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POPULATION DYNAMICS OF ENTERIC PARASITES IN THE ENDANGERED VANCOUVER ISLAND MARMOT (*MARMOTA VANCOUVERENSIS*)

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Fecal egg count
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Endangered species
Island endemics
Captive breeding

ABSTRACT

Enteric parasites can have wide-ranging effects throughout an ecosystem, often driving coevolutionary and ecological processes. Parasites have long been overlooked in conservation efforts because of the negative impact inflicted on their hosts; however, parasites make up a significant component of Earth's biodiversity and host conservation efforts need to be parasite inclusive. The Vancouver Island marmot (VIM), *Marmota vancouverensis*, is an endangered alpine rodent endemic to Vancouver Island, British Columbia, Canada. Captive-bred VIMs are released to augment the wild population, but their susceptibility to parasites is unknown. The objectives of this study were to describe the diversity, prevalence, severity, and temporal variation of VIM enteric parasites. Noninvasive fecal samples were collected from wild and captive marmots and analyzed using a modified McMaster fecal egg floatation technique to indicate parasite prevalence and relative mean abundance. We identified oocysts and ova from 3 parasite taxa including a protozoan coccidium not previously described in the VIM (prevalence 68%), an ascarid nematode *Baylisascaris laevis* (prevalence 82%), and an anoplocephalid cestode *Diandrya vancouverensis* (prevalence 8%). Depending on the species, comparisons revealed variation in parasite infection by sex, by colony, and between wild and captive VIMs, but not among age classes or by female reproductive status. Finally, captive VIMs displayed significant monthly variation in parasite prevalence and mean egg abundance, suggesting a seasonal influence on parasite egg shedding. This information is critically important for future research investigating the influences of these trends on the health, ecology, and conservation of VIMs and their parasites.

Parasites can infect every trophic level in an ecosystem with significant wide-ranging effects on their hosts including increased stress, decreased survival, and lower fitness (Van Vuren, 1996; Degen, 2006; Gooderham and Schulte-Hostedde, 2011; Patterson et al., 2013). Furthermore, parasites can drive the coevolution of their hosts through an evolutionary arms race (Hugot, 2006). As parasites continue to evolve novel ways to infect new hosts, hosts are constantly under selection to defend against parasitism. In this way, the coevolution between parasites and their hosts can result in significant adaptations to maximize fitness (i.e., production of offspring) for both the parasite and the host. One such example is the coevolution of virulence, which drives adaptations to minimize the lethal effects of the parasite on the host, increasing both host and parasite fitness (Bull, 1994). Furthermore, parasites play critical roles in promoting host proper immune functioning, regulating populations and communities of hosts on the landscape, and even promoting genetic diversity (Coltman et al., 1999; Spencer and Zuk, 2016; Ianiro et al., 2022; Selbach et al., 2022). Many parasites evolved much earlier than their contemporary hosts and therefore likely coevolved the parasitic lifestyle as the latter underwent speciation (Hugot, 2006). Hitching a ride with their host in their newly acquired niche, parasites have become widespread, occurring in every ecosystem on the planet (Krasnov et al., 2006; Nieberding and Morand, 2006).

Endoparasites of mammals commonly have complex life cycles involving multiple intermediate hosts and high host specificity (Poulin et al., 2006). Routes of transmission between hosts often include the parasite eggs being consumed through the fecal–oral route and the ingestion of larvae from consuming an infected intermediate host (Ebermann, 1976). In this way, parasites can interact with different organisms across multiple trophic levels in an ecosystem. The dispersal of small mammals throughout an ecosystem can be limited because of the physiological cost of parasite burden, meaning that small mammals can be forced to live in suboptimal habitats to avoid parasitism (Zanet et al., 2017). Similarly, the ability of the parasite to complete its life cycle often depends on trophic interactions among intermediate hosts. This suggests that the dispersal of the parasite can be severely limited to the sympatric range of their host organisms (Zanet et al., 2017). As a result, parasites both influence and are limited by the distribution of their host species. Parasites not only represent a powerful regulatory force in ecosystems but make up

a significant portion of the biodiversity on Earth, and our understanding of their importance and their need for conservation is only just beginning (Okamura et al., 2018; Lymbery and Smit, 2023). A paradigm shift toward parasite-inclusive conservation is underway, which recognizes the value of parasites for their biodiversity and critical ecological roles (Dougherty et al., 2015).

Marmots (*Marmota*, Rodentia) have many parasites commonly found in other species with complex life cycles and intermediate hosts, which has enabled further study into the ecological and evolutionary impacts of parasitism (Van Vuren, 1996; Callait and Gauthier, 2000; Zanet et al., 2017). For example, yellow-bellied marmots (*Marmota flaviventris*) showed either increased or decreased rates of foraging compared with uninfected individuals depending on the species of endoparasite with which they were infected (Chmura et al., 2016). Furthermore, Nouri and Blumstein (2019) demonstrated that yellow-bellied marmots infected with *Eimeria* have louder vocalizations than uninfected marmots and suggested that marmot vocalization could potentially be an honest indicator of physiological condition. Alpine marmots (*Marmota marmota*) had a higher risk of enteric parasite infections at lower elevations, suggesting that parasite burden may be a possible constraint on their distribution on the landscape (Zanet et al., 2017). Additionally, alpine marmots with increased ectoparasite loads have longer maternal dependence and lower offspring overwinter survival (Arnold and Lichtenstein, 1993).

