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AN EXPANDING POPULATION OF THE GIANT LIVER FLUKE (*FASCIOLOIDES MAGNA*) IN ELK (*CERVUS CANADENSIS*) AND OTHER UNGULATES IN CANADA

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ABSTRACT: Giant liver fluke (*Fascioloides magna*) populations readily expand under suitable conditions. Although extirpated from the eastern slopes of the Canadian Rocky Mountains in the early 1960s, the fluke reappeared following natural spread through mountain passes from British Columbia. Herein, we assessed epizootiology of the fluke population two decades later. Between 1984 and 1991, 534 ungulates, including 381 elk (*Cervus canadensis*), 68 mule deer (*Odocoileus hemionus hemionus*), 54 white-tailed deer (*Odocoileus virginianus*), and 31 moose (*Alces alces*) from adjacent areas of Alberta (AB) and British Columbia (BC), Canada, were examined for giant liver flukes. Prevalence in elk increased from 53% to 79% (1984–91) in Banff National Park (BNP) in AB and 77% to 100% (1985–89) in Kootenay National Park (KNP) in BC. Super-infections (>100 flukes) were more common in later years. Generally, prevalence increased over time and with increasing age of elk. Intensity was lowest in young-of-year (BNP 8±5, KNP 3), but similar in yearlings (BNP 36±11, KNP 23±8) and adults (BNP 33±5, KNP 32±6). Prevalence was similar in male and female elk. Intensity was higher in males (BNP 47±7, KNP 46±12) than in females (BNP 28±6, KNP 22±4), although the maximum number of flukes (545) occurred in a female elk. Prevalence and intensity differed among other species of ungulates but patterns were similar in each park. Prevalence was lower in mule deer (BNP 6%, KNP 4%) than in white-tailed deer (BNP 44%, KNP 28%) and moose (BNP 52%, KNP 63%). Intensity differed among these species but never exceeded 30 flukes. Gravid flukes occurred only in elk and white-tailed deer. Transmission occurred primarily in late summer-fall and in wet habitats. At least seven elk died as a direct result of fluke infection. In this region, elk and white-tailed deer maintain the *F. magna* population with spillover into moose and, rarely, mule deer.

Key words: *Alces alces*, *Cervus canadensis*, elk, epizootiology, *Fascioloides magna*, giant liver fluke, moose, Rocky Mountains.

INTRODUCTION

Mature giant liver flukes (*Fascioloides magna*) occur in fibrous capsules within hepatic parenchyma in various wild and domestic ruminants. The species has broad ecologic tolerance and can establish expanding populations from foci of natural or translocated hosts (Pybus 2001). Eggs shed with host fecal pellets hatch in water and penetrate the tissues of various aquatic snails (Swales 1935). After a period of development and replication, large numbers of cercariae leave the snail and encyst on submerged vegetation, where they persist for prolonged periods. These cysts harden and remain dormant until ingested by an herbivore. Thus they are available to any suitable host that ingests encysted infective larvae.

Fascioloides magna is of North American origin. However, it was described from specimens collected from elk (=wapiti, *Cervus canadensis*) imported to Italy from western Canada in 1865 (Bassi 1875; Kralova-Hromadova et al. 2011). Within 10 yr, extensive fluke-related mortality of elk occurred and outbreaks continue (Balbo et al. 1987). Molecular evaluation confirmed multiple introductions of *F. magna* into Europe from translocated elk and white-tailed deer (*Odocoileus virginianus*) (Kralova-Hromadova et al. 2011), and the distribution continues to expand (Novobilský et al. 2007; Rajkovic-Janje et al. 2008; Kasny et al. 2012).

In North America, *F. magna* occurs in several wild cervids including elk, moose (*Alces alces*), white-tailed deer, mule deer (*Odocoileus hemionus hemionus*), black-tailed deer (*Odocoileus hemionus columbianus*), and woodland caribou (*Rangifer tarandus caribou*) as well as in domestic sheep (*Ovis aries*) and goats (*Capra aegagrus hircus*) (Foreyt 1981) in discrete regions across Canada and the US (Pybus 2001). In eastern North America, white-tailed deer and woodland caribou are the primary hosts (Lankester and Luttich 1988; Pybus 2001; Pollock et al. 2009). In western North America, elk and mule deer are reported as hosts (Dutson et al. 1967), although few infected mule deer are documented. Early records in the west also include black-tailed deer (Kermode 1916; Cowan 1946), moose, and mule deer in British Columbia (BC) (Cowan 1951), although Cowan (1951) states that large areas of the Rocky Mountains and northern BC were free of *F. magna* in the early 1950s. The giant liver fluke is not reported from Yellowstone National Park in the western US.

Elk generally were extirpated from the Rocky Mountains of Alberta (AB) and BC by the early 1900s (Stelfox 1964) and reduced to a few remnant populations in isolated areas (Millar 1915). There were few elk in the vicinity of Banff National Park (BNP), AB (51°30′0″N, 116°0′0″W) until the population was restocked with elk from Yellowstone National Park between 1916 and 1920 (Lloyd 1927; Green 1946; Lothian 1981). Elk expanded in number and geographic distribution within BNP and by the early 1940s were periodically culled to reduce the population (Green 1946; Flook 1967).

Fascioloides magna was not detected in BNP until 1959–60 (Green 1946; Flook 1967). Prevalence quickly increased to 50% of adult elk (Flook and Stenton 1969). These authors suggested the fluke entered BNP in elk moving through the mountain passes from Kootenay National Park (KNP) in southeastern BC (51°52′59″N, 116°02′57″W).

