



Living with liver flukes: Does migration matter?

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ABSTRACT

Migration is typically thought to be an evolved trait driven by responses to forage or predation, but recent studies have demonstrated avoidance of parasitism can also affect success of migratory tactics within a population. We evaluated hypotheses of how migration alters parasite exposure in a partially migratory elk (*Cervus canadensis*) population in and adjacent to Banff National Park, Alberta, Canada. Equal numbers of elk remain year-round on the winter range or migrate to summer range. We quantified diversity and abundance of parasites in faecal elk pellets, and prevalence (number of infected individuals) and intensity (egg counts) of giant liver fluke eggs (*Fascioloides magna*) in faeces across migratory tactics. We tested whether giant liver fluke intensity in faeces was affected by elk use of wetlands, elevation, forage biomass, and elk concentration in the previous summer. We rejected the “migratory escape” hypothesis that suggests migration allowed elk to escape parasite exposure because migrant elk had the highest richness and evenness of parasite groups. We also rejected the hypothesis that prevalence was highest at highest summer densities because higher-density resident elk had the lowest diversity and giant liver fluke egg presence and intensity. Instead, the high prevalence and intensity of giant liver flukes in migrants was consistent with both the hypothesis of “environmental tracking”, because elk that migrated earlier may expose themselves to favourable parasite conditions, and with the “environmental sampling” hypothesis, because giant liver fluke intensity increased with increased exposure to secondary host habitat (i.e., wetland). Our results indicate that differential exposure of different migratory tactics that leave the winter range has a greater influence on parasites than the concentration of elk that reside on the winter range year-round.

1. Introduction

Studies of ungulate populations often focus on forage and predation interactions, but parasites can be as important in affecting individual fitness (Albon et al., 2002; Hughes et al., 2009; Tompkins and Begon, 1999). Parasites can affect host body condition (Davidson et al., 2015; Irvine et al., 2006), fecundity (Akinyi et al., 2019; Albon et al., 2002; Hicks et al., 2019), and survival (Pybus et al., 2015; Schmitz and Nudds, 1994) in ungulates. In partially migratory populations where some individuals migrate and others are sedentary (Chapman et al., 2011), parasites could alter the relative fitness of migratory tactics. The interaction between migration and parasitism is not well understood (Mysterud et al., 2016; Pruvot et al., 2016; Risely et al., 2017), but differential parasite abundance among ungulates that follow different migratory tactics has been documented. For instance, red deer (*Cervus*

elaphus) that migrated longer distances to summer at higher elevations had lower ectoparasitic tick (*Ixodes ricinus*) infestation (Mysterud et al., 2016) whereas migrant caribou (*Rangifer tarandus tarandus*) in Norway had significantly lower warble fly larvae (*Hypoderma tarandi*) abundance than those that did not migrate (Folstad et al., 1991).

Several hypotheses have been proposed for how differences in parasite infections in migrant and resident individuals may arise. The “migratory escape” hypothesis suggests migrants may reduce parasite infection by escaping contaminated ranges before a peak infectious period when conditions for parasite transmission improve (Fritzsche McKay and Hoye, 2016; Loehle, 1995; Mysterud et al., 2016; Pruvot et al., 2016; Qviller et al., 2013). Conversely, it is hypothesized that migrants may have higher parasite infections because they are exposed to novel parasites due to greater “environmental sampling” of geographic space along migration corridors or stop-over areas or to more

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Table 1 Hypotheses predicting the effects of migration on parasite infection in populations and individuals and the potential tactic-level effect on migration within the Ya Ha Tinda elk population. S1 = Supplementary Table 1.

Hypothesis	Description of hypothesis	Predictions for parasite infection of migratory tactics			
		West	Resident	East	
H1: Migratory Escape	Migration reduces exposure to concentrations of infective stages on contaminated winter range.	Medium	High	Low	
H2: Elk Density	Higher clustered resources and a predation refuge lead to concentration of infective stages	Low	High	High	
H3: Environmental tracking	Environmental tracking of early green-up at low elevation extends migrant exposure to infective stages.	Low	Medium	High	
H4: Environmental sampling	Migrant exposure to more diverse or more secondary host habitat	High	Low	High	
	Conditions on allopatric ranges				
	Eastern migrants leave the winter range 2–3 weeks earlier on average than western migrants				
	Resident and eastern elk more concentrated on summer ranges with larger group sizes due to clustered resources and predation refuges (S1)				
	The eastern summer range is at lower elevation than the resident and western summer ranges (1560 m, 1740 m, and 1880m; S1)				
	Eastern and western migrants are exposed to more diverse habitats and have more wetland habitat on their summer range than resident elk (S1)				

secondary hosts on allopatric ranges (Altizer et al., 2011; Bauer and Hoye, 2014; Koprivnikar and Leung, 2015; Leung and Koprivnikar, 2016; Vanderwaal et al., 2015). At the same time, according to the “environmental tracking” hypothesis, migrants that track favourable conditions, such as early forage green-up associated with higher temperatures at low elevation, are exposed to favourable conditions for parasite growth (Altizer et al., 2006; Teitelbaum et al., 2018) and parasite exposure may be prolonged. Finally, migrants and residents may be disproportionately exposed to parasites through contact rates or increased faecal deposition of infective stages if they are at higher density or are more concentrated, potentially due to patchy distribution of habitat or behavioural responses to predation (Fritzschke McKay and Hoye, 2016; Hegemann et al., 2019; Lankester and Peterson, 1996).