The Vancouver Island marmot (*Marmota vancouverensis*; Swarth 1911; hereafter VIM) is endemic to Vancouver Island, British Columbia and is one of Canada's most endangered mammals. The population dropped to a low of less than 30 individuals, likely from anthropogenic habitat modification, and a captive breeding program was initiated to prevent extinction and help recovery through augmentation (COSEWIC, 2019). Studies focused on the conservation of VIMs have investigated hibernation and breeding in captivity (Aymen et al., 2021; Graham et al., 2024), predator recognition (Dixon-MacCallum et al., 2021), genetic diversity (Barrett et al., 2022), and optimal release strategies (Lloyd et al., 2019), but an examination of the diversity and prevalence of their parasites is overdue. Mace and Shepard (1981) identified 2 intestinal helminth species during the necropsy of a single wild female VIM. These included an ascarid nematode, *Baylisascaris laevis* Leidy 1856, commonly found in other marmot species, and an anoplocephalid cestode that they described, on the basis of unique morphology, as a novel species *Diandrya vancouverensis*. Recent genetic analyses have confirmed that *D. vancouverensis* is a unique species endemic to the VIM and suggest that *B. laevis* on Vancouver Island is also likely divergent from the mainland population (Barrera et al., 2022). However, until now there has been no further study to characterize the patterns of endoparasitism in VIMs or to estimate the prevalence of these species.

Here, we investigated enteric parasites in the VIM using noninvasive fecal samples to assess the diversity of parasites and compare how prevalence and relative mean abundance vary by host age, sex, female breeding status, and across wild colonies. We also compared parasite load (defined here as prevalence or mean abundance) between wild and captive marmots and tested for temporal variation by repeatedly sampling captive individuals across the active season.

MATERIALS AND METHODS

Sample collection

As the VIM is an endangered species, we used noninvasive fecal samples to quantify enteric parasite load. Fecal samples from wild VIMs were opportunistically collected by the Marmot Recovery Foundation from 2003 through 2020 during live captures (June to September) and stored at −20 C. Wild marmots are tagged and monitored over their lifetime, which makes it possible to know the age of each individual and the reproductive status of each female in the sampling year. We analyzed 38 samples from wild marmots, of which 3 were collected in 2003, 1 in 2014, and the remainder from 2017 to 2020. Samples were pooled across years in all subsequent analyses because of limited sample sizes. Of the 38 wild samples, 18 were from females, 17 were from males, and 3 were of unknown sex, as the samples were collected from burrows where the identity of the marmot could not be confirmed. Of the female marmots, 8 were reproductive in the year of sampling and 10 were nonreproductive. VIMs mate upon emergence from hibernation between late March and early May, females gestate for ∼34 days, and offspring are weaned after ∼30 days of lactation, usually by July, leaving breeding females only 2 mo to prepare for hibernation by mid-September (Bryant, 1998; Keeley et al., 2012). As a result, female VIMs typically breed biennially as the cost of hibernation and reproduction is believed to be too extreme to breed annually (Bryant, 1996). Marmots were grouped into 4 age classes with approximately equal numbers of individuals, including pups that were born the same year the sample was collected ($n = 9$), yearlings that were born the year before the sample was collected ($n = 11$), 2- and 3-yr-old marmots ($n = 10$), and adult marmots ≥4 yr of age ($n = 7$). Wild samples were collected from a total of 15 colonies; however, only 3 colonies had adequate sample sizes for comparisons (Fig. 1; Suppl. Data, Table S1). Six samples were collected on Mt. Arrowsmith, 4 samples were collected from the colony at Labour Day Lake, and 10 samples were collected on Mt. Washington.

Fecal samples from captive VIMs were collected from group enclosures at the Tony Barrett Mt. Washington Marmot Recovery Centre in the first week of each month from June to October of 2020 and stored at −20 C. As these enclosures housed between 1 and 5 marmots, it was not possible to acquire a monthly fecal sample from individual marmots. However, as all members of each group lived closely together and there was limited movement of marmots among groups, samples from each enclosure were considered representative of all the individuals in that enclosure. We analyzed 1 sample from each enclosure collected during the first week of each month from June to October, resulting in 20 samples per month replicated over 5 mo. However, as marmots were occasionally moved between enclosures, we excluded enclosures that gained a new marmot throughout the study period as this could result in a nonrepresentative sample. This left us with 10 enclosures that had samples from the same group of marmots for each month of our study period.

Lab procedures

We examined fecal samples for oocysts and ova using a modified McMaster technique, which provides a standardized estimate of abundance among samples (Vadlejch et al., 2011; Ballweber et al., 2014). Briefly, 1 g of fecal material was crushed and suspended in 10 ml of Sheather's sugar solution (specific gravity: 1.27) and then

