Experimental moose reduction lowers wolf density and stops decline of endangered caribou

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The expansion of moose into southern British Columbia caused the decline and extirpation of woodland caribou due to their shared predators, a process commonly referred to as apparent competition. Using an adaptive management experiment, we tested the hypothesis that reducing moose to historic levels would reduce apparent competition and therefor recover caribou populations. Nested within this broad hypothesis were three specific hypotheses: 1) sport hunting could be used to substantially reduce moose numbers to an ecological target; 2) wolves in this ecosystem were primarily limited by moose abundance; and 3) caribou were limited by wolf predation. These hypotheses were evaluated with a before-after control-impact (BACI) design that included response metrics such as population trends and vital rates of caribou, moose, and wolves. Three caribou subpopulations were subject to the moose reduction treatment and two were in a reference area where moose were not reduced. When the moose harvest was increased, the moose population declined substantially in the treatment area (by 70%) but not the reference area, suggesting that the policy had the desired effect and was not caused by a broader climatic process. Wolf numbers subsequently declined in the treatment area, with wolf dispersal rates 2.5 × greater, meaning that dispersal was the likely mechanism behind the wolf numerical response, though reduced recruitment and starvation was also documented in the treatment area. Caribou adult survival increased from 0.78 to 0.88 in the treatment area, but declined in the reference. Caribou recruitment was unaffected by the treatment. The largest caribou subpopulation stabilized in the treatment area, but declined in the reference area. The observed population stability is comparable to other studies that used intensive wolf control, but is insufficient to achieve recovery, suggesting that multiple limiting factors and corresponding management tools must be addressed

simultaneously to achieve population growth.

1   **EXPERIMENTAL MOOSE REDUCTION LOWERS WOLF DENSITY AND STOPS DECLINE OF ENDANGERED**

2   **CARIBOU**

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20   **Abstract**

21   The expansion of moose into southern British Columbia caused the decline and extirpation of

22   woodland caribou due to their shared predators, a process commonly referred to as apparent

23   competition. Using an adaptive management experiment, we tested the hypothesis that

24   reducing moose to historic levels would reduce apparent competition and therefor recover

25   caribou populations. Nested within this broad hypothesis were three specific hypotheses: 1)

26   sport hunting could be used to substantially reduce moose numbers to an ecological target; 2)

27   wolves in this ecosystem were primarily limited by moose abundance; and 3) caribou were

28   limited by wolf predation. These hypotheses were evaluated with a before-after control-impact

29   (BACI) design that included response metrics such as population trends and vital rates of

30   caribou, moose, and wolves. Three caribou subpopulations were subject to the moose

31   reduction treatment and two were in a reference area where moose were not reduced. When

32   the moose harvest was increased, the moose population declined substantially in the treatment

33   area (by 70%) but not the reference area, suggesting that the policy had the desired effect and

34   was not caused by a broader climatic process. Wolf numbers subsequently declined in the

35   treatment area, with wolf dispersal rates 2.5 × greater, meaning that dispersal was the likely

36   mechanism behind the wolf numerical response, though reduced recruitment and starvation

37   was also documented in the treatment area. Caribou adult survival increased from 0.78 to 0.88

38   in the treatment area, but declined in the reference. Caribou recruitment was unaffected by

39   the treatment. The largest caribou subpopulation stabilized in the treatment area, but declined

40   in the reference area. The observed population stability is comparable to other studies that

41   used intensive wolf control, but is insufficient to achieve recovery, suggesting that multiple

42   limiting factors and corresponding management tools must be addressed simultaneously to

43   achieve population growth.

