RESEARCH ARTICLE

A tale of two populations: vital rates of fishers in British Columbia, Canada

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Abstract

Fishers (*Pekania pennanti*) are a forest-dependent carnivore of conservation concern in British Columbia, Canada. Ecological, spatial, and genetic evidence suggests that there are 2 distinct populations (Boreal and Columbian) that occur in forests at low to moderate elevations in the boreal and central interior regions of the province. In British Columbia, fishers occur at low densities relative to other parts of their range in North America, are trapped for their fur, and are sensitive to habitat change. Despite these factors, little demographic information exists to assist with management decisions for these populations. We collated and analyzed survival and reproductive data from 100 radio-tagged fishers from 5 independent studies conducted between 1990 and 2012 in British Columbia: 2 in the Boreal population, and 3 in the Columbian population. We also collated litter size data from 1 den box study and a translocation project of fishers from the Columbian population. Annual survival rates were not significantly different between the populations or between males and females; however, adult survival rates were higher than subadults (0.79 and 0.63, respectively). Subadult females had significantly lower survival rates than other sex or age classes. Reproductive rates were significantly different between the 2 populations (denning rate = 0.54 [Columbian], 0.82 [Boreal]; x̄ litter size = 1.7 [Columbian], 2.6 [Boreal]). These differences resulted in net reproductive rates in the Columbian population that were less than half of those in the Boreal population (0.92 kits/reproductive season compared to 2.13, respectively). Population growth rates suggest that the

Columbian population may have been declining during the studies, whereas the Boreal population may have been increasing (0.96 compared to 1.20). Consequently, we suggest that focused and intensive habitat and population management for fishers are needed in British Columbia to ensure population sustainability, particularly for the Columbian population.

Fishers (*Pekania pennanti*) are a forest-dependent carnivore that occur throughout the Boreal, Cordilleran, and northern Carolinian forests of North America (Powell et al. 2003). Compared to fisher populations in the eastern portion of its range, which are relatively abundant and occupy a variety of forested environments, fishers in western North America occur in relatively low abundance and are more closely tied to specific habitat conditions commonly associated with late-successional forests (Lofroth et al. 2010). As a result, fishers continue to be the subject of considerable study and conservation concern in western North America (Lofroth et al. 2011), focused primarily on habitat ecology (Raley et al. 2012).

Despite this concern, our knowledge of vital rates of reproduction and survival that drive the dynamics of these western populations is limited. Much of what is known about the vital rates of western fisher populations comes from 1 small, isolated, and endangered population of fishers that has been examined in 3 separate study areas in the southern Sierra Nevada, California, USA (Jordan et al. 2011, Matthews et al. 2013, Sweitzer et al. 2015, Green et al. 2018). Survival and reproductive rates vary considerably among the southern Sierra Nevada study areas and, as observed in eastern North America (Paragi et al. 1994, York 1996, Koen et al. 2007), are different among sex and age classes. Subadults typically have lower survival rates than adults, adult females typically have the highest year-to-year survival rate, and female reproductive output peaks at age 3–5 years (Douglas and Strickland 1987, Powell and Zielinski 1994). Outside of this population in California, the dynamics of other western fisher populations are largely unknown.