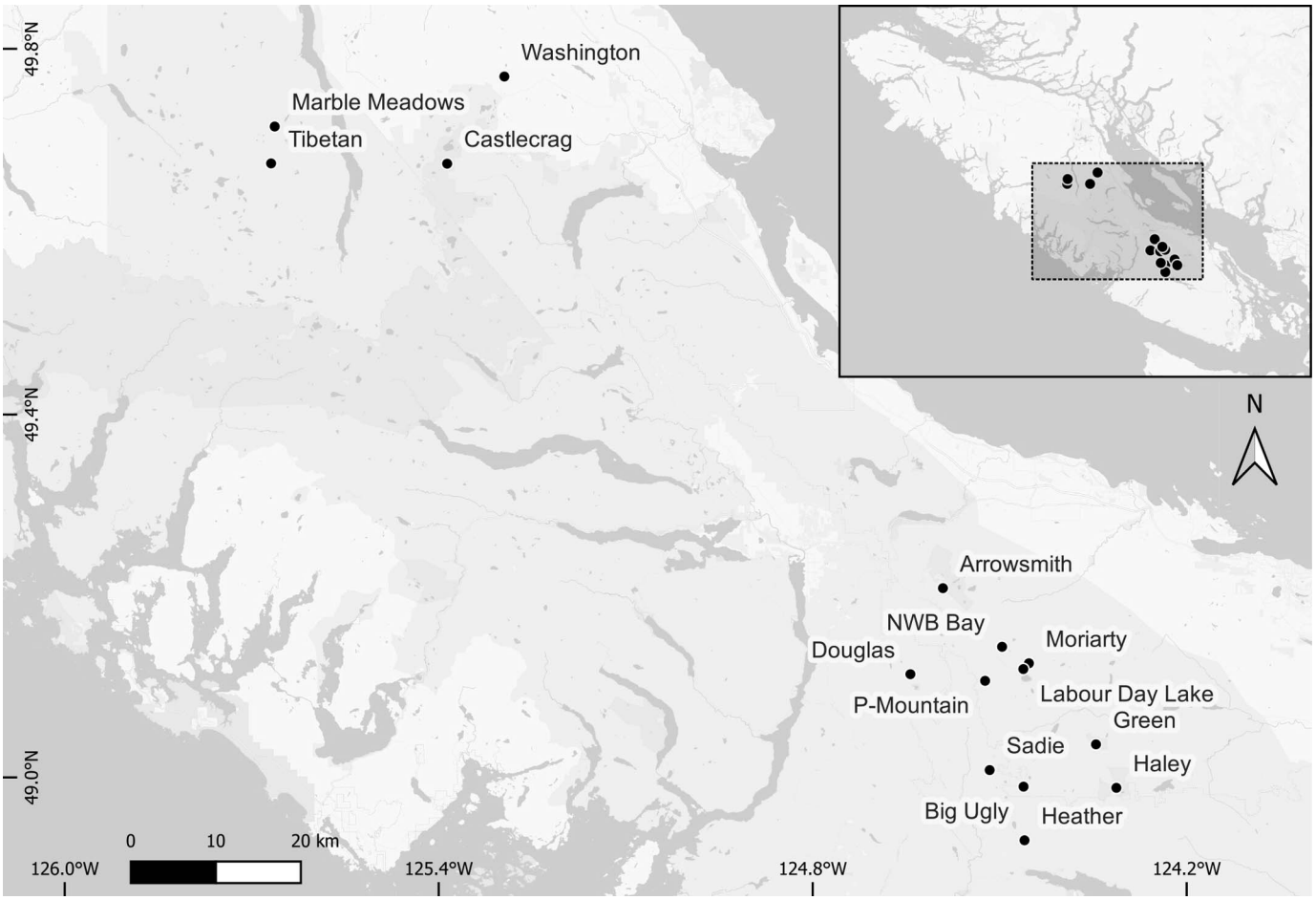

Figure 1. Location of wild Vancouver Island marmot colonies where fecal samples were collected. Base maps from CartoDB.

strained through 2 layers of cheesecloth. Each vial was topped up with Sheather's solution and spun in a washtub centrifuge for 5 min at 640 *g* to float any eggs. We then pipetted 60 µl of supernatant into each of the 2 counting chambers on a McMaster slide (120 µl total) and let the slide rest for 5 min before examination. We counted every type of egg (i.e., oocyst and ovum) separately, either inside or touching the gridlines at ×100 magnification. The total number of eggs from both chambers was then multiplied by 50 to give the number of eggs per gram for each parasite taxon. After counting, a small volume of solution (~5 µl) from a positive sample was transferred to a regular slide and covered with a coverslip for viewing at ×400 magnification. Egg size was measured using an ocular micrometer and an ocular lens camera was used to photograph eggs for morphological identification.

Statistical analysis

Egg counts determined both the presence/absence and the relative abundance of each taxon in each sample. Here we define prevalence as the proportion of positive samples and abundance as the number of eggs per gram of feces. Shapiro–Wilk tests determined that our data were not normally distributed so we conducted comparisons using nonparametric analyses.

We used Pearson's chi-square tests of independence to compare differences in prevalence including (1) between wild males and females, (2) between females that were reproductive and nonreproductive the year they were sampled in the wild, (3) among 4 age classes of wild marmots (pups, yearlings, 2–3 yr old, 4+ yr old), (4) among 3 wild colonies (Mt. Arrowsmith, Mt. Washington, Labour Day Lake), and (5) between wild and captive marmots. Similarly, we tested for differences in mean abundance among these same 5 comparisons using Mann–Whitney U-tests or Kruskal–Wallis tests followed by Conover post hoc tests with Bonferroni corrections. We also tested for pairwise covariation in the prevalence of parasite taxa among wild marmots using Pearson's chi-square tests. Last, we tested for changes in prevalence in captive marmots from June to October with a Pearson's chi-square test, whereas changes in mean abundance were investigated using a Friedman's test to account for repeatedly sampling the same groups over time followed by a Conover post hoc test with a Bonferroni correction.

As captive fecal samples could not be traced to specific marmots, we could not test for differences between sexes, between reproductive and nonreproductive females, or among age classes in captivity. However, we randomly selected a single sample from each group of captive marmots to compare parasite load between captive and wild populations. As parasite prevalence and mean abundance showed significant monthly variation, captive samples were only randomly selected from months that overlapped with the collection dates of wild samples (June to September). All statistical analyses were

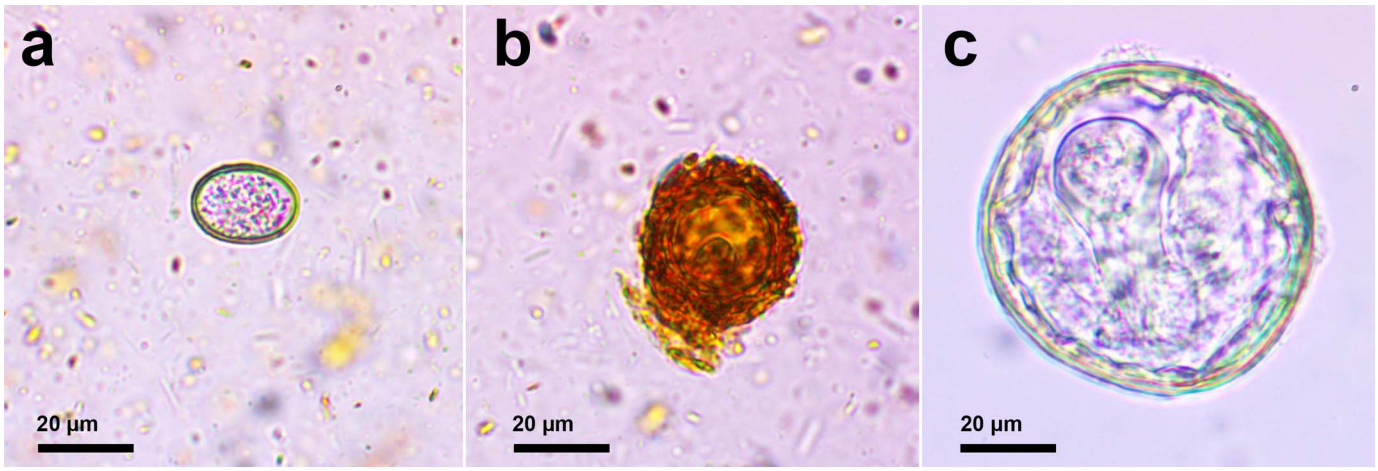

Figure 2. (**a**) Coccidia oocyst. (**b**) *Baylisascaris laevis* ova. (**c**) *Diandrya vancouverensis* ova. Color version available online.

completed using the Real Statistics Resource Package add-in for Microsoft Excel (version 6.8; Zaionitz, 2020).