44

45   **Introduction**

46   When species colonize new areas, the consequences for native organisms can be

47   profound, often with negative impacts caused by competition or predation. An exotic predator

48   can have dramatic effects on native prey (Smith and Quin 1996), particularly on islands where

49   prey have evolved few anti-predator strategies (Sinclair et al. 1998). Similarly, extreme forms of

50   interference competition can have pronounced and obvious impacts, such as the invasion of

51   the Eurasian zebra mussel (*Dreissena polymorpha*) into North America where it now dominates

52   available substrate and smothers native bivalves (Ricciardi et al. 1998). In both cases, the

53   ecological interactions can be severe but straightforward to document. Interactions involving

54   indirect processes can be more difficult to confirm because they are not well explained simply

55   by tracking the abundance of individuals. One such process is apparent competition (Holt

56   1977), which can occur when a novel prey species colonizes a new area, stimulating an increase

57   in the abundance of one or more predator species. The novel prey need not be an introduced

58   exotic, but may be expanding its range either because of natural or anthropogenic factors

59   (Dawe et al. 2014). A secondary, but native prey may then become victim of apparent

60   competition, usually because it is less fecund or less able to escape predation than the novel

61   prey. The secondary prey can be driven to extinction because there is little or no feedback

62   between secondary prey abundance and predator numbers, given that predators are sustained

63   by the more abundant novel prey (Holt 1977, Latham et al. 2011). Identifying this mechanism

64   can be difficult because the cause of the secondary prey's decline could be confused with other

65   indirect interactions such as exploitative competition.

66   Woodland caribou (*Rangifer tarandus caribou*) represent a classic case of apparent

67   competition, especially the endangered ecotype of mountain caribou that inhabit the interior

68   rain forests of British Columbia and Idaho. Increases in moose (*Alces alces*) and white-tailed

69   deer (*Odocoileus virginianus*) are leading to the unsustainable predation rates on caribou (Seip

70   1992, Latham et al. 2011). Recovery options for mountain caribou can be summarized into

71   three interrelated approaches (Seip 2008). The first is to reduce or eliminate forest harvesting

72   in caribou range because this activity increases forage for moose and deer. Forest harvesting

73   also reduces the abundance of arboreal lichens that are the primary food for mountain caribou

74   during winter. However, reducing forest harvesting will not prevent the imminent extinction of

75   many caribou subpopulations (Wittmer et al. 2010) because of the existing legacy of forestry; it

76   will take decades for natural succession to reduce forage for moose and deer. The second

77   option is to directly reduce predator numbers. In numerous locations this approach has been

78   shown to increase caribou vital rates and population trend (Bergerud and Elliot 1998, Seip

79   1992, Hayes et al. 2003, Hervieux et al. 2014). Predator reduction, however, must be

80   continuous because if the treatment is stopped, predator numbers recover quickly, as long as

81   their primary prey are still abundant (Ballard et al. 1987, Hayes et al. 2003). Predator control is

82   also much less acceptable to the public than it was in the past (Orians et al. 1997, but see

83   Boertje et al. 2010). The third option involves reducing the primary prey that supports predator

84   populations, under the premise that this action will indirectly reduce predator numbers.

85   Recent recovery actions across the range of mountain caribou have included protecting

86   > 2 million hectares of old-growth forest from logging, closing areas to snowmobiling, and

87   adhering to a minimum distance between mechanized recreation and observed caribou. Yet,

88   because these management actions do not deal with proximate limiting factors, a population

89   response from caribou has not been observed, even in herds that live in parks and have seen

90   minimal disturbance on their range (Hebblewhite et al. 2010, Serrouya and Wittmer 2010).

91   Viability analyses suggest that under current conditions, without any additional habitat

92   degradation, many mountain caribou populations are on a trajectory to extinction (Wittmer et

93   al. 2010). Clearly this means that direct management of animal populations is needed, and such

94   actions should be implemented across broad spatial scales (Carpenter et al. 1995) that large

95   mammal predator-prey systems are known to encompass (Hayes et al. 2003, Mosnier et al.

96   2008).

97   The hypothesis we tested was whether substantially reducing moose numbers, the

98   wolves' (*Canis lupus*) primary prey in this ecosystem, to an ecological target (Serrouya et al.

99   2011) would reduce wolf populations and thus positively affect caribou population growth. The

100   ecological target was based on the estimated number of moose that would exist if there had

101   been no logging, which implied a reduction of *c*. 70% over contemporary numbers (Serrouya et

102   al. 2011). Nested within our broad hypothesis were three more specific hypotheses, each

103   contingent on the previous one: 1) sport hunting could be used to substantially reduce moose

104   numbers; 2) wolves in the Columbia ecosystem were primarily limited by moose abundance;

105   and 3) mountain caribou were partially limited by wolf predation. Theoretical underpinnings of

106   the broad hypothesis were explored in Serrouya et al. (2015a) who found that the rate and

107   intensity of reducing invading prey would have a major influence on the native prey. In this

108   paper we focus on empirical data including before-after control-impact (BACI) comparisons of

109   large areas that were subject to the moose reduction, with a spatial reference area where

110   moose were not reduced, and on the vital rates of the large mammals under study (caribou,

111   moose, and wolves).