The population effects of *F. magna* in free-ranging wildlife are largely unknown. Giant liver flukes apparently contribute to mortality of heavily infected individuals (Kermode 1916; Fenstermacher and Olsen 1942; Cheatum 1951; Murray et al. 2006) and are a serious concern for wildlife managers in North America (Pybus 2001) and Europe (Kasny et al. 2012). We examined the interplay of giant liver fluke among sympatric, free-ranging ungulates in various habitats within Banff and Kootenay national parks in the Rocky Mountains of AB and BC (Fig. 1). Abundance and distribution of flukes was compared between the parks and with data from BNP in the mid-1960s.

MATERIALS AND METHODS

Hosts and flukes

Livers from elk, moose, white-tailed deer, and mule deer were collected opportunistically. Most livers were collected and frozen; others were examined fresh. Only intact livers were included. Livers were thinly sliced (5 mm) with a sharp knife. Manual pressure applied to the liver resulted in intact flukes being expressed along the cut surface. Flukes were gently extracted and placed in tap water. Liver slices were submerged and gently agitated in water, the water decanted, and all fluke pieces collected. Most flukes were collected intact but pieces of flukes damaged during slicing were sorted into heads (recognizable by a pointed anterior and an oral sucker) and tails (rounded, no openings), with one head and one tail accounting for one fluke. Flukes were staged as immature or gravid (eggs present) and counted.

Sample sizes in analyses differ because: 1) intensity of flukes was not determined in a few of the livers; data from such individuals were used only in prevalence (presence-absence) analyses. 2) Generally, host age was classified as adult (AD), yearling (YLG), or young-of-year (YOY); but in some cases, specific age was determined by counting cementum annuli in the first premolar (Matson's Lab, Milltown, Montana, USA), and only these samples were used in cohort analyses. 3) Sex of two individuals was not recorded and these data were not used in analyses related to sex.

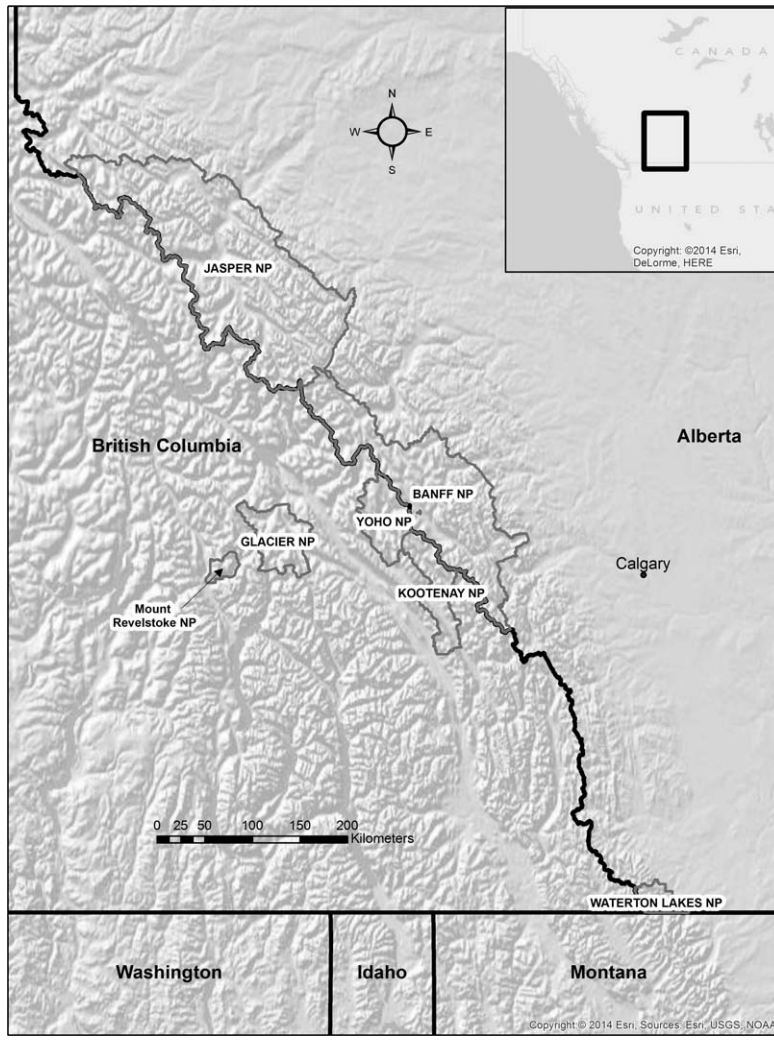

FIGURE 1. Banff and Kootenay national parks (NP) and adjacent NPs in the Canadian Rocky Mountains.

Occurrence and transmission

We examined occurrence of liver flukes within habitat types and geographic locations within the two parks. Elk show fidelity to seasonal home ranges (Morgantini and Hudson 1988; Woods 1991). Thus we considered ecosite (habitat) where they died as reflective of an individual's home range and assessed relationships between habitat and prevalence or intensity of flukes. Given the role of aquatic snails in the life cycle of giant liver flukes (Swales 1935), ecosites were classified into four 'wetness' categories: 1=dry with well-drained soils, 2=moderately wet with moderately drained soils, 3=wet with poorly drained soils, and 4=permanent water bodies.

Spatial distribution of flukes among demographic groups within each park was examined. Mortality site was used to allocate animals into five populations in BNP (Fig. 2; for details see Woods 1991). In KNP, animals were allocated to four locations based on visual assessment of clustered collection sites (Fig. 2). Prevalence in these groups was used to reflect spatial distribution of flukes in the park.

