among shared host species; *P. maxillaris* infected female and male badgers equally, whereas burdens of this species were higher in male skunks. *Taenia leonina* burdens were equivalent in female and male coyotes, but female biased in red foxes (gender comparison was not possible in raccoons). We were unable to test whether sex-specific distributions of *T. crassiceps* were similar in coyotes and foxes.

DISCUSSION

The results of this study provide limited support for the contention that helminth parasite loads in mammals tend to be male biased. Exploring sex differences in gastrointestinal parasitism in 5 sympatric carnivores with the use of 3 different metrics (prevalence, intensity, overdispersion), we detected a male bias on 8 occasions (27% of cases compared), whereas females were found to be more heavily burdened only once (3% of cases compared). Yet most of the statistical comparisons we made revealed little or no sexual bias (21 of 30, 70%), indicating that heightened susceptibility in male hosts is by no means ubiqui-

tous among mammals (Poulin, 1996; Skorping and Jensen, 2004). Instead, our findings demonstrate that the degree to which helminth parasites are found to be overrepresented in 1 sex will depend on the host considered, the helminth species targeted, and the means used to assess the nature of infection.

Patterns of parasite distribution in females and males differed markedly among the carnivore species examined. In American badgers, few sex differences were detected, with males playing host to greater numbers of 1 particular parasite, *T. taxidensis*, despite a slight, but insignificant, female bias with parasites pooled. For coyotes and raccoons, males were found to be more heavily infected than females when parasites were combined, but no other differences were evident. Conversely, female red foxes tended to be more heavily infected than males with parasites pooled; this trend was significant when *T. leonina* was considered independently. Finally, for striped skunks, males were both more likely to be parasitized by, and more heavily infected with, *B. columnaris*. Furthermore, heavily infected individuals, i.e., those in the top 20% of the distribution, were always overwhelmingly male, suggesting that male skunks may serve as primary vectors for the transmission of the parasites we recovered (Perkins et al., 2003; Ferrari et al., 2004; Skorping and Jensen, 2004).

These findings clearly illustrate 2 important points. First, they show that host selection can dramatically affect the outcome of tests for male-biased parasite distributions in mammals. For example, separate investigations targeting red foxes and skunks would have reached opposite conclusions regarding the hypothesis that males consistently serve as reservoirs for helminth parasites in our study system. By implication, even mammal species characterized by sympatry and ecological similarity, i.e., substantial niche overlap, cannot be expected to share the tendency for males to be inherently more vulnerable to parasitism, even if they are closely related, e.g., coyotes and foxes. Second, they show that, for any mammalian host, different helminth species can vary greatly in their tendency to infect 1 sex. For example, male skunks were disproportionately vulnerable to *B. columnaris*, but not to *P. maxillaris*. Thus, an investigation focusing exclusively on the latter parasite species, or on a pooled measure of infection, would have failed to detect a male bias. By extension, the degree to which helminth parasite distributions in mammals are male-biased has likely been underestimated (or at least remains to be assessed rigorously), as many past studies have considered only nematodes, leaving other helminths underrepresented (see Poulin, 1996 for a review).

Our ability to detect sexual bias also depended heavily on the metric we used to characterize parasite infection. A comparison of intensity measures for females and males revealed disparities in all 5 carnivores. Conversely, in comparing sex-specific measures of prevalence and overdispersion, we only found differences in 1 host species, skunks. Moreover, for skunks, these latter 2 measures did not agree: only 1 parasite species was more prevalent in males, whereas males were found to be prone to heavy infection by both helminths individually and when parasites were combined. Had we elected to rely solely on measures of parasite prevalence, therefore, we would have concluded that sexual bias was virtually absent from the study system. We acknowledge that the inclusion of comparisons precluded by low sample size would likely have resulted in heightened consensus among the measures used in this investigation.

Nevertheless, our results suggest that previous attempts to detect male bias using a single measure of parasite infection may have missed or underestimated existing sex differences (Skorping and Jensen, 2004).