112   The ability to use sport hunting to reduce ungulate populations is important because

113   hunter access and the fecundity rate of the prey species make some cervid populations resilient

114   to increased hunting (Brown et al. 2000, Lebel et al. 2012, Simard et al. 2013). To properly test

115   this hypothesis, we had to establish whether any change in moose abundance was caused by

116   the change in harvest policy, or a broader ecological process such as climate/weather or

117   ecosystem change that can also influence ungulate populations (Post and Stenseth 1998). The

118   spatial reference area where moose hunting was not increased helped to resolve these

119   potential confounds.

120   The hypothesis that wolves were primarily limited by moose abundance simply predicts

121   that reducing moose will reduce wolf abundance. Descriptive studies from within the study

122   area suggested that wolf diets were dominated by moose (Stotyn 2008), and across a variety of

123   ecosystems there is a broad relationship linking ungulate biomass to wolf abundance (Fuller et

124   al. 2003). However, wolf populations lag, sometimes by many years, in response to a decline in

125   their primary prey (Mech 1977, Gasaway et al. 1983). In such a case, the ratio of wolves to prey

126   would increase, at least temporarily, which could be detrimental to caribou because they would

127   become a higher proportion of available prey. There is increasing evidence that higher predator

128   to prey ratios translate to higher per capita predation rates (Vucetich et al. 2011). In addition,

129   wolf populations may not track the availability of moose biomass, but instead respond to the

130   abundance of vulnerable (old) moose (Peterson et al. 1998). These factors may result in an

131   equivocal relationship between wolf abundance and the moose reduction treatment,

132   particularly at a local scale.

133   The final hypothesis was that mountain caribou were limited in part by wolf predation

134   (Wittmer et al. 2005a), and therefore our prediction was that reduced wolf numbers would at

135   least increase caribou survival and reduce their rate of decline compared to before the

136   treatment and to the spatial reference area. This hypothesis has received support across many

137   woodland caribou subpopulations, either through manipulation (Seip 1992, Hayes et al. 2003,

138   Hervieux et al. 2014) or mensurative experiments (Seip 1992, Rettie and Messier 1998,

139   McLoughlin et al. 2003, Wittmer et al. 2005b, Latham et al. 2011). We also predicted that

140   caribou recruitment would increase following the treatment, recognizing that caribou calves

141   might be killed by bears or meso-predators to a greater extent than wolves (Adams et al. 1995,

142   Gustine et al. 2006). Again, these predictions depended on the previous hypothesis, where a

143   reduction in wolves could be achieved by reducing moose.

144   **STUDY AREA**

145   The study was located within two major mountain ranges in the interior of British

146   Columbia, the Columbia and Cariboo Mountains. The treatment area was 6500 km^2 whereas

147   the reference area was 11500 km^2, and they were separated by the Monashee Mountains, a

148   sub-range of the Columbia's with a maximum elevation of 3274 m. All these areas were

149   windward ranges of the Rocky Mountains that had wet climates dominated by interior rain-

150   forests. Both areas were rugged and remote. Half of the treatment area was on the west side of

151   Lake Revelstoke with only boat access (Fig. 1), and thus little human presence. In the reference

152   area there was a major highway and railway, whereas in the treatment area there was one

153   dead-end highway with relatively little traffic. Warm summers and cool, wet winters with

154   excessive snowfall (> 20 m) are typical in the central portion of these ranges at mid elevations

155   (1800 m a.s.l.) where caribou spend most of the winter. In valley bottoms (400 – 500 m)

156   snowfall averages 396 cm (n = 100 yr, SD = 120), which is where most other ungulates and their

157   predators spend the winter. As the snow melts in summer, moose and deer, along with wolves,

158   bears (*Ursus* spp.), and cougars (*Puma concolor*), spread out in the mountains. As a rough ratio

159   of moose to deer abundance, sampling from 17 pellet transects cleared and measured each

160   spring from 2003 to 2011 (Serrouya et al. 2011) recorded 969 moose and 61 deer pellet groups

161   (a ratio of 15.9:1).