In this research, we compared parasite infections of elk (*Cervus canadensis*) in a partially migratory population to address these hypotheses (Table 1). The Ya Ha Tinda elk population winters on a large fescue (*Festuca campestris*) grassland that borders Banff National Park in Alberta (Fig. 1). The population has declined since the early 2000s from over 1200 to ~450 elk. During the decline, there was an increase in the proportion of individuals remaining year-round on winter range (residents), as well as a shift in the behaviour of migrants from predominately westward into Banff National Park (western migrants) to about equal numbers of elk that also migrate eastward (eastern migrants) onto low-elevation, industrial lands forest along the Red Deer river (Eggeman et al., 2016). We predicted that if migrant elk escaped high parasite exposure on the winter range in spring (Table 1: H₁), both western and eastern migrants would have lower parasite infections than resident elk that remain on winter range year-round. In addition, if elk density was key in influencing parasite exposure (H₂), we predicted that parasite levels would be highest in residents because there are more residents than migrants and they concentrate at the Ya Ha Tinda because it is a human refuge from predation (Eggeman et al., 2016). Alternatively, if migrating to low-elevation ranges 2–3 weeks earlier than western migrants exposed elk to favourable conditions for parasite infection earlier (H₃), eastern migrants would have the highest parasite infestations. Lastly, if conditions on allopatric summer ranges rather than timing of migration contributed to parasite infection (H₄), differences in parasite infection would be consistent with habitat diversity and the extent of suitable habitat of secondary hosts across the ranges (Bauer and Hoye, 2014; Vanderwaal et al., 2015; Teitelbaum et al., 2018).

We quantified differences in parasites among migratory tactics at two levels. At the population level, we compared parasite diversity and faecal egg counts from unmarked elk collected during summer on the allopatric ranges. At the individual-animal level we collected faeces from Global Positioning System (GPS)-collared elk in late winter. We also related giant liver fluke (*Fascioloides magna*) prevalence (number of infected individuals) and intensity (egg counts in those individuals) to habitat characteristics used in the previous summer because the prepatent period for *F. magna* (time from infection to egg excretion in faeces) is ≥ 6 months (Foreyt, 1996; Pybus et al., 2015). The giant liver fluke is an environmentally transmitted trematode where the adults infect the liver of an ungulate definitive host, releasing eggs into the faeces that hatch and invade secondary hosts (aquatic snail), multiply, and develop into infective stages that encyst on aquatic vegetation to be consumed by other definitive hosts (Pybus, 2001; Pybus et al., 2015). Our study is among the first that relates diversity, prevalence, and intensity of parasites of individual, free-ranging cervids to their use of the environment and contributes to a growing understanding of the relationship between parasitism and migration (Kołodziej-Sobocińska, 2019; Satterfield et al., 2018).

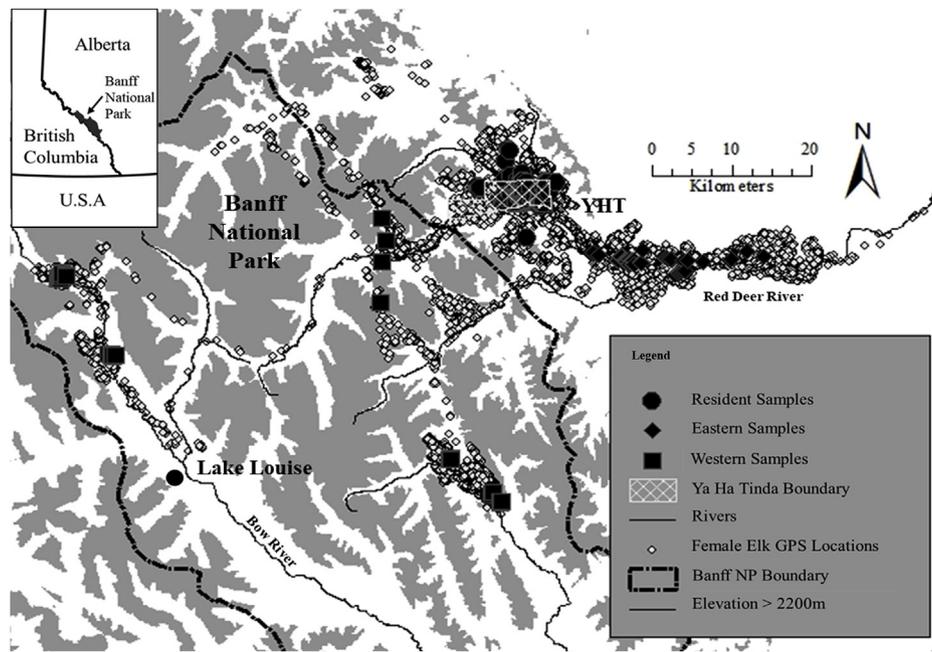


Fig. 1. Study Area Map. The Ya Ha Tinda in relation to Banff National Park in western Canada and locations of elk faecal samples collected in 2017–2018 by migration tactic.