RESULTS

Wild marmots

We identified eggs from 3 different parasite taxa across 38 fecal samples from wild marmots including a protozoan coccidium with a prevalence of 68%, an ascarid nematode with a prevalence of 82%, and an anoplocephalid cestode with a prevalence of 8% (Figs. 2, 3; Table I). We presumed the nematode to be *B. laevis* and the cestode to be *D. vancouverensis* on the basis of egg morphology and prior identification in VIMs (Mace and Shepard, 1981; Barrera et al., 2022).

The prevalence of *B. laevis* in the wild was significantly higher in males (94%) than in females (67%, $\chi^2 = 4.1$, $P < 0.05$, Fig. 3). However, the sexes showed no significant difference in their prevalence of coccidia (76% in males and 61% in females, $\chi^2 = 1.0$, $P > 0.32$) or *D. vancouverensis* (0% in males and 17% in females, $\chi^2 = 2.9$, $P > 0.08$) even though *D. vancouverensis* was only found in females. We found no significant variation in the prevalence of any parasites among the 4 age classes (all $P > 0.25$), between reproductive and nonreproductive females (all $P > 0.28$), or among the 3 colonies (all $P > 0.20$, Tables I, II). Furthermore, we found no evidence of pairwise covariation in prevalence among parasites in wild marmots (all $P > 0.39$, Table S2), suggesting that marmots that were positive for 1 species were not more or less likely to be positive for another species.

Mean abundances of all 3 parasite taxa did not vary significantly by sex, age class, or female reproductive status (all $P > 0.09$, Tables I, II). Coccidia oocyst mean abundance varied across the 3 colonies ($H[2] = 8.0$, $P < 0.02$), with Labour Day Lake having higher counts than Mt. Washington ($P < 0.01$) but was not different from Mt. Arrowsmith after Bonferroni correction ($P = 0.03$, adjusted alpha = 0.016), and there was no difference between Mt. Washington and Mt. Arrowsmith ($P > 0.21$, Fig. 4). The mean abundance of *B. laevis* ova also varied across the 3 colonies ($H[2] = 6.8$, $P < 0.04$), with Mt. Arrowsmith having higher egg counts than Mt. Washington ($P < 0.01$), but was not different from Labour Day Lake ($P = 0.03$,

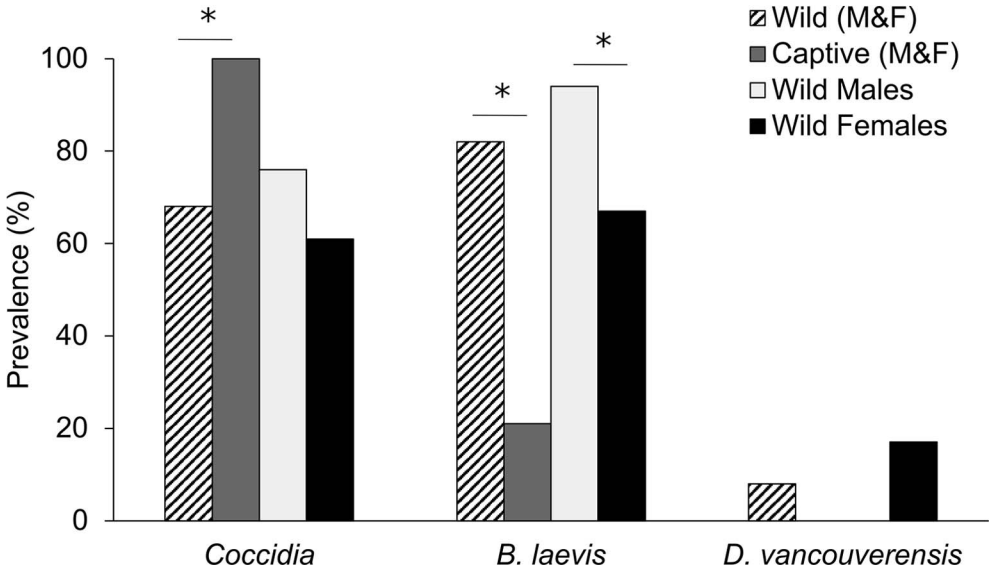

Figure 3. Prevalence of coccidia, *Baylisascaris laevis*, and *Diandrya vancouverensis* in wild (n = 38) and captive (n = 19), as well as wild male (n = 17) and wild female (n = 18), Vancouver Island marmots. Three marmots were of unknown sex. Significant differences between pairs denoted by *, $P < 0.05$.

Table I. Prevalence and mean abundance of oocysts and ova from coccidia, *Baylisascaris laevis*, and *Diandrya vancouverensis* in fecal samples from different groups of Vancouver Island marmots.