To assess transmission of flukes, we focused on the period when YOY were first found with flukes. Elk in BNP are partially migratory; some individuals migrate seasonally, others are sedentary year-round (Woods 1991). Collection dates of YOY elk were grouped into

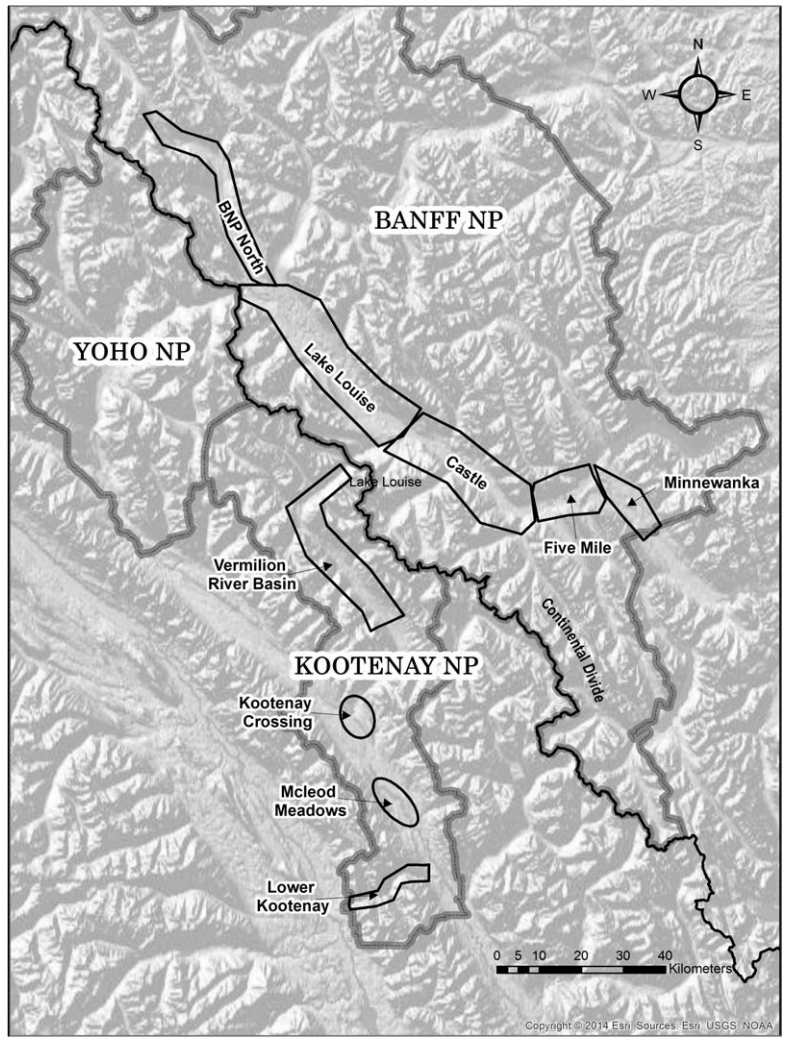

FIGURE 2. Elk (*Cervus canadensis*) population ranges within Banff and Kootenay national parks (NP), Canada.

seasons based on patterns of potential elk movement and behavior: winter (sedentary, December–April); spring (migration to summer grounds, May–June); summer (on summer grounds, July–September); and fall (migration to winter grounds, October–November), recognizing that behavioral activities related to these periods are general and can be affected by climate or predator activities (Morgantini and Hudson 1988; Woods 1991). Prevalence in calves during these four periods was used to assess timing of transmission.

Statistical analyses were done in SYSTAT for Windows (Wilkinson 1986) with significance at the 95% level. Data were checked for distribution and variance factors. Nonparametric tests were used where assumptions of normality or homogeneity of variances could not be met by transformation. If sample sizes were too small to allow statistical analysis, general patterns were described.

RESULTS

Potential definitive hosts for *F. magna* ($n=534$) from BNP ($n=412$) and KNP ($n=122$) were examined for giant liver flukes from 1984 to 1991. The majority were elk, but moose, mule deer, and white-tailed deer also were examined (Table 1). In BNP, mortality was associated with vehicle collisions (71%), miscellaneous mortality

TABLE 1. Prevalence (% of sample size, *n*), intensity (mean±SE), and range of the giant liver fluke (*Fascioloides magna*) in various ungulates, all ages combined, from Banff (BNP) and Kootenay (KNP) national parks, Canada.

	BNP				KNP			
Species[a]	%	Intensity	Range	*n*	%	Intensity	Range	*n*
Elk	61	37±5	1–545	312	70	30±5	1–193	69
Mule deer	4	1, 2[b]	1, 2	52	6	1	1	16
Moose	52	16±9	1–30	23	63	2±1	1–4	8
White-tailed deer	44	4±3	1–9	25	28	3±3	1–10	29

[a] Elk = *Cervus canadensis*; mule deer = *Odocoileus hemionus*; moose = *Alces alces*; white-tailed deer = *Odocoileus virginianus*.

[b] Two mule deer each had one fluke in liver; one of these also had one fluke in the lungs.

(drowning, poaching, found dead; 8%), railway collisions (6%), research collections (4%), predation (1%), or unrecorded causes (10%). Cause of mortality in KNP often was not recorded but generally was vehicle collisions.

Infection data differed among the four host species and between the two parks (Table 1); thus data are presented by species and park. The majority of animals examined were elk from BNP.

Elk

Prevalence of *F. magna* in elk increased over time (Table 2). When adjusted for year effect from 1985 to 1988 (samples large enough to compare), prevalence differed between parks, with a generally higher prevalence in KNP (Mantel-Haenszel chi-square test; $\chi^2=4.35$, $P=0.039$). Therefore subsequent analyses were conducted for each park separately.

Intensity of flukes in elk (Table 2) increased significantly in BNP between 1984 and 1991. Increased intensity is most evident in elk with >100 flukes during 1988–91. Annual intensity in elk from KNP did not increase.