2. Materials and methods

2.1. Pellet collection

We collected faecal pellets from adult female elk for analysis of *F. magna* eggs using two sampling designs. At the population level, we collected samples from unmarked individuals in elk groups located by tracking a collared female elk with the goal of collecting fresh pellet samples from ~30 unknown individuals in each of the migratory tactics in each of 2 time periods ($n = 60/\text{migratory tactic}/\text{year}$). Collections were made in spring (11–31 May in 2017, 4–27 May in 2018) on winter range from collared elk and in summer (2 July – 24 August in 2017, 30 June – 23 August in 2018) from unmarked elk on allopatric summer ranges (Supplementary Table 2). Using collared elk avoided resampling the same group, improving the independence of samples. Pellets were sampled after elk groups had moved away. We collected pellets of different size, shape, and colour at least 5 m apart (Vanderwaal et al., 2015), and in proportion to $\leq 20\%$ of the number of elk in the group to maximize the likelihood that pellets came from different animals. We collected only fresh pellets (< 1 day old), which were identified as being wet on the outside with a mucous coating present and green and wet on the inside (Brambilla et al., 2013). To minimize variation in parasite infections due to sex and age, we avoided sampling male elk groups by collecting from groups composed mainly of adult female elk ($> 70\%$) and did not include pellets of calves, which were identified by size.

At the individual elk level, we collected 3 pellet samples from each of 55 GPS-collared elk (35 residents, 9 western migrants, 11 eastern migrants) on the winter range from 25 March to 21 April in 2018 and 2019. Fifteen (10 residents, 2 western migrants, 3 eastern migrants) elk were sampled in both years. Pellets were collected by watching focal elk from horseback 10–50 m away, noting the location visually or with a small flagging-taped rock, and waiting until the elk had moved from the immediate area to collect the sample. All elk monitoring and pellet sampling were consistent with Canadian Council on Animal Care Guidelines and approved by Animal Care and Use committees (the University of Alberta Animal Care and Use Committee Protocol # AUP00000624; University of Montana Institutional Animal Care and Use Committee Protocol # AUP004-16) and by Parks Canada (Permit #

YHTR-2017-26977) and Alberta Environment and Parks (Permit # GP-19-003).

2.2. Parasite egg and larvae extraction from pellets

Pellet material was analysed fresh within 1–7 days of being stored in an air-tight plastic bag in a cool place to prevent development of parasite eggs and larvae before analysis. For sampling giant liver flukes, we analysed haphazardly selected subsamples of 2 g (2 ± 0.2 g) of pellets, using one subsample/individual from unmarked elk in groups and 3 subsamples/individual from collared elk. Giant liver fluke eggs were isolated from pellets using the FlukeFinder® method of differential sieving and sedimentation and examined under a dissecting scope (protocol provided by S. Kutz Lab, University of Calgary). For all other parasites, we selected 4 g (4 ± 0.2 g) of faecal pellets and isolated eggs and larvae using the Wisconsin Double-Centrifugation technique which floats eggs onto slide covers via lower specific gravity than a sugar solution as described by Western College of Veterinary Medicine Parasitology Diagnostic Techniques Handbook. Eggs and larvae were examined under a compound microscope at 100x power and identified based on morphology, to the lowest taxonomic classification possible. We present measures of parasite richness (number of species groups) and evenness (Simpson's evenness; Heip et al., 1998) of eggs per 4 g of pellets for all parasites including liver fluke, whose egg counts we multiplied by two because sampling occurred at 2 g instead of 4 g. We also present average abundance (egg counts in both infected and uninfected individuals) of all parasite groups and giant liver fluke prevalence (proportion of infected individual elk), median intensity (egg counts in those individual elk), and average abundance at the population and individual levels as eggs per 1 g of pellets (EPG) to allow direct comparison to results from other studies.

2.3. Statistical analyses

We derived migration status of collared elk from sequential locations of 2-h or 6-h fixes using a net-squared displacement approach (Bunnfeld et al., 2011) and visual inspection with migrants classified as moving > 15 km from their winter range for > 30 days (Egeman et al., 2016). We assumed elk did not switch between migratory tactics

even though it has been reported in this population (Eggeman et al., 2016), but address the potential bias in the discussion. At the population level, we first tested for differences in presence and intensity of giant liver fluke eggs in early (May) and late summer (July/August) and found no difference in presence ($p = 0.16$, $df = 1$, ANOVA $F = 2.02$) or intensity ($p = 0.28$, $df = 1$, ANOVA $F = 1.19$) in either year. Therefore, we pooled samples across these two periods within years for further analyses. We used a Kruskal-Wallis rank sum test with a post-hoc Dunn's multiple comparisons test to compare population-level richness, Simpson's evenness, and abundance of parasite groups among migration tactics using the lowest possible taxonomic classifications possible ($\alpha = 0.05$; `vegan` and `dunn.test`; Dinno, 2017; Okansanen et al., 2019). We also tested for differences in fluke occurrence between the three migratory tactics (resident as reference) and year of collection (2017 as reference) based on presence/absence using logistic regression and egg intensity with a zero-truncated negative binomial regression at the population level (`glm` and `vglm` from the R packages `stats` and `VGAM`, respectively; R Core Team, 2019; Yee, 2010).