			Coccidia		*B. laevis*		*D. vancouverensis*	
Comparison	Group	n	Prevalence (%)	Mean abundance (eggs/g ± SE)	Prevalence (%)	Mean abundance (eggs/g ± SE)	Prevalence (%)	Mean abundance (eggs/g ± SE)
Sex	Male	17	76	5,817.7 ± 3,740.3	94	2,741.2 ± 1,136.9	0	0
	Female	18	61	4,586.1 ± 2,895.4	67	10,188.9 ± 9,167.7	17	44.4 ± 38.8
Age	Pups	9	44	294.4 ± 234.1	78	916.7 ± 576.3	0	0
	Yearlings	11	64	5,750.0 ± 4,672.3	82	2,881.8 ± 1,720.7	0	0
	2–3 yr	10	80	8,205.0 ± 6,292.1	90	18,235.0 ± 16,406.4	20	10.0 ± 6.7
	4+ yr	7	86	5,092.9 ± 1,834.4	71	1,864.3 ± 1,294.4	14	100.0 ± 100.0
Colony	Arrowsmith	6	67	10,800.0 ± 10,700.1	100	6,641.7 ± 2,761.1	17	8.3 ± 8.3
	Washington	10	50	250.0 ± 156.9	80	780.0 ± 556.2	0	0
	Labour Day	4	100	16,450.0 ± 11,853.2	50	600.0 ± 476.1	0	0
Female Status	Reproductive	8	75	2,068.8 ± 933.4	63	21,293.8 ± 20,632.1	25	93.8 ± 86.8
	Nonreproductive	10	50	6,600.0 ± 5,191.0	70	1,305.0 ± 1,076.1	10	5.0 ± 5.0
Environment	Wild	38	100	515.8 ± 98.5	21	15.8 ± 7.7	0	0
	Captive	19	68	4,835.5 ± 2,140.3	82	6,421.1 ± 4,349.7	8	21.1 ± 18.4

adjusted alpha = 0.016), and there was no difference between Mt. Washington and Labour Day Lake ($P > 0.95$, Fig. 4). The mean abundance of *D. vancouverensis* did not vary significantly across the 3 colonies, although it only appeared in one of the colonies that were included in this comparison.

Captive marmots

Only the coccidium and *B. laevis* were observed in captive marmot fecal samples, with a prevalence of 100% and 21%, respectively, whereas *D. vancouverensis* was absent from captive marmots. The prevalence of coccidia was significantly higher in captive VIMs compared with wild individuals ($\chi^2 = 7.6$, $P < 0.01$, Fig. 3; Table II), whereas the prevalence of *B. laevis* was significantly lower in captive VIMs compared with wild individuals ($\chi^2 = 19.6$, $P < 0.001$, Fig. 3; Table II). Though the cestode *D. vancouverensis* was only detected in wild VIMs, prevalence was not significantly lower in captive marmots ($\chi^2 = 1.6$, $P > 0.20$, Fig. 3). Mean abundance of *B. laevis* ova was significantly higher in wild marmots than in captive individuals ($U = 86.5$, $n_1 = 38$, $n_2 = 19$, $P < 0.001$), whereas mean abundance of coccidia oocysts and *D. vancouverensis* ova did not vary between wild and captive individuals (all $P > 0.22$, Table II).

The prevalence of coccidia did not vary significantly during June to October ($\chi^2 = 6.3$, $P > 0.09$, Fig. 5). However, the prevalence of *B. laevis* did vary significantly over the same 5 mo ($\chi^2 = 7.9$, $P < 0.05$, Fig. 5), which can be characterized as low in July and October, interrupted by a peak in August and September. The mean abundance of coccidia oocysts varied over the season ($\chi^2[4] = 18.5$, $P < 0.001$), with July being higher than August ($P < 0.001$) and October being lower than June ($P < 0.01$) and July ($P < 0.01$, Fig. 6; Table S3). *Baylisascaris laevis* showed no significant variation in ova shedding from June to October ($\chi^2[4] = 6.4$, $P > 0.16$, Fig. 6; Table S3).

DISCUSSION

To better understand trends of enteric parasite loads in the VIM, we used noninvasive fecal samples to assess the diversity, prevalence, and mean abundance of parasite eggs and compared these across host sex, female reproductive status, age class, and colonies. We also compared parasite loads between wild and captive marmots and examined if parasite load fluctuated over the active season. This information provides a better understanding of both host and parasite biology, the potential influences on host health or fitness, and the ongoing conservation efforts to protect this endangered host species. We identified 3 parasite taxa including oocysts from a protozoan coccidium, ova from an ascarid nematode presumed *B. laevis*, and ova from an anoplocephalid cestode presumed *D. vancouverensis*. Comparisons revealed variation in parasite load by sex, by colony, and between wild and captive VIMs. Captive marmots

Table II. Summary of statistical analyses for prevalence and mean abundance of 3 parasite taxa among groups of Vancouver Island marmots. Mean abundance was analyzed using 2-tailed Mann–Whitney (*U*) tests or Kruskal–Wallis tests (*H*) with a post hoc Bonferroni-adjusted critical alpha of 0.016. Significant *P*-values in bold.

	Coccidia				*Baylisascaris laevis*				*Diandrya vancouverensis*			
	Prevalence		Abundance		Prevalence		Abundance		Prevalence		Abundance	
Comparison	χ^2	*P*	*U*/*H* (df)	*P*	χ^2	*P*	*U*/*H* (df)	*P*	χ^2	*P*	*U*/*H* (df)	*P*
Sex	0.96	0.33	137.0	0.60	4.12	**0.04**	103.0	0.10	2.93	0.09	127.5	0.09
Age	4.03	0.26	6.2 (3)	0.09	0.02	0.80	1.2 (3)	0.75	4.02	0.26	0.9 (3)	0.28
Reproduction	1.17	0.28	31.0	0.44	0.11	0.74	35.5	0.72	0.72	0.40	33.5	0.41
Wild/captive	7.60	**0.006**	310.0	0.39	19.58	**<0.001**	86.5	**<0.001**	1.58	0.21	332.5	0.22
Colony	3.15	0.21	8.0 (2)	**0.02**	3.75	0.15	6.8 (2)	**0.03**	2.46	0.29	0.3	0.88
Mt. Arrowsmith–Labour Day Lake				0.03				0.03				
Mt. Arrowsmith–Mt. Washington				0.21				**0.01**				
Labour Day Lake–Mt. Washington				**0.002**				0.95				

Figure 4. Mean abundance of coccidia oocysts and *Baylisascaris laevis* ova per gram of fecal material at 3 wild colonies on Vancouver Island. Errors bars indicate standard error; significant differences between colonies denoted by * indicate post hoc $P <$ Bonferroni-adjusted critical alpha of 0.016.

also demonstrated significant temporal variation in prevalence and mean abundance of shed parasite egg counts. Additionally, this is the first study to characterize the prevalence of *D. vancouverensis* since its initial description from 1 individual host (Mace and Shepard, 1981).