In British Columbia, Canada, fishers occur at the northwestern extreme of their distribution where forests are substantially different than those found anywhere else in the range of the species (Kuchler 1964, Meidinger and Pojar 1991, McNab and Avers 1994, Ecological Stratification Working Group 1995). In British Columbia, fishers are a species of conservation concern with <2,100 individuals in the province in 2020 (British Columbia Conservation Data Centre 2020). Fishers are geographically separated into 2 populations in British Columbia (Figure 1), with each population occurring in very different ecological conditions. For instance, snow is deeper in most areas of the Columbian population (e.g., average annual snowfall = 316 cm, Sub-Boreal Spruce biogeoclimatic zone; DeLong 2004) compared to the Boreal population (e.g., average = 169 cm, Boreal White and Black Spruce biogeoclimatic zone; MacKenzie et al. 2020). Furthermore, forests in the Boreal population typically support higher abundances of key prey for fishers than in the Columbian population. For example, snowshoe hares (*Lepus americanus*) occur at <1 hare/ha in the Columbian population (Kelly and Hodges 2020), but there are 1.6–8.1 hares/ha in the Boreal population (Keith et al. 1984). Other prey including North American red squirrels (*Tamiasciurus hudsonicus*; Rusch and Reeder 1978, Sullivan et al. 2017) and ruffed grouse (*Bonasa umbellus*; Fischer and Keith 1974, Davies and Bergerud 1988) also have higher densities in the Boreal population compared to the Columbian population. Fishers in the Columbian population occur at the lowest densities documented (8.8 fishers/1,000 km²; Weir and Corbould 2006), half of that recorded for the Boreal population (16.3 fishers/1,000 km²; Weir et al. 2011). Additionally, recent evidence suggests that these 2 populations of fishers are genetically distinct (R. D. Weir, BC Ministry of
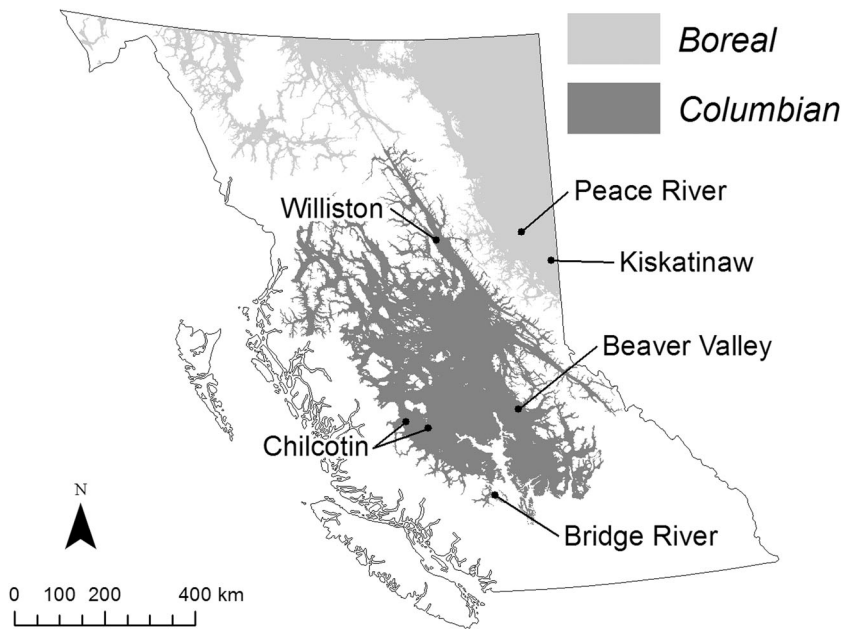
FIGURE 1 Location of study areas within the range of fishers within the Boreal (light gray) and Columbian (dark gray) fisher populations, British Columbia, Canada, 1990–2018.

Environment and Climate Change Strategy, unpublished data). Both populations are exposed to threats from habitat change and fur harvest (British Columbia Conservation Data Centre 2020). Forested habitat, particularly within the Columbian population, has been affected by mountain pine beetle (*Dendroctonus ponderosae*) outbreaks and resulting intensive forest management since the early 1990s (Eng et al. 2005). In addition, large areas of productive fisher habitat were disturbed in this region in 2017 and 2018 by uncharacteristically large and severe wildfires (Province of British Columbia 2017, 2019).

Given the close linkage that western fishers have to specific habitat features in late-successional forests (Lofroth et al. 2010), and the substantial differences in habitat conditions and climate between the forests of British Columbia and elsewhere, we expect vital rates of fisher populations in British Columbia may be different. Because of this, managers need clear population-specific information on rates of survival and reproduction to understand the capacity of these fisher populations to respond to changes in their environment and ensure a sound foundation for prudent management and conservation.

The purpose of our study was to estimate rates of survival and reproduction specific to 2 fisher populations in British Columbia by analyzing data collected on fishers during 6 research studies and 1 translocation project conducted throughout the range of fishers in the province. We specifically wanted to determine any differences in vital rates between the populations because these would affect conservation and management actions needed to ensure population sustainability.

STUDY AREA

We compiled survivorship and reproduction data from radio-telemetry studies of fishers conducted between 1990 and 2012 at 5 study areas throughout the range of fishers in British Columbia and additional litter size data from a study of artificial den boxes between 2015 and 2018 (Table 1). All studies were conducted in non-mountainous

TABLE 1　Characteristics of fisher study areas, British Columbia, Canada, 1990–2018.