For parasites at the individual elk level, we first determined whether date of faecal collection influenced fluke egg abundance in winter. We related egg abundance to Julian day in 2018 and 2019 independently, and with years combined comparing the fit of a linear, quadratic, cubic, and logarithmic functions to the data based on AIC. We found no linear or nonlinear relationship between sampling date (25 March to 21 April) and giant liver fluke egg abundance in samples collected from individual elk during the winter in either 2018, 2019 or combined (Supplementary Table 3) and thus sampling date was not included in further models. Second, because we did not have data on body condition and calf-at-heel for all individual elk, yet these two factors could influence our comparison among migratory tactics if they differed in sampled animal, we assessed whether body condition and calf-at-heel differed among with migratory tactics. We used χ^2 goodness of fit to determine if equal number of elk within migratory tactics had calves-at-heel in mid-summer ($n = 55$, 91%), and parametric Analysis of Variance (ANOVA) to determine if body condition differed between elk in the three migratory tactics ($n = 24$, 44%). Calf at heel mid-summer was determined from cow-calf resight and elk body condition was determined from scores (Cook et al., 2010) at capture in late February/early March.

We modelled giant liver fluke presence as a function of age and migratory tactic using a logistic mixed-effects model (`glmer` from the R package `lme4`; Bates et al., 2015) and used a zero-truncated negative binomial, mixed-effects model for intensity, with individual elk as a random effect to account for individuals repeated in both years (`glmmTMB` from the R package `glmmTMB`; Brooks et al., 2017). Using the same modeling approach, we also modelled the relationship between giant liver flukes and 4 environmental covariates (elevation, wetlands, herbaceous forage, elk utilization) to address our hypotheses. We weighted values of the 4 environmental covariates by the intensity of use of the landscape of the respective, individual GPS-collared elk during 1 May – 31 October (see below).

We derived elevation from a digital 30-m elevation model (DEM). Wetlands (0 or 1 presence/absence of a wetland) areas were determined by digitizing aerial imagery taken on September 29, 2015 (Google Earth Pro) using a 250-m buffer around flat treeless areas that included water features from a hydrology map to create wetland polygons. For herbaceous forage biomass, we used peak growing season (1 August) herbaceous forage biomass determined by Hebblewhite et al. (2008). As a metric of the concentration of elk use on the landscape, we derived a resource utilization function (RUF; Marzluff et al., 2004). We modelled the RUF by first developing a 100% fixed kernel utilization distribution (UD) using 6-h GPS-relocations of 66 adult female elk monitored across the study area from 2013 to 2016 in Geospatial Modelling Environment (GME version 0.7.4, <http://www.spatial ecology.com>, accessed 10 Sept 2018). We then modelled the values of the UD as a function of herbaceous forage biomass (Hebblewhite et al., 2008), burned areas

(Hebblewhite, 2006), distance to the nearest forest edge, and wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) resource selection functions (Hebblewhite and Merrill, 2007; Nielsen et al., 2002).

In contrast to the RUF, to quantify exposure to each of the 4 variables (elevation, wetland, herbaceous forage biomass, and RUF) within an individual elk's home range, we derived a weight for the relative use each 30 m² cell within the individual's home range. The weights were derived based on a dynamic Brownian Bridge approach (R packages `move`, `raster`, and `rgdal`; Bivand et al., 2019; Hijmans, 2019; Kranstauber et al., 2019) and were multiplied by the value of environmental covariates within the cell. We standardized the weighted covariate values to a mean of 0 and standard deviation of 1 prior to modeling. Herbaceous forage biomass and RUF values were positively correlated ($r = 0.90$) because RUF was a function of herbaceous forage biomass; any other covariates with Pearson correlations $> |0.5|$ correlation also were not used in the same model.

3. Results

3.1. Population-level

We detected several endoparasite groups (where a group is defined as a set of morphologically indistinguishable eggs/larvae) in faecal pellets of the Ya Ha Tinda elk population including *Capillaria* sp., *Dictyocaulus* sp., *Eimeria* spp., *Moniezia* sp., Nematodirines, Protostrongylidae, *Trichuris* sp., Trichostrongyle-type eggs, *Strongyloides* sp., and *Fascioloides magna* (giant liver fluke; Table 2). Richness of parasite groups in faeces of western migrants (0.81) and eastern migrants (0.71) in summer did not differ ($p = 0.12$, $df = 2$, Kruskal-Wallis $\chi^2 = 1.43$) but both were higher than parasite richness for residents (0.45; $p < 0.001$, $df = 2$, Kruskal-Wallis $\chi^2 = 32.4$; Table 2). Western migrants in summer also had higher Simpson's evenness ($p = 0.01$, $df = 2$, Kruskal-Wallis $\chi^2 = 18.2$) and a higher mean abundance for most parasite groups compared to eastern migrants and residents (Table 2). The exceptions were *Eimeria* spp. and giant liver fluke. *Eimeria* spp. abundance was highest in residents ($p = 0.01$, $df = 2$, Kruskal-Wallis $\chi^2 = 6.54$; Table 2) whereas giant liver fluke abundance was higher in eastern migrants ($p < 0.001$, $df = 2$, Kruskal-Wallis $\chi^2 = 42.00$; Fig. 2).

There was high uncertainty among models predicting the presence and intensity of giant liver fluke eggs in elk faeces at the population level (Table 3). The most parsimonious model predicting giant liver fluke presence included only migration tactic, with the odds of eastern migrants excreting fluke eggs being at least 8 times ($\exp \beta = 8.24$) higher than that of the other two migratory tactics. Similarly, intensity of giant liver fluke egg infection was greatest in eastern elk (0.98 ± 0.41 ; $\beta \pm SE$), with higher intensity in 2018 compared to 2017 (0.80 ± 0.40 ; Fig. 2, Supplementary Table 4).