Wild marmots

The nematode *B. laevis* and the cestode *D. vancouverensis* have been previously reported in the VIM (Mace and Shepard, 1981), whereas coccidians have been observed (VIMRT, 2008) but never characterized in the population until now. Oocysts from *Eimeria* spp. have been recorded in several *Marmota* spp. from North America and Eurasia (Wilber et al., 1998). Given the lack of morphological detail in unsporulated oocysts, we were unable to identify the coccidium observed in our study. However, with the isolation of *M. vancouverensis* on Vancouver Island and the confirmation of *D. vancouverensis* as a novel species, this coccidium may also be unique. Detailed study and genetic sequencing

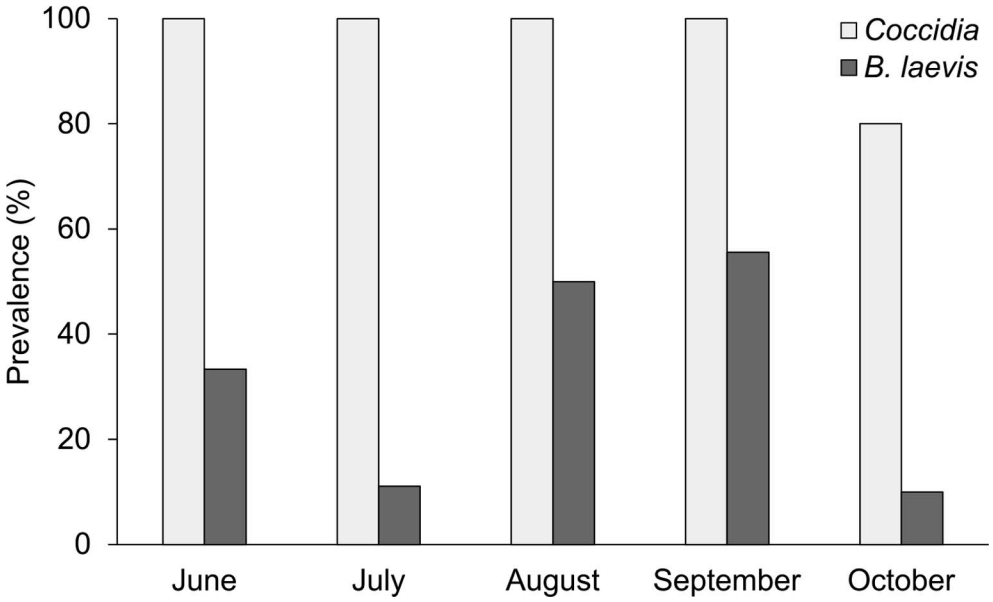

Figure 5. Prevalence of coccidia oocysts and *Baylisascaris laevis* ova from June to October in 10 groups of captive Vancouver Island marmots. Prevalence of *B. laevis* varied temporally ($P <$ 0.05), whereas prevalence of Coccidia did not.

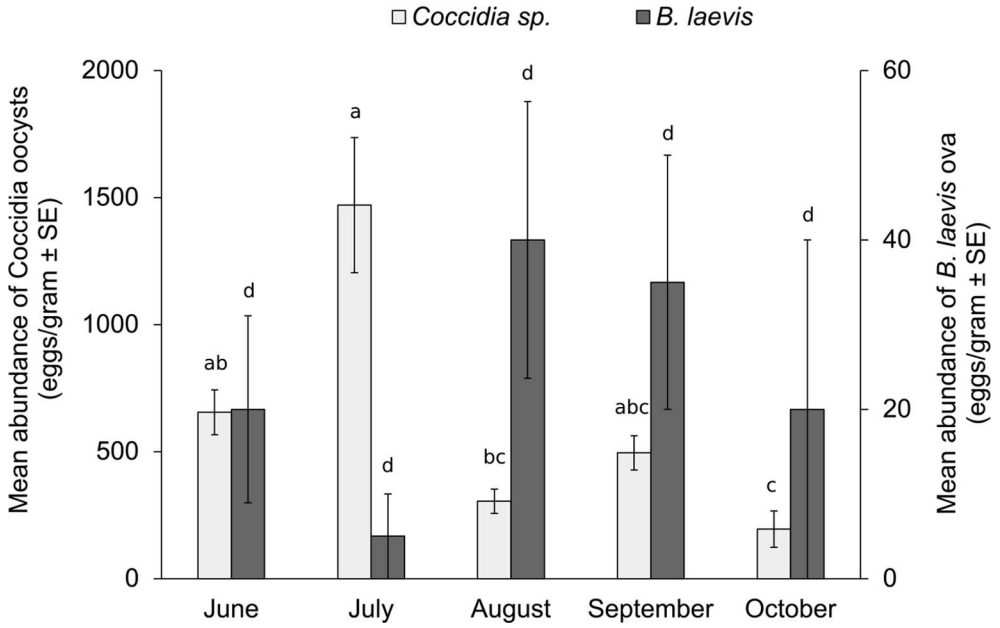

Figure 6. Mean abundance of coccidia oocysts and *Baylisascaris laevis* ova shed from June to October in 10 groups of captive Vancouver Island marmots. Coccidia oocyst counts varied temporally and months with different letters above their standard error bars (i.e., a, b, c, d) were significantly different from one another on the basis of post hoc $P <$ Bonferroni-adjusted critical alpha of 0.005.

of sporulated oocysts from nonfrozen fecal samples would be required to identify this coccidium in the future.