Study area	Study dates	Size (km²)	Biogeoclimatic zone[a]	Trapping pressure	Source	Population
Beaver Valley	1990–1993	1,500	SBS	Normal	Weir (1995)	Columbian
Williston	1996–2000	1,830	SBS	Normal	Weir and Corbould (2008)	Columbian
Chilcotin	2005–2008	1,700	IDF, SBPS, MS	Reduced	Davis (2009)	Columbian
Bridge River[b]	2015–2018	990	IDF, SBPS	Normal	Davis (2020)	Columbian
Kiskatinaw	2005–2009	950	BWBS	Reduced	Weir et al. (2013)	Boreal
Peace River	2011–2012	850	BWBS	Reduced	Simpson et al. (2013)	Boreal

[a]BWBS, Boreal White and Black Spruce; IDF, Interior Douglas-fir; MS, Montane Spruce; SBS, Sub-Boreal Spruce; SBPS, Sub-Boreal Pine-Spruce.
[b]Only litter size data obtained from this den box study.

areas with low to moderate elevations (610–1,200 m). Three radio-telemetry study areas were situated west of the Rocky Mountains in the plateau forests of the central interior region (Columbian population), and 2 were located east of the Rocky Mountains in the boreal forest region (Boreal population; Figure 1). The den box study occurred in 2 of the Columbian population radio-telemetry study areas (Chilcotin and Beaver Valley) along with the Bridge River study area (Columbian population).

　　The Beaver Valley and Williston study areas occurred within the Sub-Boreal Spruce biogeoclimatic zone (Meidinger and Pojar 1991), where forests were primarily coniferous and dominated by hybrid spruce (*Picea glauca* x *engelmannii*), lodgepole pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*) or Douglas-fir (*Pseudotsuga menziesii*), with localized deciduous and mixed forests containing trembling aspen (*Populus tremuloides*) and black cottonwood (*Populus balsamifera trichocarpa*). The Chilcotin study area was within the driest ecological zones of all 6 studies and included the Sub-Boreal Pine Spruce, Montane Spruce, and Interior Douglas-fir biogeoclimatic zones (Meidinger and Pojar 1991), where forests were dominated by lodgepole pine with lesser components of Douglas-fir, hybrid spruce, and trembling aspen. The Bridge River study was in the Interior Douglas-fir and Montane Spruce biogeoclimatic zones (Meidinger and Pojar 1991), where forests were dominated by Douglas-fir, hybrid spruce, lodgepole pine and trembling aspen. The Kiskatinaw and Peace River studies both occurred in the Boreal White and Black Spruce biogeoclimatic zone (Meidinger and Pojar 1991) and the mixed-wood forests found there were predominantly white spruce (*Picea glauca*) or black spruce (*Picea mariana*) and trembling aspen with minor components of balsam poplar (*Populus balsamifera balsamifera*).

　　The climate in all study areas consisted of warm, dry summers (Jun–Sep) and cold, snowy winters (Nov–Mar), with annual mean temperatures ranging from 7.2°C in parts of the Interior Douglas-fir (Steen and Coupé 1997) to 1.7°C in Boreal White and Black Spruce zone (DeLong et al. 2011). Snowfall was greatest in the Beaver Valley and Williston study areas with an average annual snowfall of 334 cm (DeLong 2003) and 786 cm (DeLong 2004), respectively. Reproductive data were collected from late March to early May (reproductive season). Legal trapping seasons for fishers existed on registered traplines in all study areas from 1 November to 15 February of each winter (Province of British Columbia 2018). Trappers agreed to not harvest fishers in 3 study areas (Chilcotin, Peace River, Kiskatinaw), which reduced (but did not eliminate) trapping pressure. Trapping activity occurred in the Beaver Valley, Bridge River, and Williston study areas but was lower than before these studies because most trappers did not trap during the period of the studies and those that did set fewer traps for shorter time periods. During our studies, an average of 184 ± 70 (SD) fishers were trapped each year from the Columbian population (*n* = 21 seasons) and 72 ± 21 were trapped from the Boreal population (*n* = 16 seasons; M. Wolowicz, Biometrics and Report Officer, Province of BC, unpublished data). Additional study area details are available from the original studies (Table 1).

METHODS

We compiled survival, whelping rate, and litter size data from 5 radio-telemetry studies conducted on fishers in British Columbia from 1990–2012. We monitored the survival and reproduction of 100 free-ranging radio-tagged fishers (33 males, 67 females) within 5 study areas. We compiled litter size data from 2 additional sources: data from a study on the use of artificial den boxes by 9 untagged female fishers conducted in the Bridge River, Beaver Valley, and Chilcotin study areas from 2015–2018 (Davis 2020) and from 4 female fishers that were translocated from the Columbian population to Olympic National Park in Washington, USA, in 2009 and 2010 (Happe et al. 2019).