3.2. Individual elk

We found no difference in body condition scores ($p = 0.99$, $df = 2$, $F = 0.007$), among migratory tactics. Western migrants had a lower number of calves-at-heel detections mid-summer (50%) than residents (100%, $p < 0.001$, $df = 1$, $\chi^2 = 13.82$) but not lower than eastern migrants (92%, $p = 0.11$, $df = 1$, $\chi^2 = 2.50$) and residents and eastern migrants did not differ ($p = 0.17$, $df = 1$, $\chi^2 = 0.94$; $n = 50$). In the subset of collared elk, we found no correlation between abundance of giant liver fluke eggs and body condition score ($r = -0.06$, $p = 0.60$, $n = 24$). Abundance of giant liver fluke eggs in elk with calves-at-heel did not differ from those without calves-at-heel ($p = 0.83$, $df = 1$, $F = 0.048$).

Overall, giant liver fluke eggs were detected in 90.6% and 89.6% of individual elk sampled in 2018 and 2019, respectively. There also was high uncertainty among models in predicting presence and intensity of giant liver fluke eggs in the faeces of individual elk (Table 4,

Table 2

Prevalence of *Fasciolodes magna* in elk faeces in and adjacent to Banff National Park, Alberta, Canada. Mean prevalence is reported with 95% confidence intervals, mean (\pm SD) abundance, and median (with range) intensity of infection of parasite eggs in 1 g (EPG) of elk faeces collected from unmarked elk in groups (population-level) on their summer ranges from 11 May through 24 August in 2017 and 2018 and of liver flukes eggs in 1 g (EPG) of faeces collected from individually marked elk from 25 March to April 21, 2018 and 8 April to April 18, 2019. For population-level parasite groups, significant differences ($\alpha = 0.05$) indicated with ^{a, b, c} where no letters indicate no significant difference.

	Eastern	Resident	Western	Overall
Population-level	n = 96	n = 183	n = 51	n = 330
Parasite Richness	0.71 \pm 0.60 ^a	0.45 \pm 0.62 ^b	0.81 \pm 0.65 ^a	0.58 \pm 0.63
Pielou's Evenness	0.15 \pm 0.33 ^a	0.079 \pm 0.24 ^a	0.31 \pm 0.43 ^b	0.12 \pm 0.30
Abundance				
<i>Capillaria</i> sp.	0 ^a	0 ^a	0.04 \pm 0.20 ^b	0.005 \pm 0.08
<i>Dictyocaulus</i> sp.	0.04 \pm 0.18	0.05 \pm 0.54	0.02 \pm 0.08	0.04 \pm 0.40
<i>Eimeria</i> sp.	0.02 \pm 0.15 ^a	0.48 \pm 3.24 ^b	0 ^a	0.26 \pm 2.39
<i>Moniezia</i> sp.	0.03 \pm 0.28 ^a	0 ^a	0.17 \pm 0.96 ^b	0.04 \pm 0.41
Nematodirines	0 ^a	0.004 \pm 0.06 ^a	0.02 \pm 0.07 ^b	0.005 \pm 0.06
Protostrongylidae	0	0.004 \pm 0.04	0.02 \pm 0.12	0.005 \pm 0.06
<i>Trichuris</i> sp.	0.01 \pm 0.11	0.005 \pm 0.04	0.03 \pm 0.13	0.01 \pm 0.08
Trichostrongyle-type egg	0.04 \pm 0.29 ^a	0.03 \pm 0.29 ^a	0.11 \pm 0.33 ^b	0.05 \pm 0.30
<i>Strongyloides</i> sp.	0.03 \pm 0.16 ^a	0.04 \pm 0.39 ^a	0.10 \pm 0.36 ^b	0.04 \pm 0.33
<i>Fascioloides magna</i>				
Prevalence	0.65 (0.54,0.74)	0.29 (0.23,0.36)	0.39 (0.26,0.54)	0.41 (0.36,0.46)
Abundance	11.93 \pm 3.45	1.54 \pm 0.55	2.47 \pm 1.16	5.31 \pm 1.72
Intensity	5.8 (0.5–189.5)	2.0 (0.5–150.0)	3.0 (0.5–11.0)	4.0 (0.5–189.5)
Individual elk -level	n = 11	n = 35	n = 9	n = 55
<i>Fascioloides magna</i>				
Prevalence	0.51 (0.41,0.62)	0.34 (0.29,0.40)	0.38 (0.28,0.50)	0.38 (0.34,0.43)
Abundance	5.88 \pm 9.8	1.32 \pm 2.19	3.02 \pm 5.34	2.56 \pm 5.44
Intensity	7.5 (0.5–33.5)	3.5 (0.5–16)	5.5 (0.5–24)	4.5 (0.5–33.5)

Supplementary Table 5). The most parsimonious model for predicting egg presence included wetland and herbaceous forage biomass, whereas the most parsimonious model predicting egg intensity was elevation (Table 4). Migration tactic was among the top models for giant liver fluke egg intensity where eastern migrants had highest egg intensity, but not in the top model for individual giant liver fluke egg prevalence (Tables 2 and 4).