Interestingly, particular helminth species infecting multiple carnivores generally did not manifest consistent distribution patterns among the sexes. Indeed, even a nematode parasite (*P. rara*) using 2 closely related canids (coyotes and red foxes) failed to show a consistent sex bias. Consequently, we can surmise that these parasites do not possess traits that universally led them, in our study system, to infect sympatric and ecologically similar hosts in a particular way, e.g., to always overburden males. Instead, we infer that sexual bias (or the lack thereof) was not consistently observed in parasites with multiple hosts because of host species-specific immune responses (Bize et al., 2005), variability in the degree to which their hosts are characterized by subtle sex-specific differences in exposure or susceptibility (Poulin, 1995, 1996; Haukisalmi and Henttonen, 1999; Pulkkinen and Ebert, 2004), and/or interactions with other parasites (Haukisalmi and Henttonen, 1993).

The debate surrounding the role played by males as reservoirs for parasites has been fueled both by a paucity of data and disagreement over the best means to quantify infection (Skorping and Jensen, 2004). Our study provides results that are germane to both problems. First, using sympatric mammalian carnivores as models, it adds to a growing literature showing that males are indeed more likely than females to harbor heavy parasite loads (Poulin, 1996; Schalk and Forbes, 1997; Moore and Wilson, 2002), but that the existence, direction, and degree of bias in particular cases are both host and parasite dependent. Thus, analyses that target multiple hosts and parasites across a variety of systems are essential if we are to gain a full understanding of the scope of this phenomenon (Altizer et al., 2003). Second, and perhaps more importantly, it reveals the profound impact that methodological considerations can have on tests for male bias. Thus, different techniques used to measure parasite loads in a particular host species can lead to divergent conclusions. By implication, spatiotemporal comparisons of parasite burdens within and across taxa must be based upon equivalent measures of parasitism. Moreover, future tests for sexual bias should seek to measure rates of parasitism multilaterally.

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LITERATURE CITED

- ANDERSON, R. M., AND R. M. MAY. 1985. Helminth infections of humans: Mathematical models, population dynamics, and control. *Advances in Parasitology* **24**: 1–101.
- ALTIZER, S., C. L. NUNN, P. H. THRALL, J. L. GITTLEMAN, J. ANTONOVICS, A. A. CUNNINGHAM, A. P. DOBSON, V. EZENWA, K. E. JONES, A. B. PEDERSON, M. POSS, AND J. R. C. PULLIAM. 2003. Social organizations and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics* **34**: 517–547.
- ARNEBERG, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: Comparative analyses of directly transmitted nematodes of mammals. *Ecography* **25**: 88–94.
- AZEVEDO, F. C. C., V. LESTER, W. GORSUCH, S. LARIVIÈRE, A. J. WIRSING, AND D. L. MURRAY. 2006. Dietary breadth and overlap among five sympatric prairie carnivores. *Journal of Zoology* **269**: 127–135.
- BIZE, P., A. ROULIN, J. L. TELLA, AND H. RICHNER. 2005. Female-biased mortality in experimentally parasitized Alpine Swift *Apus melba* nestlings. *Functional Ecology* **19**: 405–413.
- BUNDY, D. A. P. 1988. Population ecology of intestinal helminth infections in human communities. *Philosophical Transactions of the Royal Society of London, Series B* **321**: 405–420.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: A practical information-theoretic approach. Springer, New York, New York, 353 p.
- DOBSON, A. J. 2002. An introduction to generalized linear models. Chapman and Hall, London, U.K., 192 p.
- FERRARI, N., I. M. CATTADORI, J. NESPEREIRA, A. RIZZOLI, AND P. J. HUDSON. 2004. The role of host sex in parasite dynamics: Field experiments on the yellow-necked mouse *Apodemus flavicollis*. *Ecology Letters* **7**: 88–94.
- FOLSTAD, I., AND A. J. KARTER. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* **139**: 603–622.
- GALVANI, A. P. 2005. Age-dependent epidemiological patterns and strain diversity in helminth parasites. *Journal of Parasitology* **91**: 24–30.
- GEORGE-NASCIMENTO, M., G. MUÑOZ, P. A. MARQUET, AND R. POULIN. 2004. Testing the energetic equivalence rule with helminth endoparasites of vertebrates. *Ecology Letters* **7**: 527–531.
- HAUKISALMI, V., AND H. HENTTONEN. 1993. Coexistence in helminths of the bank vole *Clethrionomys glareolus*. I. Patterns of co-occurrence. *Journal of Animal Ecology* **62**: 221–229.
- , AND ———. 1999. Determinants of helminth aggregation in natural host populations: Individual differences or spatial heterogeneity? *Ecography* **22**: 629–636.
- HUDSON, P. J., AND A. P. DOBSON. 1995. Macroparasites: Observed patterns in naturally fluctuating animal populations. *In Ecology of infectious diseases in natural populations*, B. T. Grenfell and A. P. Dobson (eds.). Cambridge University Press, Cambridge, U.K., p. 144–176.
- MOORE, S. L., AND K. WILSON. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. *Science* **297**: 2015–2018.
- PALMER, R. A. 1999. Detecting publication bias in meta-analyses: A case study of fluctuating asymmetry and sexual selection. *American Naturalist* **154**: 220–233.
- PERKINS, S. E., I. M. CATTADORI, V. TAGLIAPIETRA, A. P. RIZZOLI, AND P. J. HUDSON. 2003. Empirical evidence for key hosts in persistence of a tick-borne disease. *International Journal for Parasitology* **33**: 909–917.
- PERNEGER, T. V. 1998. What's wrong with Bonferroni adjustments. *British Medical Journal* **316**: 1236–1238.
- POULIN, R. 1995. Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs* **65**: 283–302.
- . 1996. Sexual inequalities in helminth infections: A cost of being a male? *American Naturalist* **147**: 287–295.
- . 1997. Species richness of parasite assemblages: Evolution and patterns. *Annual Review of Ecology and Systematics* **28**: 341–358.
- PULKKINEN, K., AND D. EBERT. 2004. Host starvation decreases parasite load and mean host size in experimental populations. *Ecology* **85**: 823–833.
- REIMCHEN, T. E., AND P. NOSIL. 2001. Ecological causes of sex-biased parasitism in three-spine stickleback. *Biological Journal of the Linnean Society* **73**: 51–63.
- ROLFF, J. 2002. Bateman's principle and immunity. *Proceedings of the Royal Society of London B Biological Sciences* **269**: 867–872.
- SCHALK, G., AND M. R. FORBES. 1997. Male biases in parasitism of mammals: Effects of study type, host age, and parasite taxon. *Oikos* **78**: 67–74.
- SHAW, D. J., AND A. P. DOBSON. 1995. Patterns of macroparasite abun-