162   Below approximately 1300 m, western redcedar (*Thuja plicata*) and western hemlock

163   (*Tsuga heterophylla*) are the typical climax tree species, whereas above this elevation the forest

164   transitions to Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*).

165   Forest age classes are typically bi-modal, with either old (> 250 yr) or young (< 40 yr)

166   regenerating stands following harvesting, and relatively little (<15 %) mid-seral vegetation.

167   Natural shrub openings occur in avalanche paths, marshes, and at higher elevation as the forest

168   transitions to alpine areas.

169   The caribou subpopulations in the treatment area included Columbia North, Columbia

170   South, and Frisby-Queest. The latter two each numbered less than 50 caribou when the moose

171   reduction treatment began, while Columbia North numbered *c.*150 when the treatment began

172   (McLellan et al. 2006). A portion of the Frisby-Queest range was located in the reference area,

173   but the vast majority (> 80%) of caribou occurrences from that subpopulation were located in

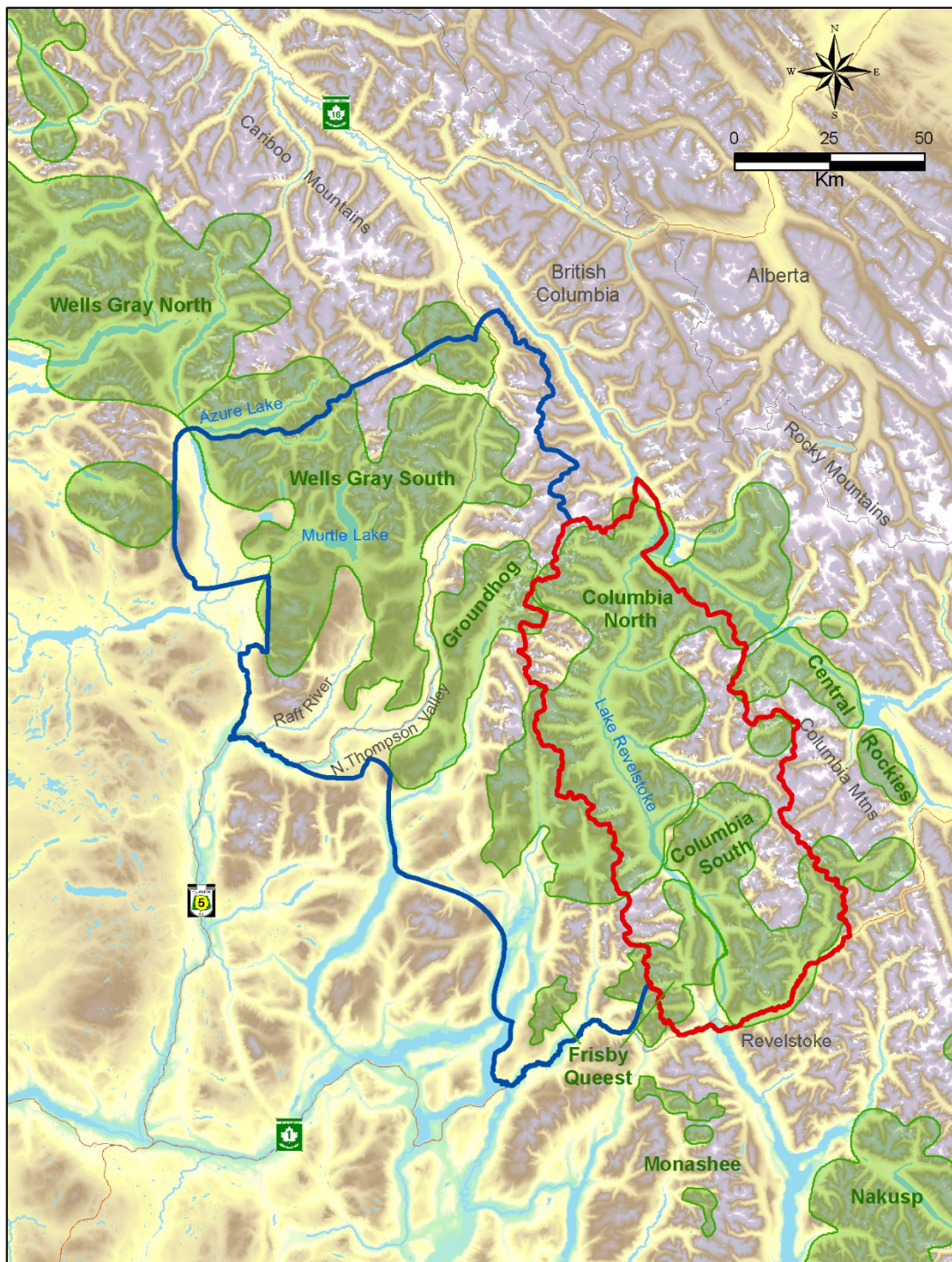
174   the treatment area (Apps et al. 2006). In the reference area, caribou subpopulations were Wells