4. Discussion

Our results indicate that, with the exception of *Eimeria* spp., migrant elk had higher diversity, prevalence, and intensity of parasites than resident elk, which is consistent with the environmental sampling and not the migratory escape hypothesis (Loehle, 1995; Altizer et al., 2011; Teitelbaum et al., 2018). Higher infestation in eastern migrants is not a sampling bias because we controlled for elk age and sex differences, which can influence infection levels in many parasites (Albery et al., 2018). Ranges of eastern elk also were the only ones grazed by cattle, but cattle are dead-end hosts for giant liver fluke (i.e., do not excrete eggs; Swales, 1935; Pybus, 2001). For this reason, Pruvot et al. (2016) hypothesized that consumption of giant liver fluke eggs by cattle may reduce infection of elk, which is contrary to our results. However, grazing pressure of cattle on summer ranges of the eastern migrants is much lower than in those populations classified as 'exposed to cattle' in the study by Pruvot et al. (2016). Instead, we hypothesize the difference in parasite infestation in eastern migrants is due to environmental sampling. First, eastern migrant elk move to low-elevation summer ranges 2–3 weeks earlier and their pronounced increase in giant liver flukes may be exacerbated by the early development of parasites associated with temperature-dependent environmental conditions. If warmer temperatures at lower elevations are sufficient to induce earlier larval production in snails (Olsen, 1944), then eastern migrants are likely exposed to giant liver fluke infective stages for a longer period than residents and western migrants. Second, we suggest eastern migrants are more exposed to snail secondary host habitat because there are more wetlands in the summer ranges of elk migrating east, and we

found a positive relationship between giant liver fluke prevalence in faeces of individual elk and their use of wetlands.

We also did not find evidence for increased infection of giant liver flukes with increasing definitive host concentration in space. Resident elk comprised the largest proportion of the Ya Ha Tinda elk population (Eggeman et al., 2016) and consistently maintained larger group sizes than migratory elk during summer (Hebblewhite and Merrill, 2009), yet they had the lowest parasite diversity and giant liver flukes. Vanderwaal et al. (2015) also reported that giant liver fluke infection in white-tailed deer (*Odocoileus virginianus*) in Minnesota was not correlated with deer abundance (pellet counts); instead, they also report an increase in liver flukes with an increase in the extent of wetlands (rooted-floating aquatic marshes). As a result, for parasites that involve a secondary host, definitive host local density alone may not reflect potential risk of infection. Although we found the extent of secondary host habitat (i.e., wetlands) within an individual elk's summer range influenced giant liver fluke infection, we found no direct link to the relative intensity of use of an area by collared individuals or an interaction between intensity of use of an area and extent of wetlands. We suspect it will require a more rigorous assessment of infection pressure to discern their joint impact on risk of infection.

The higher diversity and the abundance of some parasite groups in western migrants may be related to sharing summer ranges with elk from Banff National Park, which could foster infestation of parasites among elk populations (Teitelbaum et al., 2018). Summer ranges of western migrants are within 20 km of the town of Banff and there is overlap in summer range with elk from the town of Banff (Morgantini and Hudson, 1988; Woods, 1991). Supporting the intermixing between these two populations in summer is the fact that western migrants were the only elk where we found *Capillaria* sp., a nematode detected in elk populations near the town of Banff (Edwards, 2013) but not detected in residents or eastern migrant elk from the Ya Ha Tinda. If this hypothesis is true, western migrants may be responsible for the eastern expansion of giant liver fluke into the Ya Ha Tinda elk population. In the 1920s, giant liver fluke was rare in resident elk of the Bow Valley in Banff National Park; however, by the late 1960s prevalence of giant liver