Prevalence increased with increasing age class in elk from BNP and KNP (likelihood ratio $\chi^2=176$ and $\chi^2=32$, respectively; Table 3). Within age classes, samples were too small to adjust for differences among years. In addition, the proportion of YOY elk decreased over time (likelihood ratio $\chi^2=39.9$, df=14, $P=0.00$). However, no YOY collected in BNP from 1984 to 1988 ($n=76$) were infected, but eight of 16 (50%) from 1989 to 1991 were infected: two of four in 1989, zero of two in 1990, and six of 10 in 1991. One of 13 YOY from KNP was infected. Evaluation of prevalence in cohort classes indicated >20% of the cohorts had too few cases for statistical assessment, particularly in older elk. However, the youngest cohorts (except in 1991) often had lower prevalence than did older cohorts in BNP (Table 4). Generally, annual prevalence was >75% in elk born prior to 1983 and <75% in those born in 1983 or later. Data from KNP were insufficient to detect trends.

In elk from BNP, intensity of *F. magna* was higher in YOY than in YLG or AD when adjusted for year effect ($F=3.33$, $P=0.038$). However, this was due entirely to calves of 1990–91. These calves were examined specifically because they had unusually high intensity and depicted an aberrant situation (see upcoming text). Without these calves, intensity in YOY was less than in YLG and adults (Table 3). In KNP, elk samples were too small to adjust for year effects and there was only one infected YOY. Mean intensity did not differ in YLG and AD in either park.

Prevalences were similar in male and female elk in BNP when adjusted for year effects (Table 5). Similarly, for all years combined, prevalence between sexes did not differ ($\chi^2=0.18$, $P=0.675$). Calves

TABLE 2. Prevalence of infection (% of sample size, *n*) and intensity of infection with giant liver flukes (*Fascioloides magna*) in elk (*Cervus canadensis*), all age classes combined, from Banff National Park (BNP) (Kruskal-Wallis $H=23$, $P=0.00$) and Kootenay National Park (KNP), Canada (Kruskal-Wallis $H=7.7$, $P=0.1$).[a] CV = coefficient of variation.

	BNP					KNP				
	Prevalence		Intensity			Prevalence		Intensity		
Year	%	*n*	Mean±SE	Range	CV	%	*n*	Mean±SE	Range	CV	*n*
1984	53	17	17±8.1	1–80	1.5	9	n/a	0	n/a	n/a	n/a	n/a
1985	43	54	28±6.7	1–104	1.1	22	77	13	19±5.2	1–45	0.9	10
1986	46	70	14±2.8	2–65	1.1	32	65	26	26±4.8	1–81	0.8	17
1987	55	47	23±3.8	2–80	0.8	26	67	12	63±22.7	7–193	0.9	7
1988	73	38	57±19.9	1–545	1.8	28	67	15	24±11.8	1–98	1.4	9
1989	87	41	37±10.5	1–131	1.2	20	100	3	32±17.2	5–64	0.9	3
1990	81	21	36±7.1	3–116	0.8	17	n/a	0	n/a	n/a	n/a	n/a
1991	79	24	88±20.7	2–254	1	19	n/a	0	n/a	n/a	n/a	n/a
Overall	—	—	37±4.5	1–545	1.6	174	—	—	30±5	1–193	1.1	46

[a] CV = coefficient of variation; n/a = not applicable.

rarely were infected and thus prevalence between sexes was analyzed without YOY. However, there was still no difference in specific years or over time. In KNP, prevalence also did not differ between male and female elk ($\chi^2=0.01$, $P=0.92$; Table 5). In contrast, in both parks intensity was significantly higher in male elk when adjusted for year effects (Table 6), with approximately twice as many flukes in males than in females.

Lesions associated with giant liver fluke infections are well documented (Bassi 1875; Swales 1935, 1936; Pybus 2001) and not detailed herein. However, the severity of pathologic changes tended to increase with increasing host age and fluke intensity. Liver damage in YOY elk generally was limited to a few hemorrhagic tracks associated with immature flukes (no gravid flukes were found in calves). Lesions in YLG and AD elk differed only in the extent of damage. Infected livers often were enlarged, with rounded margins and scattered streaks of black pigment (Fig. 3). Severely infected livers were four to five times larger than uninfected livers from the same age class of elk. Fibrous adhesions ranging from small (2–3 mm) tags to extensive solid sheets occurred on abdominal serosal surfaces and, occasionally, the latter adhered to the peritoneal wall. Irregular protuberances extended beyond the normal contours of the liver (Fig. 4). Thin black fluid often exuded from cut surfaces of such livers. Extensive fibrous tissue occurred within the hepatic parenchyma, primarily as discrete, thin-walled (2–3 mm) capsules around gravid flukes (Fig. 5) and as a generalized increase in connective stroma within the liver. Occasionally dark, round, hard nodules of accumulated fluke eggs were found within the parenchyma in severely infected elk (Fig. 6). Recognizable dead flukes, deteriorating capsules, or secondary bacterial infection were rare. At low intensity, damage tended to occur adjacent to

TABLE 3. Prevalence (% infected) and intensity (mean number in infected hosts) of giant liver flukes (*Fascioloides magna*) in three age classes of elk (*Cervus canadensis*) from Banff (BNP) and Kootenay (KNP) national parks, Canada.

	BNP			KNP		
Age class[a]	%	*n*	Intensity	%	*n*	Intensity
YOY	8[b]	88	8±5	8	13	3
YLG	57	44	36±11	64	11	23±8
AD	88	178	33±5	89	45	32±6

[a] YOY = young-of-year; YLG = yearling; AD = adult.