The prevalence of the coccidium among wild VIMs was 68%, which was within the prevalence range seen in *Marmota monax* (between 12 and 82% prevalence depending on the species of *Eimeria*; Fleming et al., 1979), though *M. flaviventris* had prevalences of *Eimeria* sp. between 93 and 100% (Lopez et al., 2013). We found the ascarid *B. laevis* in 82% of VIMs, which was significantly higher than previous studies reporting prevalences ranging from 1 to 27% in *M. monax* (Fleming et al., 1979; Berry, 1985) and between 3 and 28% in *M. flaviventris* (Lopez et al., 2013). Compared with the coccidium and ascarid *B. laevis*, we found the cestode *D. vancouverensis* to have a much lower prevalence at only 8% in VIMs. This also seems lower in comparison with the prevalence of *Diandrya composita* in 72% of *Marmota caligata*, 42% of *Marmota broweri*, and 62% of *Marmota olympus* (Rausch and Rausch, 1971). Though not statistically significant, *D. vancouverensis* was only observed in wild mature females from 3 colonies, Mt. Arrowsmith, Douglas Peak, and Big Ugly.

Although the mean egg abundance of each parasite did not vary by sex, *B. laevis* had a higher prevalence in males than in females. This partially conflicts with previous findings showing no effect of sex on *B. laevis* worm prevalence or mean intensity in necropsied *M. monax* (Berry, 1985). However, the increased prevalence is consistent with the general trend among mammals that males have higher parasite loads than females, possibly due to decreased immunity resulting from the energetic trade-offs for larger body size, larger home ranges, and higher aggression and fighting during mating (Poulin, 1996; Moore and Wilson, 2002; Gorrell and Schulte-Hostedde, 2008; Waterman et al., 2013). There were too few positive individuals for *D. vancouverensis* to show significant differences between sexes, but this parasite was found only in 3 female marmots.

Surprisingly, we found no significant difference in the prevalence or mean abundance of any of the 3 parasites among marmot age classes. Similar studies with *M. monax* also found no difference in prevalence or mean intensity of several helminths and coccidia between juveniles and adults (Fleming et al., 1979; Berry, 1985), which suggests that parasites are evenly distributed across the host population. However, Lopez et al. (2013) found a higher prevalence of endo- and ectoparasites (including an ascarid) in yearlings compared with adults among *M. flaviventris*. The prevalence of *Eimeria* sp. in *M. flaviventris* also varied between yearlings and adults but showed opposite patterns depending on sex. Hence, differences among age classes can be complicated, and teasing apart these relationships could be challenged by our small sample sizes. Presumably, marmots are born free of endoparasites, and the relatively high prevalence of coccidia and *B. laevis* in pups (44% and 78% respectively) indicates that transmission of parasites occurs rapidly in the marmots' first season of life but varies depending on parasite type. This is consistent with other findings of age-related parasite infection trends in *M. flaviventris* (Lopez et al, 2013) and feral horses (*Equus ferus*; Debeffe et al., 2016). After feeding *B. laevis* ova to *M. monax,* Berry (1985) noticed shed ova in their feces 63–69 days postinfection, suggesting that pups infected early in the season could be shedding *B. laevis* ova by mid- to late summer. *Diandrya vancouverensis* ova were not detected in pups and yearlings but were only detected in adults. This may indicate that pups and yearlings are less likely to become infected with *D. vancouverensis* than marmots 2 yr of age and older, or that the cestode takes more than 1 season to reach maturity (Georgiev et al., 2006). Before hibernation, marmots appear to go through a transition period when they pass soft stool that often contains adult parasites (Rausch and Rausch, 1971; Callait and Gauthier, 2000; M. L. McAdie, pers. obs.). However, larvae of *B. laevis* may persist in the host by migrating out of the intestine and entering a diapause while the marmot is hibernating (Callait and Gauthier, 2000). Fleming et al. (1979) found that several helminth species and coccidia could survive hibernation in *M. monax*. Nevertheless, this feat seems to regulate adult marmot parasite loads and make them indistinguishable from juveniles in our study.

Mt. Arrowsmith and Mt. Washington are home to two of the largest colonies of marmots on Vancouver Island. The colony at Labour Day Lake is a small colony located within ~14 km of the Mt. Arrowsmith colony. Because of the proximity of these colonies, migration may occur between them (Bryant, 1998) as at least

1 marmot has been observed dispersing from Mt. Moriarty (1 km from Labour Day Lake) to Mt. Arrowsmith. Not surprisingly, no difference was found in the prevalence or mean abundance of any of the 3 parasite species between these 2 locations. However, Mt. Washington had a significantly lower mean abundance of *B. laevis* ova than Mt. Arrowsmith and a significantly lower mean abundance of coccidia oocysts than Labour Day Lake. This may be due to the high number of captive-released marmots on Mt. Washington that are routinely administered an anthelmintic drug before their release into the wild, as well as the higher frequency of capture and treatment of wild marmots compared with other colonies (Lloyd et al., 2019). Immunological naivety due to administering anthelmintics can lead to increased susceptibility to parasitism later in life (Stringer and Linklater, 2014). For example, the release of naïve black rhinoceros (*Diceros bicornis*) into trypanosome (*Trypanosoma* spp.)-endemic areas of East Africa must be done when infection rates are seasonally low to be successful (Mihok et al., 1995). Further research is needed to understand the effects of anthelmintic drugs and immunological naivety on the infection and reacquisition rates of parasites pre- and post-release into the wild.

We found no difference in parasite prevalence or mean abundance between reproductive and nonreproductive female marmots. This is contrary to results showing that female horses that have undergone parturition have increased susceptibility to parasitism due to the energetic expense of gestating and caring for offspring (Debeffe et al., 2016). Furthermore, several studies show that parasitism can have a negative effect on reproductive success in *M. flaviventris* (Van Vuren, 1996) and North American red squirrels (*Tamiasciurus hudsonicus*; Patterson et al., 2013). However, parasite removal experiments found no increase in reproductive success in male and female Columbian ground squirrels (*Urocitellus columbianus*; Raveh et al., 2011, 2015), suggesting that sometimes parasite load bears little to no fitness cost.