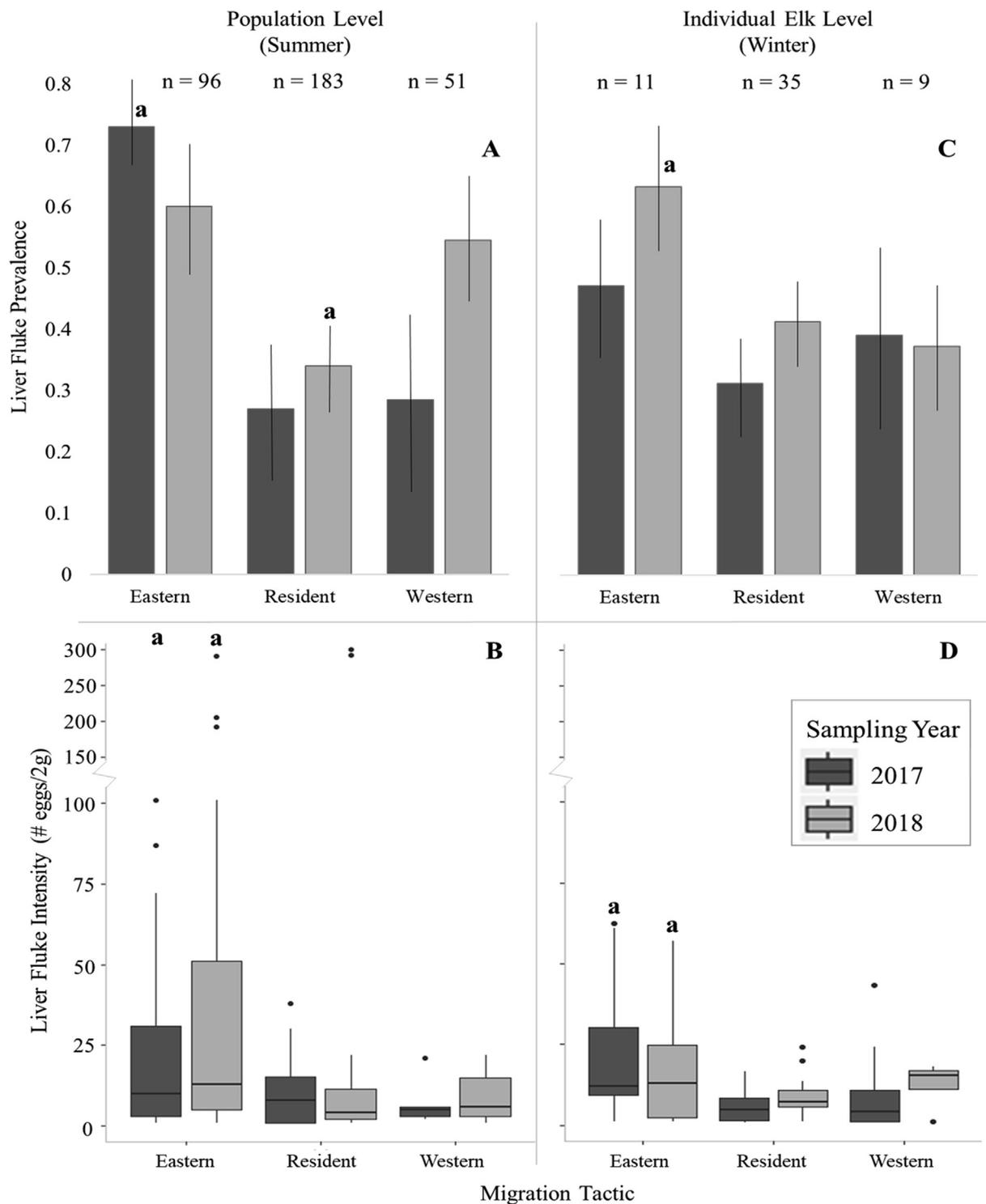


Fig. 2. Liver fluke prevalence and intensity. Liver fluke prevalence (top; infected animals/all animals sampled) and liver fluke intensity (bottom; EPG) detected in faecal pellets of each elk migrant tactic at the population (left) and individual level (right) separated by sampling year (2017 in dark grey, 2018 in light grey). Bars represent 95% confidence intervals for prevalence and standard error for intensity. Significant differences within years ($\alpha = 0.5$) are indicated with a,b,c where no letters indicate no significant difference.

flukes in elk approached 50% (Pybus et al., 2015). In contrast, in the early 1960s, < 1% of the 339 elk harvested from the Red Deer River valley in Banff National Park, which likely included western migrants from the Ya Ha Tinda population, were infected with liver fluke (Flook and Stenton, 1969). It is possible that overlapping ranges between the western migrants and the Bow Valley elk on summer range resulted in spill-over and amplification of giant liver fluke that subsequently

resulted in the translocation of the parasite into the broader Ya Ha Tinda elk population.

The consistency of the patterns we observed in how migration influences parasite infections compared to other studies are mixed. In their review of 93 ungulate species from the Global Mammal Parasite Database 2.0, Teitelbaum et al. (2018) reported higher parasite richness in migrants. Shaw et al. (2018) also reported from their review of 19

Table 3
Summary of model selection for *F. magna* egg presence in 1 g of faeces at the population level based on AICc by migration tactic and year.

Model Structure	k	AICc	Δ AICc	AICc Wt.
Presence				
Migration tactic + year + migration tactic x year	5	417.4	0.00	0.60
Migration tactic	3	419.4	2.05	0.21
Migration tactic + year	4	419.7	2.30	0.19
Year	2	447.2	29.77	0.00
Null	1	448.5	31.12	0.00
Intensity				
Migration tactic + year	4	1028.3	0.00	0.60
Migration tactic	3	1029.7	1.43	0.30
Migration tactic + year + migration tactic x year	5	1032.2	3.91	0.09
Year	2	1035.7	7.34	0.02
Null	1	1313.8	285.5	0.00

studies that parasite richness was most often higher in individuals that migrated than were resident, but the same was not true of intensity and prevalence. In this study, we found migrants had both the highest diversity of parasites overall and the highest intensity and prevalence of giant liver flukes compared to residents. In contrast, in studies of parasites of caribou (Folstad et al., 1991) and red deer (Mysterud et al., 2016) in Norway, intensity of warble flies (*Hypoderma tarandi*) and ticks (*Ixodes ricinus*), respectively, were lower in migrating individuals, which lead to the conclusion that migration leads to escape from ectoparasites.

Mixed results among studies highlight the importance of considering sampling designs and the context of migratory patterns in populations. For example, Pruvot et al. (2016) sampled liver flukes in 10 elk populations (including the Ya Ha Tinda) in Alberta, most of