We captured, radio-tagged and monitored free-ranging fishers in each of the radio-telemetry study areas using similar methods. We captured fishers in Havahart (Havahart, Lititz, PA, USA) and Tomahawk (Tomahawk Livetrap, Hazelhurst, WI, USA) cage live traps and box traps (Weir and Corbould 2008) and occasionally in log-cabin box traps set for wolverines (*Gulo gulo*; Lofroth et al. 2008). We immobilized fishers in the field using ketamine hydrochloride and xylazine hydrochloride (Weir 1995), tiletamine hydrochloride and zolazepam hydrochloride (Weir and Corbould 2008), or ketamine hydrochloride and midazolam (Simpson et al. 2013). We fitted fishers with radio-collars (Lotek Engineering SMRC-5, Lotek, Newmarket, ON, Canada; Holohil MI-2M, Holohil, Carp, ON, Canada; Telonics MOD 205 or Telonics MOD 080, Telonics, Mesa AZ, USA) in the field (Weir 1995, Weir and Corbould 2010) or had licensed veterinarians surgically implant transmitters (Telonics IMP 300, IMP325L, or IMP140L) under sterile conditions (Weir and Corbould 2010, Simpson et al. 2013). Transmitters were equipped with motion sensors that increased the transmission rate when they had not moved appreciably for 12 hours (i.e., a mortality signal).

We sexed fishers based on physical examination for external genitalia and weighed each fisher with a spring balance once immobilized. We classified fishers as subadults (<2 yr) or adults based on tooth cementum annuli where possible (Matson's Laboratory, Manhattan, MT, USA) and tooth wear; otherwise, we classified fishers as adults if sagittal crests were noticeably evident by palpation, if chest girth was ≥23 cm for males, or if nipples were swollen enough to be easily visible. We collected locations of radio-tagged fishers using standard radio-telemetry techniques (Resource Inventory Committee 1998b) daily to weekly during winter and less frequently (e.g., weekly to monthly) during snow-free periods. We investigated mortalities of radio-tagged fishers as soon as possible (usually within 48 hr) after a mortality signal was received to confirm and identify mortality sources. We recorded a mortality date as the midpoint between the last radio-location at which the animal was recorded alive and the first date it was recorded as dead. We collected all carcasses for detailed necropsy by the provincial wildlife veterinarian, during which carcasses were dissected, and all injuries and wounds described and photographed. We collected tissue samples from organs and sent them to the British Columbia Provincial Veterinary Laboratory for toxicant and disease screening. We classified mortality sources as anthropogenic (i.e., trapping, poisoning), natural (i.e., accidental, starvation, predation), or unknown. The Beaver Valley study included a mix of resident and translocated animals (from the Columbian population), but we did not include any monitoring data collected prior to transplanted fishers establishing home ranges (using the metrics of Weir 1995) in our analyses. We evaluated differences in body mass of captured fishers using *t*-tests with acceptable Type 1 error set to 0.05 using t.test from the base package of R (R Core Team 2017).

We estimated annual survivorship rates for each sex and age class by population (Columbian or Boreal; Figure 1) using monitoring data collected on the radio-tagged fishers. We estimated survival using a multiple staggered-entry approach (Pollock et al. 1989, Krebs et al. 2004) that facilitated the inclusion of right-censored data (i.e., tagged fishers for which radio-telemetry signals could not be found and fate was not determined). We defined the population year as beginning 1 April, which is when females in British Columbia generally give birth to kits (Weir 1995, Weir and Corbould 2008, Davis 2009, Weir et al. 2012). Fishers with failed radio-transmitters that were subsequently recaptured were integrated into the data set as a new entry. We used the survfit function from the survival package of R (R Core Team 2017) to calculate estimates of annual survival. We evaluated differences in survival rates among sexes, age classes, and populations by comparing observed and expected survival outcomes

using the survdiff function from the survival package of R (R Core Team 2017), which evaluates the difference between ≥2 survival curves using G^p rank test procedures and chi-square statistics (Harrington and Fleming 1982).

We estimated reproductive output for fishers in each population using several metrics and data sources. We calculated denning rate for each radio-tagged female as the proportion of times it produced litters in the number of reproductive seasons (late Mar–early May) that it was monitored. We considered female fishers to have produced a litter if the female was located using the same tree cavity consistently and repeatedly for ≥3 weeks during the reproductive season or if a litter was observed. We measured litter sizes of kits using remote camera photo or video observations within or immediately outside reproductive dens. We were not able to observe litters in the Beaver Valley or Williston studies because of safety issues associated with the nature and condition of den trees. We collected data on litter sizes from 4 female fishers that were captured while pregnant in the Chilcotin region of British Columbia and produced litters immediately following translocation to Washington. These fishers were monitored immediately post-translocation with telemetry and remote cameras and litter sizes recorded. We also obtained litter size data from a study of artificial den boxes used by 9 female fishers in the Bridge River, Beaver Valley, and Chilcotin study areas (Davis 2020), where video evidence of litters was collected inside den boxes.