[b] Does not include the year 1991 (see text).

the portal fissure; at high intensity tissue changes occurred throughout the liver.

Giant liver flukes were associated with mortality of two radio-collared male elk (see Woods 1991); a yearling found unable to rise and then died and an adult found soon after it died. In each case, the abdominal cavity contained copious blood and a few liver flukes. Each liver was greatly enlarged and contained extensive fibrosis and >200 adult and immature flukes. Cause of death was acute peritonitis and exsanguination associated with rupture of the hepatic capsule and hepatic portal vein, respectively, in the two elk. Similarly, *F. magna* was a significant factor in mortality of five YOY elk found dead in April 1991. Mean intensity in these calves was 184±65. Damage to livers was extreme, most flukes were tiny (5–10 mm), and there were extensive migratory tracks throughout each liver. No other significant gross or histologic lesions were found. To assess the role of liver flukes in the mortality, four YOY sympatric with the dead calves were collected in July 1991. Three of four were uninfected and the livers were normal. The remaining calf had 162 flukes, severe damage to the liver, and was undersized in comparison to the three other calves.

TABLE 4. Prevalence (% infected) of giant liver flukes (*Fascioloides magna*) in elk (*Cervus canadensis*) from Banff National Park, Canada.

Cohort year	Prevalence	*n*
1964	100	1
1969	50	2
1970	100	1
1971	100	1
1973	100	2
1975	80	5
1976	100	1
1977	100	4
1978	80	5
1979	88	8
1980	78	9
1981	100	13
1982	83	12
1983	71	14
1984	52	29
1985	16	43
1986	27	26
1987	36	25
1988	27	15
1990	60	15
1991	100	6

Other species

Prevalence of giant liver flukes in mule deer, moose, and white-tailed deer differed markedly among species but the pattern was similar in both parks (Table 1). Prevalence was highest in moose, followed by white-tailed deer and then mule deer. Where appropriate, data were evaluated for yearly differences (Table 7). In BNP, prevalence in white-tailed deer increased between 1986 and 1990, while prevalence in moose differed from year to year in the few samples examined. Infected mule deer ($n=2$) were found only in 1987. In KNP, samples for these species were too small to detect annual patterns.

Intensity of flukes differed among the four cervid species in BNP (Kolmogorov-

TABLE 5. Annual prevalence (% infected) of giant liver flukes (*Fascioloides magna*) in male and female elk (*Cervus canadensis*), all ages combined, from Banff (BNP) and Kootenay (KNP) national parks, Canada.[a]

	BNP				KNP			
	Female		Male		Female		Male	
Year	%	*n*	%	*n*	%	*n*	%	*n*
1984	56	10	44	7	n/a	n/a	n/a	n/a
1985	61	29	39	25	78	9	75	4
1986	78	46	22	23	65	20	87	6
1987	71	24	43	21	67	6	67	6
1988	64	22	88	16	67	12	100	2
1989	86	21	89	19	100	1	100	2
1990	75	8	92	12	n/a	n/a	n/a	n/a
1991	73	11	82	11	n/a	n/a	n/a	n/a
Total	62	171	60	134	67	48	75	20

[a] n/a = not applicable.

Smirnov=21.2, df=3, P=0.00; Table 1) but was consistently lower than in elk. Annual differences were confounded by small sample sizes but, in general, moose had a higher intensity than did white-tailed deer (Table 8). Very few flukes were seen in mule deer. Fewer flukes were seen in moose from KNP than from BNP, but intensities in deer from each park were similar.

Tissue damage associated with giant liver fluke infection in moose (Fenstermacher and Olsen 1942; Lankester 1974) and white-tailed deer (Swales 1936) has been described and is not detailed herein. The primary lesion in moose livers was extensive hemorrhagic tracks associated with individual, immature flukes. Very few flukes were paired and these occurred in thick-walled (5–10 mm) capsules. Paired flukes were not gravid. Damage tended to occur throughout the liver, regardless of fluke intensity. Occasionally, one or two immature flukes were encapsulated in lung tissue of severely infected moose. The primary lesion in white-tailed deer was a pair of gravid flukes within a thin-walled (2–3 mm), fibrous capsule in the hepatic parenchyma. Very few flukes were found in mule deer, and tissue damage was localized at the site of the immature fluke in the liver (n=2 deer) or lung (n=1). No gravid flukes were seen in mule deer.

Spatial and temporal distributions

Based on data from eight radio-collared elk (Woods 1991) with necropsy data, we examined the proportion of time individuals spent in specific habitats in BNP

TABLE 6. Intensity of infection with giant liver flukes (*Fascioloides magna*) in male and female elk (*Cervus canadensis*) from Banff (BNP) and Kootenay (KNP) national parks, Canada.

	BNP		KNP	
Parameter[a]	Female	Male	Female	Male
n	97	74	31	15
Mean intensity	28	47	22	46
SE	6.4	6.5	4	12.1
CV	2.22	1.18	0.99	1.01
Range	1–545	1–254	1–81	6–193
ANCOVA	F=10.8, df=1 P=0.003		F=4.9, df=1 P=0.032	

[a] CV = coefficient of variation; ANCOVA = analysis of covariance on log-transformed data.

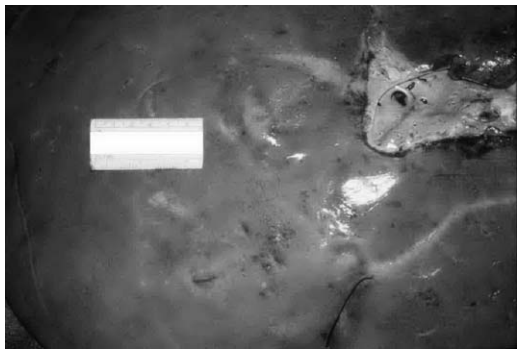

FIGURE 3. Minor liver damage in elk (*Cervus canadensis*) infected with giant liver fluke *Fascioloides magna*: rounded margins and minor black streaks below the hepatic capsule. Ruler=5.8 cm.