175   Gray South and Groundhog, which numbered *c.* 120 and 20, respectively, at the beginning of

176   the experiment. Although Wittmer et al. (2005a) considered Wells Gray North and South to be

177   one subpopulation, more recent analyses revealed limited demographic exchange between

178   these areas (van Oort et al. 2011, Serrouya et al. 2012), so the comparison was limited to the

179   Wells Gray South portion (Fig. 1) of the larger Wells Gray subpopulation.

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181   **Figure 1.** Map of treatment (red) vs. reference areas (blue). Caribou subpopulations are shaded
182   green.

183

184 **METHODS**

185   To estimate population size, trend, recruitment, survival, mortality causes and dispersal

186 rates, animals were captured and fitted with VHF or GPS radio collars. Caribou and moose were

187 captured by aerial net-gunning, whereas wolves were captured using leg-hold traps and net-

188 gunning. To reduce confounding effects of age for estimates of vital rates, we avoided capturing

189 animals that were < 2 years old (and to avoid risks with radio collaring). Net-gunning was

190 conducted in winter when snow facilitated tracking and minimized the risk of injury to animals,

191 whereas leg-hold traps were used in summer only. Captures adhered to BC Provincial

192 Government and University of Alberta animal care protocols (permit # VI08-49757, and 690905,

193 2004-09D, 2005-19D).

194   Animals were monitored every two to four weeks from fixed-wing aircraft using VHF

195 telemetry. If an animal was not found during a monitoring session, the pilot (D. Mair, Silvertip

196 Aviation) scanned for these animals while *en route* to other projects centered 150 to 300 km

197 away in BC and Alberta, flying at a high altitude (> 2500 m) to maximize collar detection. We

198 occasionally searched a 50 – 100 km buffer around the study area using a meandering flight

199 path to try to locate missing animals.

200 **Study design and response metrics**

201   The design was based on an ecosystem-level perturbation intended to reduce moose

202 populations in one area (treatment) and compare the results to the reference area where no

203 attempt was made to reduce the moose population. In the treatment area, a 10-fold increase in

204 the number of moose hunting permits began in 2003 (Fig. 2; Serrouya et al. 2015b), but no

205 major change in policy occurred in the reference area. In the treatment and reference areas we

206 estimated moose survival and population trend, wolf survival and dispersal, and caribou

207 survival, abundance, trend, and recruitment. In the treatment area alone, we also estimated

208 wolf abundance, trend, and recruitment (Table 1). Caribou monitoring began in 1992

209 (summarized in Wittmer et al. 2005a), so we compared population parameters before and after

210 the moose reduction treatment began, and against the spatial reference area, conforming to a

211 BACI design. Moose abundance and survival estimates began in 2003, but population trend

212 based on hunter harvest data could be estimated in both areas prior to this date. Wolf survival

213   and dispersal comparisons began in 2004, but abundance estimates began in 2007. For moose

214   and wolves, we present animal abundance and density because density fluctuates within a year

215   as the available habitat changes 3-fold in summer vs. winter when snow restricts the

216   distribution of moose and wolves to the valley bottom. Winter densities can be obtained by

217   dividing abundance by c. 1100 km^2, but summer densities are roughly 3-fold less as snow melts

218   and animals disperse into adjacent mountains (Serrouya et al. 2011).