We compared denning rates and litter sizes among populations using t-tests with acceptable Type 1 error set to 0.05 using t.test from the base package of R (R Core Team 2017). We calculated the net reproductive rate for each population as the denning rate multiplied by the mean litter size for all adult females monitored in each population. We calculated population growth rates (λ) from the net reproductive rates for female kits (i.e., female kits/adult female/year) and survival rates for adult and subadult females using the Lotka equation (Eberhart and Siniff 1977). We assumed a 1:1 sex ratio in litters (York 1996, Matthews et al. 2013) in our calculations and an age of first reproduction of 2 years. In the absence of data for juvenile survival (age 0–1), we conservatively used the survival rate for subadults. Sweitzer et al. (2015), using comparable methods, reported juvenile survival rates similar to those of subadults (juvenile survival = 0.823 during den season, 0.79 post denning; subadult survival = 0.724). To estimate variance in λ, we assumed an underlying normal distribution to fisher survival and reproductive rates, and we used rnorm from the base package of R (R Core Team 2017) to simulate each variable 1,000 times. To reflect real values of survival and reproduction, we assigned a value of 0 to any negative values. For each realization, we solved for λ and derived summary statistics ($\bar{x}$, SD).

RESULTS

We monitored 100 radio-tagged fishers (33 males, 67 females; 30 subadults, 70 adults) between 1 and 1,257 days (Table 2). Two male fishers in the Williston study, and 2 male and 3 female fishers in the Peace River study were monitored as subadults and adults; we segregated data for these fishers as separate entries into the appropriate age classes. We monitored more than twice as many adult females as any other sex or age class (48 adult females, 21 adult males, 22 subadult females, 16 subadult males). We collected more monitoring-days of data in the Kiskatinaw study area (12,996; Table 2) than any other study area, but overall, we collected nearly an equal number of monitoring-days between the Columbian (18,207) and Boreal populations (16,606). We monitored adult fishers for more days ($\bar{x} = 376 \pm 310$, $n = 70$) than subadults ($\bar{x} = 265 \pm 283$, $n = 32$). We censored 55 sessions because of transmitter failures, 19 because of removal of collars or completion of the study, and 3 because the fishers appeared to have dispersed from the study area or we lost contact with the radio-transmitter. We observed that body masses of captured female fishers in the Columbian population ($\bar{x} = 2.6 \pm 0.3$ kg, $n = 23$) were lower than those in the Boreal population ($\bar{x} = 2.9 \pm 0.2$ kg, $n = 20$; $t_{41} = 3.31$, $P < 0.02$).

We documented 25 mortalities of fishers over the study periods (Table 3). Seventeen occurred during winter (Nov–Mar). Nine mortalities were anthropogenically related, 9 were due to predation, 2 were accidental, 1 was due to starvation, and 4 were of unknown cause. All 8 fur-trapping mortalities were females (5 subadults, 3 adults).

TABLE 2 Number of radio-tagged fishers and mean number of days monitored in British Columbia, Canada, 1990–2012.

| | Adults | | | | | | Subadults | | | | | | |
| | Males | | | Females | | | Males | | | Females | | | |
Study area	n	Days	Range	n	Days	Range	n	Days	Range	n	Days	Range	Total monitoring-days
Columbian population													
Beaver Valley	1	209		8	324	123–783	2	100	63–137	2	87	22–152	3,174
Williston	4[a]	166	42–265	8	454	21–1,148	4[a]	265	32–681	8	73	15–391	5,942
Chilcotin	6	301	51–792	14	488	29–935	2	40	31–48	1	375		9,091
Boreal population													
Kiskatinaw	6	206	56–606	11	628	1–1,257	4	465	5–772	5	598	319–818	12,996
Peace River	4[b]	342	40–540	7[c]	249	35–587	4[b]	42	1–78	6[c]	55	17–118	3,610
Total	21	5,278		48	21,714		16	3,368		22	4,453		34,813

[a]Two male fishers in the Williston study were monitored as both subadults and adults.

[b]Two male fishers in the Peace River study were monitored as both subadults and adults.

[c]Three female fishers in the Peace River study were monitored as both subadults and adults.

TABLE 3 Sources and numbers of documented mortalities among radio-tagged fishers, British Columbia, Canada, 1990–2012.