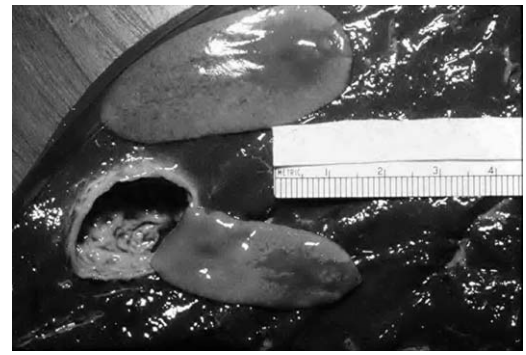

FIGURE 5. Thin-walled white fibrous capsule surrounding two gravid giant liver flukes, *Fascioloides magna*, in an elk (*Cervus canadensis*) liver. Ruler=4.5 cm.

(Table 9). Individuals with relatively high occurrence in wet habitats had a higher intensity of giant liver flukes. In the assessment of distribution among herds, prevalence of flukes in adult or YLG elk was similar among locations but infected YOY were more common in wetter areas, including the Vermilion Lakes wetlands (Five Mile Bridge and Minnewanka; Table 10 and Fig. 2). All infected YOY were collected in winter, December–April. Infected white-tailed deer and moose occurred in all areas of BNP; however, sample sizes were too small to detect differences in geographic distribution. Infected mule deer were found only in the Castle and North BNP areas.

In KNP, giant liver flukes were present in elk throughout the park and prevalences were similar among locations. In each location there were more infected elk than uninfected. Sample sizes for other cervid species were too small to analyze. The only obvious pattern was that moose were found mainly in the northern part of the park (Vermilion River Basin, seven of eight moose examined) and most (five of seven) were infected.

DISCUSSION

Contiguous national parks in AB and BC provide a case study in natural dispersal of giant liver flukes and their population expansion within a suite of cervids. The rapid expansion of elk in the

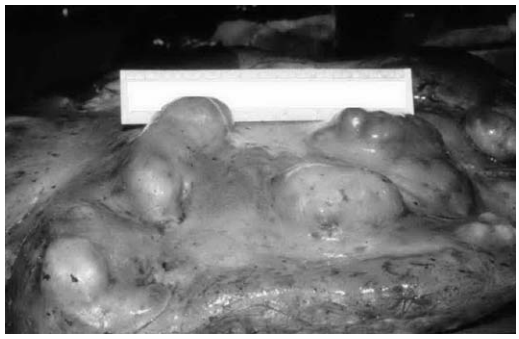

FIGURE 4. Severe liver damage in elk (*Cervus canadensis*) infected with giant liver fluke *Fascioloides magna*: fibrous capsules extending beyond the liver surface. Ruler=10 cm.

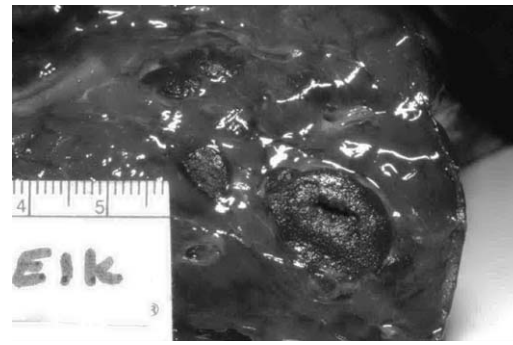

FIGURE 6. Accumulation of giant liver fluke eggs, *Fascioloides magna*, within elk (*Cervus canadensis*) liver tissues.

TABLE 7. Annual prevalence (% infected) of giant liver flukes (*Fascioloides magna*) in various cervids collected from Banff (BNP) and Kootenay (KNP) national parks, Canada.[a]

	BNP					KNP				
	Mule deer		White-tailed deer		Moose	Mule deer		White-tailed deer		Moose
Year	%	*n*	%	*n*	No. infected	%	*n*	%	*n*	No. infected
1985	n/a	0	n/a	0	3 of 3	n/a	0	n/a	0	0
1986	0	1	0	1	0 of 1	n/a	0	n/a	0	0
1987	13	16	29	7	3 of 3	14	7	36	14	3 of 4
1988	0	17	50	14	3 of 6	0	6	20	10	2 of 4
1989	0	9	n/a	0	2 of 6	0	3	20	5	0
1990	0	9	67	3	0 of 3	n/a	0	n/a	0	0
1991	n/a	0	n/a	0	1 of 1	n/a	0	n/a	0	0

[a] Mule deer = *Odocoileus hemionus hemionus*; white-tailed deer = *Odocoileus virginianus*; moose = *Alces alces*; n/a = not applicable.

Rocky Mountains in AB in the 1920s did not appear to include *F. magna*. Although elk were culled for population control in BNP starting in 1944 (Table 11; Green 1946, 1957), and livers often were salvaged for food in work camps (Lothian 1981), no *F. magna* were found until 1959–60 (Flook 1967), despite similar sample sex ratio and age distribution as elk in the current study. Prevalence increased slowly during the early 1960s, and flukes were first recorded in YOY and YLG elk in 1966–67 (Flook and Stenton 1969). Our data indicate the expansion continued geographically, numerically, and across suitable host species.