The lack of covariation among any of the parasites in wild marmots indicates that infection with one parasite does not influence the likelihood of being infected by another parasite. This is contradictory to the hypothesis that helminth infection has a positive effect on concurrent microparasite infections, which has been demonstrated under some circumstances in *M. marmota* (Václav and Blažeková, 2014). This may suggest that an infection from a single parasite taxon may not inflict enough of an energetic expense on its host to facilitate increased infection of other parasites (Maizels and McSorley, 2016).

Captive marmots

Of the 3 parasite taxa detected in the wild, only *B. laevis* and the coccidium were present in captive marmots. A possible explanation for why *D. vancouverensis* was not detected in captive marmots is the lack of an obligate intermediate host that is likely involved in the life cycle of this anoplocephalid cestode (Georgiev et al., 2006). As all cestodes require at least 1 intermediate host to complete their life cycle, captive marmots likely do not become infected by the cestode if the intermediate host is not present in captivity. A common intermediate host of other anoplocephalid cestodes is oribatid soil mites (Ebermann, 1976; Shimano, 2004; Georgiev et al., 2006). More research is necessary to determine the life cycle and intermediate hosts of *D. vancouverensis*.

VIMs are administered an anthelmintic drug regularly if born in captivity (ivermectin to treat nematode infections; Graham et al., 2024) or within the first 30 days since capture if introduced into the captive breeding program from the wild. Wild marmots are also sometimes administered anthelmintic drugs when caught for monitoring/health checkups, although not as frequently as captive marmots. Not surprisingly, *B. laevis* showed significantly lower prevalence and mean abundance in captive marmots than in wild marmots, though captive marmots were not completely cleared of helminths despite the anthelmintic treatment. However, the high prevalence of coccidia in captive marmots is contrary to what we expected as anthelmintic treatment of wild *M. marmota* temporarily reduced both the number of cestode ova and coccidia oocysts released in the feces (Václav and Blažeková, 2014). Still, these interactions can be context specific as coccidia may initially be protected from host immunity through helminth coinfection but can also have a negative association once helminths mature and begin to reproduce, suggesting that established infections of coccidia may have higher fitness in the absence of competition from helminths (Václav and Blažeková, 2014). Captive VIMs are housed close to each other, possibly resulting in increased transmission among individuals compared with wild marmots (Patterson and Ruckstuhl, 2013; Václav and Blažeková, 2014). Lopez et al. (2013) found that coccidia (*Eimeria* sp.) were prevalent in nearly 100% of *M. flaviventris* and concluded that parasite richness, but not coccidia prevalence, was correlated with colony size. Both coccidia and *B. laevis* do not require intermediate hosts to complete their life cycles but instead transmit directly among hosts via the fecal–oral route (Todd, 1967; Sapp et al., 2017).

Although coccidia maintained nearly 100% prevalence in captive VIMs throughout the active season, the mean abundance of shed oocysts peaked in July and decreased again from August to October. Similar results were seen in *M. marmota* where oocyst counts were positively related to helminth ova counts early in the season when helminth infections were low but became negatively correlated later in the season when helminth infections were higher (Václav and Blažeková, 2014). Our study followed these trends as the mean abundance of coccidia loosely appears to be inversely correlated to the mean abundance of *B. laevis* from July to October; however, our small sample size limits our statistical power to make a stronger conclusion. We found that the prevalence of *B. laevis* peaked in August and September but then dropped in October, which is similar to results in *M. monax* and *M. marmota* where the prevalence of *B. laevis* and a cestode peaked at the end of the active season in August–October (Berry, 1985; Callait and Gauthier, 2000; Zanet et al., 2017). The significant decrease in *B. laevis* prevalence in October supports the hypothesis that marmots possess a mechanism to expel enteric helminths before commencing hibernation (Callait and Gauthier, 2000; Václav and Blažeková, 2014).

It is worth discussing the limitations of the sampling technique used in this study. The McMaster technique is a common noninvasive and therefore indirect approach to estimating parasite load but is unable to confirm the absence of parasites (Ballweber et al., 2014). Although a low egg count may suggest few or no parasites, there are other reasons why a fecal sample may have a low egg count. First, only female, but not male, ascarids release ova and only during periods of reproduction, which would underestimate the number of worms present (Callait and Gauthier, 2000). However, cestodes are monoecious and coccidia exhibit asexual reproduction, which reduces the concern over undetected individuals. Furthermore, a direct comparison revealed that egg counts from fecal samples followed a similar pattern to worm counts collected by

necropsy in *M. marmota* over the active season (Callait and Gauthier, 2000). Second, a lack of ova shedding during the developmental delay between host infection and parasite sexual maturity would erroneously suggest that the host is parasite free (Ballweber et al., 2014). This could explain the sharp rise in *B. laevis* prevalence from July to August and even though we found no difference in parasite load among age classes, this delay could influence comparisons between juveniles and adults if young marmots are infected early but the parasites may not be detected until later that season. Larvae of *B. laevis* reach the intestine 42 days postinfection, after first visiting the liver and lungs, though ova do not appear in the feces until 63–69 days postinfection (Babero, 1960; Berry, 1985). We also note that Berry (1985) reported a mean intensity of 5.8 and 7.0 *B. laevis* worms per infected *M. monax* host across 2 yr of study.

CONCLUSION

By examining fecal samples from VIMs, we identified oocysts/ova from 3 parasite taxa including a protozoan coccidium, an ascarid nematode presumed *B. laevis,* and an anoplocephalid cestode presumed *D. vancouverensis*. Comparisons among individuals revealed variation in parasite load by sex, by colony, and between wild and captive VIMs, but not among age classes or by female reproductive status. Additionally, significant variation in parasite prevalence and mean egg abundance occurred throughout the active season in captive marmots. Natural fluctuations in parasite populations and their host interactions provide insight into the ecology of these species, whereas the intrinsic value of parasites as components of a healthy ecosystem and their role in regulating host fitness make them equally deserving of research and conservation focus. By focusing on the marmot and its inhabitants as a system worth preserving, rather than simply on the conservation of the endangered host, we can better preserve the biodiversity, ecological functions, and ecosystem services they provide together. Further research is needed to determine the role of these parasites in the ecology, evolution, and health of this endangered community.

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