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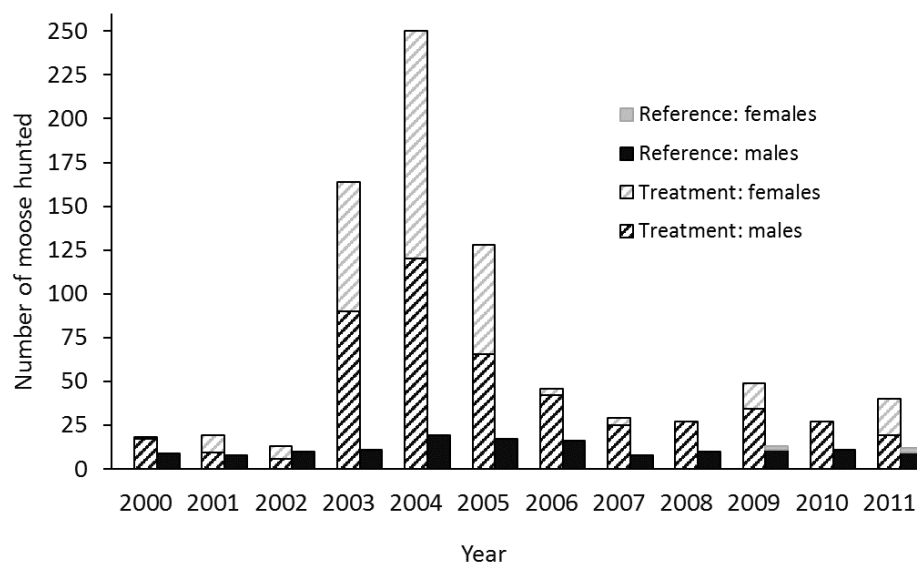
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221
222   **Figure 2.** Number of moose harvested in the treatment and reference areas. The moose
223   reduction treatment began in 2003. From Serrouya et al. (2015b).

224

225

226   **Table 1.** Response metrics within the treatment and reference areas (Yes (Y) or No (N)). Y in
227   brackets also indicates whether data exist before the moose reduction treatment began (i.e.
228   BACI).

Metric	Treatment	Reference	
Wolf survival and dispersal	Y	Y	
Wolf abundance	Y	N	
Wolf trend	Y	N	
Wolf recruitment	Y	N	
Moose trend	Y (Y)	Y	(Y)
Moose abundance	Y (Y)	Y	
Moose survival	Y	Y	
Caribou abundance and trend	Y (Y)	Y	(Y)
Caribou survival	Y (Y)	Y	(Y)
Caribou recruitment	Y (Y)	Y	(Y)

229

Moose abundance, trend, and survival

231   Methods to estimate moose abundance and trend were described in Serrouya et al.

232   (2011). Briefly, in the treatment area moose abundance was estimated using stratified random

233   block aerial surveys (Gasaway et al. 1986) and trend was monitored using annual pellet

234   transects (Serrouya et al. 2011). Catch per unit effort (CPUE) hunting data were calibrated

235   against these values (Serrouya et al. 2015b) and compared to CPUE data from the reference

236   area. In the reference area, moose abundance was estimated in 2007 in the northern third of

237   the area (see reference area in Serrouya et al. 2015b), and in the Raft River in 2009 (Klafki et al.

238   2009). These two point estimates were not used to estimate population trend, which was

239   estimated using CPUE data.

240   We calculated daily survival as 1 − (no. deaths) / (days monitored) for 2 risk periods:

241   winter (i.e., Nov–Apr) and summer (May–Oct). To produce seasonal survival rates for winter

242   and summer, we exponentiated daily survival rates by 181.25 for winter and 184 for summer

243   (the no. of days in each period). We then calculated annual survival as the product of the 2

244   seasonal risk periods (Heisey and Fuller 1985). Several authors argue for alternative approaches

245   such as cumulative incidence functions (Heisey and Patterson 2006, Murray 2006), but because

246   we were not using any covariates to explain variation in survival, the Heisey-Fuller method was

247   appropriate and is still commonly used in survivorship studies (Sparkman et al. 2011). To obtain

248   95 % confidence intervals, we bootstrapped the distribution of animals 3000 times and used

249   the percentile method. P-values for comparisons between areas were based on matching each

250   bootstrap iteration from the treatment and reference, counting the number of times the

251   treatment values were greater, and converting this to a percentile.