Telemetry studies (Woods 1991) revealed a significant exchange of elk between KNP and BNP through Vermilion Pass, providing a natural dispersal mechanism for *F. magna* from BC into AB, as reflected in the initial presence of flukes in western populations of elk in BNP (Flook 1967; Flook and Stenton 1969) and a subsequent local increase in prevalence and intensity. Our data indicate that *F. magna* later became well established in eastern portions of BNP and reflect the increased number, concentration, and relatively sedentary habits of elk (Woods 1991) in areas of large montane marshes with abundant aquatic snails—excellent habitat for perpetuating *F. magna*. Nonmigratory elk in the vicinity of the marshes year-round contribute to a continual release of eggs into

TABLE 8. Annual intensity (mean±SE) of giant liver flukes (*Fascioloides magna*) in various cervids from Banff (BNP) and Kootenay (KNP) national parks, Canada.[a]

		BNP				KNP			
Species	Year	Intensity	Range	CV	*n*	Intensity	Range	CV	*n*
Mule deer	1987	1, 2	n/a	n/a	2	1	n/a	n/a	1
White-tailed deer	1987	3.0±1.0	2–4	0.47	2	3.8±1.6	1–10	0.97	5
	1988	3.8±1.2	1–9	0.78	6	2±1.0	1–3	0.71	2
	1989	n/a	n/a	n/a	0	1	n/a	n/a	1
	1990	3.0±2.0	1–5	0.94	2	n/a	n/a	n/a	0
Moose	1985	16.3±6.0	8–28	0.64	3	n/a	n/a	n/a	0
	1987	16.7±7.3	5–30	0.75	3	2.7±0.3	2–3	0.22	3
	1988	10.0±4.5	1–15	0.78	3	2.5±1.5	1–4	0.85	2
	1989	7.5±6.5	1–14	1.23	2	n/a	n/a	n/a	0
	1991	25	n/a	n/a	1	n/a	n/a	n/a	0

[a] CV = coefficient of variation; mule deer = *Odocoileus hemionus hemionus*; white-tailed deer = *Odocoileus virginianus*; moose = *Alces alces*; n/a = not applicable.

TABLE 9. Intensity of infection (number of flukes) for radio collared elk (*Cervus canadensis*) infected with giant liver flukes (*Fascioloides magna*) in wet ecosites in Banff National Park, Canada. All elk were in the adult age class.

Elk no.	Intensity	Sex	% Wet[a]
254	3	Female	0
383	0	Female	0
684	35	Male	17
787	143	Male	20
826	545	Female	57
966	++[b]	Male	56
1,354	36	Male	18
1,529	25	Male	0

[a] % occurrences in ecosites classified as wet (see text).

[b] ~100 flukes, exact number not recorded.

the environment and accumulation of infective cysts on vegetation.

Giant liver fluke infection is considered relatively benign in elk, white-tailed deer, and caribou (Foreyt 1981; Pybus 2001). Flukes generally do not cause clinical disease in these species but may cause extensive damage to individuals under stress or with high numbers of parasites. The latter situation can occur within enclosed herds with year-round access to infective larvae (Bassi 1875; Balbo et al. 1987). Such a situation developed in BNP as the expanded fluke population resulted in mortality of individual elk. Although we documented fluke-related mortality in only two radio-collared elk, it is likely that additional elk died as a result of vascular ruptures associated with severe hepatic damage. Some radio-collared elk died in situations similar to the cases described herein, but the livers were unavailable for examination, and intact livers of uncollared elk that die of natural causes rarely are found (Woods 1990). Severe acute peritonitis also occurred in an elk calf experimentally exposed to liver flukes (Foreyt 1996). Similar mortality occurred in heavily infected white-tailed deer (Swales 1950; Cheatum 1951; Pursglove et al. 1977), black-tailed deer (Kermode 1916; Cowan 1946), moose (Fenstermacher and Olsen 1942; Karns 1972; Berg 1975), and red deer (*Cervus elaphus*; Bassi 1875; Balbo et al. 1987).

Clusters of mortality in elk also occur. Extremely high intensity of flukes in the 1990–91 elk cohort in BNP followed a period of higher than average precipitation (particularly October and November 1990) and temperature (average February temperature 1984–92 was below freezing, except in 1991) (Environment Canada 2015). Because temperature and rainfall directly influence development of flukes and snails (Olsen 1944; Boray 1969), these environmental conditions may have contributed to increased production of cercariae in snails during summer 1990 and survival of metacercarial cysts on vegetation through fall and winter. Deep snows in winter 1990–91 also may have resulted in increased use of marsh vegetation by YOY elk and thus greater exposure to flukes. The resulting high intensity and extreme hepatic damage was expressed in the mortality of heavily infected calves of this cohort, in contrast to survival of uninfected calves of the same cohort.

TABLE 10. Prevalence (% infected) of giant liver flukes (*Fascioloides magna*) in elk (*Cervus canadensis*) by age class at various locations in Banff National Park (BNP), Canada, 1984 to 1991.[a]

	Adult		Yearling		Young-of-year		Total	
Location	%	*n*	%	*n*	%	*n*	%	*n*
Minnewanka	83	29	61	13	12	17	58	59
Five Mile Bridge	85	52	60	10	13	31	60	93
Castle	89	57	43	14	4	28	59	99
Lake Louise	100	22	71	7	0	14	63	43
North BNP	100	1	n/a	0	n/a	0	100	1

[a] n/a = not applicable.

TABLE 11. Prevalence (% infected) of giant liver flukes (*Fascioloides magna*) in elk (*Cervus canadensis*) by age class in Banff National Park, Canada, 1944 to 1995.[a]

	Young-of-year		Yearling		2-yr old		>2 yr	
Period	%	*n*	%	*n*	%	*n*	%	*n*
1944–54[b]	0	197	0	147	n/a	n/a	0	906
1959–65[c]	0	138	6	126	13	117	13	462
1985–89[d]	3	69	57	30	69	16	89	70
1989–95[e]	28	32	74	27	n/a	n/a	94	77

[a] n/a = not applicable.