- dance and aggregation in wildlife populations: A quantitative review. *Parasitology* **111**: S111–S153.
- , B. T. GRENFELL, AND A. P. DOBSON. 1998. Patterns of macro-parasite aggregation in wildlife host populations. *Parasitology* **117**: 597–610.
- SKORPING, A., AND K. H. JENSEN. 2004. Disease dynamics: All caused by males? *Trends in Ecology and Evolution* **19**: 219–220.
- SPINAGE, C. A. 1973. A review of the age determination of mammals by means of teeth, with especial reference to Africa. *East African Wildlife Journal* **11**: 165–187.
- STIEN, A., R. J. IRVINE, E. ROPSTAD, O. HALVORSEN, R. LANGVATN, AND S. D. ALBON. 2002. The impact of gastrointestinal nematodes on wild reindeer: Experimental and cross-sectional studies. *Journal of Animal Ecology* **71**: 937–945.
- WILSON, K., AND B. T. GRENFELL. 1997. Generalised linear modeling for parasitologists. *Parasitology Today* **13**: 33–38.
- , O. N. BJORNSTAD, A. P. DOBSON, S. MERLER, G. POGLAYEN, S. E. RANDOLPH, A. F. READ, AND A. SKORPING. 2002. Heterogeneities in macroparasite infections: Patterns and processes. *In* The ecology of wildlife diseases, P. J. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek, and A. P. Dobson (eds.). Oxford University Press, Oxford, U.K., p. 6–44.
- , B. T. GRENFELL, AND D. J. SHAW. 1996. Analysis of aggregated parasite distributions: A comparison of methods. *Functional Ecology* **10**: 592–601.
- ZAR, J. H. 1999. *Biostatistical analysis*. Prentice Hall, Englewood Cliffs, New Jersey, 663 p.