Study	Anthropogenic		Natural			Unknown	Total
	Trapping[a]	Poison	Predation	Accident	Starvation		
Columbian population							
Beaver Valley			2				2
Williston	3		3	1	1	1	9
Chilcotin		1	3	1			5
Boreal population							
Kiskatinaw	3		1			2	6
Peace River	2					1	3
Total	8	1	9	2	1	4	25

[a]Commercial fur harvest.

TABLE 4 Annual survival rates (95% CI) for radio-tagged fishers monitored, British Columbia, Canada, 1990–2012.

Population	Adults		Subadults		All fishers
	Males	Females	Males	Females	
Columbian	0.90 (0.72–1.00)	0.79 (0.64–0.98)	0.86 (0.61–1.00)	0.41 (0.06–0.76)	0.74 (0.60–0.88)
Boreal	0.60 (0.29–1.00)	0.86 (0.69–1.00)	1.00[a]	0.54 (0.26–1.00)	0.75 (0.61–0.93)
Overall	0.72 (0.49–1.00)	0.82 (0.70–0.95)	0.92 (0.79–1.00)	0.48 (0.27–0.85)	0.74 (0.64–0.85)

[a]No observed variation in survival for this segment.

Fishers were predated upon by coyotes (*Canis latrans*), cougars (*Puma concolor*), fishers, lynx (*Lynx canadensis*), wolverines, and predators we could not identify.

Survival rates varied among sex, age class, and population (Table 4). The data did not provide evidence of a difference in overall (i.e., all fishers) survival rates between the Columbian (0.74, 95% CI = 0.61–88) and Boreal populations (0.75, 95% CI = 0.61–0.93; $\chi^2_1 = 1.3$, $P = 0.30$) or between males (0.79, 95% CI = 0.61–1) and females (0.72, 95% CI = 0.61–0.86; $\chi^2_1 = 0.5$, $P = 0.50$) but did indicate differences between subadult (0.64, 95% CI = 0.46–0.89) and adult fishers (0.79, 95% CI = 0.68–0.92; $\chi^2_1 = 6.4$, $P = 0.01$). These findings were consistent within each population: we did not detect differences in survival rates between sexes but survival rates of adult fishers were higher than those of subadults (Columban $\chi^2_1 = 8.3$, $P \leq 0.004$; Boreal $\chi^2_1 = 6.4$, $P \leq 0.01$).

Reproductive rates of fishers were different between the 2 populations. Denning rates (i.e., litters/reproductive seasons monitored) were higher in the Boreal population (0.82 ± 0.33, $n = 20$) than in the Columbian population (0.54 ± 0.41, $n = 27$; $t_{45} = 2.50$, $P \leq 0.01$). Litter sizes were also larger in the Boreal population ($\bar{x} = 2.6 \pm 0.70$ kits/litter, $n = 18$ litters) than in the Columbian population ($\bar{x} = 1.7 \pm 0.69$ kits/litter, $n = 17$ litters; $t_{33} = 3.87$, $P \leq 0.001$). Overall, net reproductive rate was ≥ 70% higher in the Boreal (2.13 kits/reproductive season) than in the Columbian population (0.92 kits/reproductive season).

The survival and reproductive rates that we documented resulted in the highest estimated growth in the Boreal population ($\lambda = 1.20$, 95% CI = 0.92–1.48), suggesting a positive rate of increase, and lowest growth rates in the Columbian population ($\lambda = 0.96$, 95% CI = 0.70–1.21), suggesting a potentially declining population.

DISCUSSION

Vital rates of fishers varied by population, age, and sex, all of which have implications for the resilience of their populations in British Columbia. Most notably, reproductive rates varied between the Columbian and Boreal populations and this difference was largely responsible for the differences in potential growth rate between the populations.

Survival rates of fishers in British Columbia were affected by several different mortality factors and appeared to be dependent upon age class of the individual. Overall, the year-to-year survival rates of adults were >60%. Survival rates of male and female fishers in British Columbia were comparable to those reported elsewhere; annual survival rates of female fishers (0.72) were similar to those in Ontario (0.71; Koen et al. 2007) and California (0.72; Sweitzer et al. 2016b). Male fishers in British Columbia had an overall annual survival rate (0.79) that was moderately higher than that in California (0.62; Sweitzer et al. 2016b) and much higher than male fishers in Ontario (0.39; Koen et al. 2007), although adult males in the Boreal population had a survival rate (0.60) closer to that reported for fishers in California. Although we did not find differences in overall survival rates between populations, we did find differences in some sex-age classes. Survival rates of subadult females were lower than those of other sex-age classes. This may be indicative of the innate vulnerability of each age class and differences in the productivity of the ecosystems that support fishers.