which included both migratory and resident individuals. They reported that giant liver fluke prevalence and intensity were lower in migratory populations. This led them to conclude that migrant elk escape parasite exposure, which is contrary to our results. In sampling parasites, Pruvot et al. (2016) collected faecal pellets from March to May 2010 from individual elk of unknown migratory status on their wintering grounds and related the parasite levels to an estimate of the proportion of migratory elk in each population. Pruvot et al. (2016) found a $27 \pm 10\%$ prevalence in the Ya Ha Tinda population in 2010 compared to our overall prevalence between 36 and 41% during 2017 and 2018. Assuming random sampling of the population, results of Pruvot et al. (2016) may reflect a lower prevalence of infection because approximately ~50% of the population are low-infection residents, and only half of the migrants are the high-infection eastern migrants. In contrast, our samples were collected from marked individuals of known migratory status on the winter range, and our population-level collection of faeces was on allopatric ranges during spring and summer, which also accounted for migration tactic of unmarked individuals. Switching by elk among migratory tactics, as has been documented for the Ya Ha Tinda (Eggeman et al., 2016), further complicates interpretations and could bias results towards a lack of differences between tactics. These discrepancies between studies highlight the importance of unique migratory patterns. Migratory elk in the Ya Ha Tinda elk population move to two distinct areas, with western migrants moving onto higher elevation ranges in Banff National Park and eastern migrants moving to lower-elevation, warmer landscapes that are likely better suited to liver fluke intermediate hosts. Our studies at the Ya Ha Tinda illustrate the challenge of generalizing the effect of migration on parasite levels when individuals migrate to summer ranges differing in landscape and climate.

Declines in migratory behaviour of ungulates with increasing resident populations is becoming a regional phenomenon (Barker et al.,

Table 4
Summary of model selection results based on AICc for liver fluke egg presence and counts in 1 g of individual elk faeces in 2018 and 2019. All models include a random effect of elk ID and threshold of zero (2018 was used as the reference year and elk resource utilization function is RUF). Beta coefficients (β) with standard error (SE), upper and lower 95% confidence intervals (CI) for the top model parameters based on AICc for a logistic and zero-truncated negative binomial model predicting liver fluke egg counts in 1 g of individual elk faeces in 2018 and 2019. The elk resource utilization function is RUF.

Model	AICc	Δ AICc	AICc Wt.	Variable	$\beta \pm SE$	95% CI Lower	Upper
Presence (logistic)							
Model 1	190.0	0.00	0.21	Intercept	-0.18 ± 0.36	-0.94	0.56
				Wetland	1.54 ± 0.60	0.55	2.93
				Forage	-1.46 ± 0.58	-2.83	-0.47
Model 2	190.8	0.89	0.14	Intercept	-0.31 ± 0.38	-1.13	0.45
				Wetland	1.59 ± 0.61	0.58	3.02
				Forage	-1.49 ± 0.59	-2.91	-0.49
				Year 2018	0.57 ± 0.52	-0.44	1.63
Model 3	191.6	1.63	0.09	Intercept	-0.02 ± 0.42	-0.89	0.88
				Wetland	1.41 ± 0.64	0.22	2.84
				Forage	-1.44 ± 0.61	-2.83	-0.37
				Wetland x forage	-0.26 ± 0.38	-1.08	0.47
Intensity (zero-truncated negative binomial)							
Model 1	545.3	0.00	0.13	Intercept	2.06 ± 0.30	1.47	2.64
				Elevation	-0.46 ± 0.21	-0.88	-0.03
				Year	0.24 ± 0.23	-0.22	0.70
Model 2	545.4	0.17	0.12	Intercept	2.10 ± 0.28	1.55	2.64
				Elevation	-0.49 ± 0.20	-0.88	-0.10
				RUF	-0.32 ± 0.24	-0.79	0.13
Model 3	545.9	0.62	0.10	Year	0.21 ± 0.24	-0.26	0.68
				Intercept	2.12 ± 0.27	1.60	2.65
				Elevation	-0.68 ± 0.26	-1.19	-0.16
				Wetland	-0.16 ± 0.24	-0.63	0.31
Model 4	546.2	0.93	0.08	Elevation x Wetland	-0.30 ± 0.18	-0.65	0.05
				Year	0.19 ± 0.24	-0.27	0.66
				Intercept	1.85 ± 0.37	1.12	2.58
				Eastern Migrants	1.12 ± 0.52	0.08	2.15
				Western Migrants	0.02 ± 0.62	-1.21	1.25

2019; Phillips and Szkorupa, 2011), but whether parasites play a role in this is unknown. At the Ya Ha Tinda, there is evidence that elk are top-down rather than bottom-up limited primarily by density-independent wolf predation (Hebblewhite et al., 2018). Nevertheless, we also have argued that differences in summer range conditions may influence body condition, thus influencing pregnancy and calf weights (Hebblewhite et al., 2009). Parasite infection may act in conjunction with body condition to impact the fitness of individuals through sub-lethal effects (Altizer et al., 2011). For example, if increased giant liver fluke infection persists or worsens in eastern migrant elk from the Ya Ha Tinda, fitness benefits experienced by eastern migrants from earlier green-up during calving (Berg, 2019), which may have contributed to the recent increase of elk following the migration tactic, may be off set by parasites. While elk can survive with low level endoparasite infection, severe infections of giant liver fluke are known to cause mortality and even moderate cases could have impacts on survival when acting in conjunction with forage quality and predation (Pybus, 2001). Understanding how parasites contribute to altering these trade-offs is a key question for parasitologists to address if we are to understand the role of parasites in the maintenance of partial migration (White et al., 2018; Shaw et al., 2018; Berg et al., 2019). Further, current land use and future climate changes may modify host-parasite interactions (Barker et al., 2019; Jore et al., 2011; Kutz et al., 2013) indirectly by altering the spatio-temporal dynamics of habitat suitability for both secondary and definitive hosts (Pybus et al., 2015). Here we have illustrated an approach to assess endoparasite infections of elk following migratory tactics but conclude that as in our study, results may be context specific.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijppaw.2020.05.002>.

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