[b] Calculated from Green (1957).

[c] Calculated from Flook (1967).

[d] Current study.

[e] Shury (1996).

Contrary to our study, Flook and Stenton (1969) report significantly higher prevalence of giant liver flukes in adult female elk than in males. They suggest males have a different liver physiology, particularly prior to and during the rut, and that adult males range at higher elevations than females for much of the year (Cowan 1950; Flook 1967), thus taking them away from foci of transmission around lowland marshes. Alternatively, there may be a 'founder effect' as *F. magna* disperses into new populations. Male elk travel further, have greater home ranges, and are more likely to migrate farther (Morgantini and Hudson 1988; Woods 1991), thus distancing them from the limited population of flukes in the initial stages of colonizing new areas. However, once flukes are established in a watershed, the increased mobility may expose male elk to more larvae and lead to higher intensity than in females. In addition, many elk in BNP forego migration to higher elevations in the summer, in part as a predator avoidance strategy (Hamer and Herrero 1991; Huggard 1993), and therefore the differential exposure of males and females to flukes as detected in the early 1960s may no longer occur and may in fact be reversed.

All elk appear susceptible to *F. magna* infection, and the opportunity for transmission may be essential in determining individual host intensity. Infections in elk, particularly in BNP, exceed the prevalence and intensity of flukes reported in other species or areas. Individual elk with >600 flukes now occur in BNP and >100 flukes per elk is not uncommon (Shury 1996; M.J.P and J.G.W. unpubl. data). High intensity in the 1990–91 cohort and a calf elk collected in nearby Yoho National Park in April 1988 (>200 flukes, M.J.P. unpubl. data.) also support high species susceptibility. In contrast, in white-tailed deer prevalence rarely exceeds 70% and mean intensity usually is <10 flukes (Olsen 1949; Foreyt et al. 1977; Addison et al. 1988; Forrester 1992). Similarly, in our study white-tailed deer had significantly lower prevalence and intensity despite co-occurring with heavily infected elk in a highly contaminated environment.

Moose are dead-end hosts for *F. magna* (Lankester 1974; Pybus 2001), yet they can have significant prevalence, intensity, and severity of hepatic damage. The extent of damage suggests the potential for compromised liver function and possible implications for long-term productivity or survival of at least individual moose. Similar implications are noted by Murray et al. (2006) but are somewhat disputed by Lankester and Foreyt (2011). A definitive evaluation of giant liver fluke in moose populations remains elusive.

Our data support a premise that elk and white-tailed deer are primary hosts for giant liver flukes in the Canadian Rocky

Mountain region. These hosts provide sufficient parasite reproduction to maintain the fluke population, with spillover into moose and, rarely, mule deer. No gravid flukes were recovered nor were fluke eggs found in moose or mule deer. Further, given the considerable overlap in habitat use among ungulates in BNP (Holroyd and van Tighem 1983; Woods 1990), the lack of infections in mule deer implies an innate resistance to infection or an ecologic barrier that limits natural transmission. Published reports of giant liver flukes in mule deer are limited: Senger (1963) reported infections in Montana but gave no details; nine mule deer given metacercariae of *F. magna* died (Foreyt 1992; 1996); while three survived and shed eggs in feces (Foreyt 1996). Thus mule deer can serve as suitable definitive hosts, but our results and the lack of literature reports suggest natural infections are rare. The relatively limited amount of aquatic vegetation in the diet of mule deer (Walmo and Regelin 1981) may minimize natural exposure to infective stages, at least in the montane habitats in our study region.

A review of current literature reveals similar epizootiologic patterns of *F. magna* within primary host populations (white-tailed deer, elk, and caribou); however, the general pattern appears to differ over time. Following initial dispersal into susceptible populations, infections occur primarily in mature animals, particularly those that are relatively transient. Prevalence and intensity generally are low and males are more commonly infected than females. As the fluke population becomes established in a local area, overall prevalence and intensity increase. At some threshold level, prevalence increases with age but only in 1- and 2-yr olds, not in adults. Intensity differs widely among individuals but mean intensity does not change significantly with age beyond YOY. The change may relate to the density of definitive hosts, prevalence in intermediate hosts, and accumulation of metacercariae on aquatic vegetation. In established populations, giant liver flukes maintain an aggregated distribution within primary hosts: most individuals have a few flukes while the majority of the fluke population occurs in a few heavily infected individuals.

Management implications

Giant liver flukes readily disperse with infected elk through natural migrations (as evidenced herein and in Europe) or translocation with imported elk (Bassi 1875; Kingscote 1950; Erhardová 1961; Hood et al. 1997) or white-tailed deer (Kralova-Hromadova et al. 2011). The fluke's habitat tolerances are relatively broad: standing water, ubiquitous aquatic snails, and emergent vegetation. These conditions occur frequently within the natural range of wild elk and in large fenced paddocks used by game-farmed elk. A drenching protocol was developed to remove flukes from a population with relatively low prevalence and intensity (Pybus et al. 1991); however, its efficacy in one-time application in elk from a free-ranging population with high prevalence and intensity is unknown. Wildlife managers considering such populations as source animals for translocation should consider the potential for translocation of liver flukes. Similarly, managers of zoos or game farms where captive cervids have access to natural wetlands should consider incorporating fluke control methods into the general herd husbandry to limit a build-up of *F. magna* on pastures and ranges. While incompletely documented, giant liver flukes in free-ranging cervids can be associated with mortality of individuals in various species and with localized mortality events in elk.

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