Several characteristics of fisher populations may have contributed to the differential survival rates that we observed among the sex-age classes and populations. Subadult fishers (i.e., <2 yr) in British Columbia typically do not establish permanent home ranges during their first 2 years and wander widely throughout the landscape (Weir et al. 2009); we expected that this naïve age class would have more frequent encounters with predators and be less effective at acquiring food resources than older more experienced fishers with established home ranges. Indeed, in our studies, all trapping mortalities recorded were of females, most of which were subadults.

The survival rate of subadult males across all our study areas (0.92) was high relative to that expected for this sex-age class, which are often believed to be vulnerable to inter- and intra-specific conflict, starvation, and fur trapping (Douglas and Strickland 1987). It is unclear as to why subadult males would have the highest survival rate of any age-sex class in our studies, but it is possible that subadult males may disperse farther than subadult females (L. R. Davis, Davis Environmental, unpublished data) and thus our ability to monitor them through dispersal to determine their ultimate fates may have influenced our observations.

The prevalence of different mortality sources among age and sex classes likely contributed to the variability in survival rates that we observed. Our observation of a strong effect of age on survival rates was unlike that found in California, where there was very little evidence for age-related differences in survival (Sweitzer et al. 2016b). In our studies, human-caused deaths accounted for 36% of mortalities, most of which were related to fur harvest. Subadult female fishers had the lowest overall survival rate of any sex or age class, with only 48% of individuals surviving from year to year, which is substantially lower than that observed in California (0.72; Sweitzer et al. 2016b). Our data suggested that subadult female fishers may be more at risk to this mortality source than other sex and age classes; 5 of 8 of the documented trapping-associated mortalities in our sample were subadult females. This is at odds with findings from other fisher populations (Krohn et al. 1994) and other populations of mustelids exposed to fur harvest (Krebs et al. 2004) where males, particularly subadults, are generally more at risk to trapping mortalities (Koen et al. 2007). By comparison, in populations that are not exposed to commercial fur harvest, predation is the primary source of mortality (e.g., California; Sweitzer et al. 2016a), which was the second-most common mortality source in the populations that we studied.

We observed differences in survival among age and sex classes between the 2 populations, most notably among males. This may be related, in part, to the variability in space needs of males. Although survival rates for other sex and age classes were similar between the 2 populations, adult male fishers in the Columbian population had survival rates that were higher than those in the Boreal population. The reasons for this difference are not clear, but we suspect it may be partially due to differences in space use between the 2 areas. Adult male fishers in the Boreal population had

home ranges that were approximately 30% larger than those in the Columbian population (Columbian: 161.3 km², Weir et al. 2009; Boreal: 210.3 km², Weir et al. 2013). It is possible that this increase in area in the Boreal population disproportionately affected their mortality risk, either through increased encounters with sources of mortality (e.g., trapping, predators, vehicles), increased energetic demands associated with larger-scaled movements, or interactions among these factors. Alternatively, we collected relatively fewer monitoring-days of data on adult male fishers (i.e., 2,676 and 1,668 monitoring-days in the Columbian and Boreal populations, respectively) and early censoring due to transmitter malfunction of 8 of 10 adult male fishers in the Boreal population could have led to somewhat spurious results that under-estimated actual survival rates in the Boreal population. Collecting additional data would be helpful to clarify the factors that affect the differential survival of fishers between the 2 populations.

The frequency with which females produced litters was different between the 2 populations, and this likely contributed significantly to the overall observation of lower reproductive output in the Columbian compared to the Boreal population. Female fishers do not typically produce offspring every year (Powell 1993), and female fishers that we studied produced litters more frequently in the Boreal than the Columbian population (0.82 vs. 0.54 litters/yr). Overall, the denning rate of females in the Boreal population was very similar to the average observed for wild fishers elsewhere in western North America (0.74; Green et al. 2018), whereas the proportion of females producing litters in the Columbian population was among the lowest recorded for wild populations anywhere (Green et al. 2018). The denning rates and the number of kits produced in each litter were lower in the Columbian population than in the Boreal population. The average litter sizes in the 2 populations were near the extremes documented for wild fisher populations. Fishers in the Columbian population had an average litter size (1.7 kits/litter) that was only moderately higher than in California, which has the lowest recorded average litter size of anywhere in the range of fishers (e.g., 1.6, Sweitzer et al. 2015; 1.57, Green et al. 2018). In the Boreal population, however, litters were amongst the largest recorded (2.6 kits/litter) in wild populations anywhere (e.g., 2.83 in MA, USA, York 1996; 2.5 in ME, USA, Paragi et al. 1994). The net effect of these differential rates of kit production and litter size resulted in the net reproductive rate being >70% higher in the Boreal than in the Columbian population.

This variability in frequency of reproduction and litter size between populations in British Columbia may be related to several factors. The proportion of each age class of female fishers that successfully reproduces varies with maternal age; in California, 2-year-old females produced offspring only about 78% of the time, whereas females between ages 3 and 5 typically produced offspring in 90% of reproductive seasons, and older females only produced litters about 75% of the time (Sweitzer et al. 2015). If the age structure of female fishers in the Columbian study areas was skewed towards old or young, we would expect this population to have lower denning rates and consequently, lower reproductive output. Alternatively, the body condition of female fishers affected their denning rate, with larger females having higher rates of parturition than those that weighed less (Green et al. 2018). Morphometric data that we collected during handling of radio-tagged female fishers supported this hypothesis; the body masses of adult female fishers in the Columbian population were lower than those in the Boreal population. Furthermore, we consistently observed abundant omental fat deposits in females in the Boreal population during surgical implantation of radio-transmitters, whereas fat deposits were virtually non-existent in females from the Columbian population (R. D. Weir, personal observation). This discrepancy in fat levels may have also contributed to the differences in number of kits that females in each population produced; females in the Boreal population produced more kits per litter than did females in the Columbian population.

Environmental conditions likely contributed to differences in energy available for females to invest in reproduction and, more generally, for all fishers to avoid starvation. Snow conditions can affect the energy expenditure required and ability of fishers to move about their environment (Raine 1983). Fishers may have higher movement costs and greater energetic demands in the Columbian population than in the Boreal population because of differences in snow conditions. Prey abundance and availability may also contribute to these differences; however, we have no specific data with which to evaluate these hypotheses.

This variance in reproductive and survival rates between the 2 populations manifested as different potential population growth rates. Although the Boreal population had survival rates typical for the species, the relatively

frequent, large litters produced by females suggested a positive population growth rate. In contrast, the Columbian population, despite having similar survival rates, had low reproductive output that suggested that this population may have been in decline.

We recognize that factors affecting population vital rates likely varied over the 22-year period of data collection. Landscapes that support fishers in British Columbia underwent change between 1990 and 2012, primarily as a result of ongoing forest harvest, including the beginning stages of expedited salvage harvest of forests affected by a widespread outbreak of mountain pine beetles that affected approximately 18.6 million ha in the province (Corbett et al. 2015). Each study occurred at different points in the progression of landscape alteration and, although we do not have a clear understanding of the effects of these changes on vital rates, we know that fishers appear to be unable to occupy landscapes with extensive amounts of open area (Weir and Corbould 2010) and so, in all likelihood, vital rates did not increase as landscape disturbance increased over the period of our studies.

MANAGEMENT IMPLICATIONS

The 2 populations of fishers that occur in British Columbia had substantially dissimilar abilities to respond to population perturbations, which likely puts them at differential risks to decline and endangerment. That is, the Boreal population, with its positive growth rate, could likely recover from landscape and population disturbance more easily than the Columbian population. The negative population growth rate of the Columbian fisher population is particularly concerning given the widespread habitat disturbances that have occurred since most of our studies occurred. Between 2009 and 2020, 16% of the range of the Columbian fisher population was burned or logged. These disturbances likely reduced the ability of much of the landscape in which the Columbian population occurs to support fishers. Trapping mortality from fur harvest also likely continues to negatively affect the vital rates of this population ($\bar{x}$ = 169 ± 37 fishers annually since 2009). Despite low trapping pressure during our studies, 32% of the documented mortalities were due to fur trapping, all of them females. Enhancing the survival rates of the female segment of the population could result in considerable improvements in the growth rate, particularly as recruitment of new individuals into the breeding-age cohort would be expected to enhance the reproductive output of the population.

CONFLICTS OF INTEREST
The authors declare no conflicts of interest.

ETHICS STATEMENT
All capture, handling, and radio-tagging methods met or exceeded capture and handling guidelines outlined in the protocols for Wildlife Capture and Handling (Resource Inventory Committee 1998*a*), were approved by a member

of the Canadian Council on Animal Care, and were carried out under Wildlife Act permits C076979, WL05-19549, FSJ05-9483, and FJ10-67379.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Associate Editor: Kerry Nicholson.