252

253   **Wolf abundance, trend, and vital rates**

254   Wolf survival, dispersal, and cause-specific mortality rates were compared between the

255   treatment and reference (Table 1). These rates were estimated again using the Heisey-Fuller

256   method (Heisey and Fuller 1985), but relative to ungulates, wolf mortality patterns vary

257   unpredictably throughout the year. Therefore, to help reduce potential biases stemming from

258   changing mortality risk throughout the year, we chose 12 risk periods corresponding to each

259   calendar month, which converges to the Heisey-Patterson approach (Heisey & Patterson 2006).

260   We again bootstrapped individual animals to obtain confidence intervals and p-values for

261   survival, cause-specific mortality rates, and dispersal rates. We also calculated an effective

262   survival rate by considering a dispersed animal to be "dead" from the study system. Cause-

263   specific mortality was separated into five categories: starvation, road kill, hunting and trapping,

264   predation, and unknown cause.

265   We defined dispersal as animals leaving the treatment or reference area by at least 50

266   km and not returning by the time the study ended – which was the same as used in a similar

267   study conducted on the Parsnip caribou herd in central British Columbia (Steenweg 2011).

268   However, because the reference unit was substantially larger than the treatment unit, the

269   opportunity for dispersal in the reference area could be negatively biased. Therefore, we also

270   quantified a more conservative dispersal rate from the treatment unit, by simulating an 11.3

271   km buffer around the treatment unit, which made it as large as the reference unit. The end

272   result was that in the treatment area wolves would have to disperse at least 61.3 km from the

273   edge. This adjustment was likely overly conservative, because the treatment area was bounded

274   by large mountains so if a wolf left this area it probably reflected an important decision to

275   expend energy and search for resources in a different area where its primary prey were not

276   declining rapidly. Dispersals included wolves that may have been lost from monitoring but were

277   subsequently found outside the study area (*sensu* Steenweg 2011, Webb et al. 2011) either

278   because they were harvested or were recaptured by another project. Potential dispersers were

279 also estimated and included animals whose radio-signal was lost before the expected end of

280 the collar's life span (Mills et al. 2008, Steenweg 2011). Annual dispersal rates were calculated

281 independently from the other cause-specific rates because including dispersals would have

282 caused a negative bias in the other cause-specific rates (see equations in Heisey and Fuller

283 1985), particularly since emigrants are normally right censored from analyses. One annual risk

284 period was used to estimate the dispersal rates.

285 Wolf abundance and trend were estimated in two ways. From 2008 to 2014 each valley

286 below 1200 m elevation in the treatment area was surveyed within a short time frame (2 – 4

287 days). Surveys began one or two days after sufficient snowfall to allow fresh tracks to be

288 detected and easily counted. Helicopters were used extensively, but ground work was done

289 simultaneously on the east side of Lake Revelstoke. Flight paths focussed on areas where tracks

290 could be easily spotted such as forestry roads, cutblocks and wetlands. Ground transects were

291 surveyed using snowmobiles or trucks along plowed and unplowed roads. An attempt was

292 made to locate all wolves in the survey area by trailing each pack until the group size could be

293 counted or at least estimated from tracks. The 2007 estimate was based on an integrated count

294 from multiple data sources over the second half of the winter, including 7 track transects

295 sampled 2 – 3 times, an aerial survey, ground observations, and GPS telemetry for 3 of the 6

296 packs to define pack boundaries. The aerial survey was not a complete census but focussed on

297 counting members of the packs with collared animals and the 3 known packs without a collared

298 member (*sensu* Hayes et al. 2003). This estimate was considered a minimum because only

299 known packs with territorial animals were enumerated. When trailing wolves, a minimum

300 estimate was always produced. These estimates were obtained from tracking evidence such as

301 splitting of routes followed, or from visual observations of the pack. A maximum estimate was

302 also recorded which provided an upper limit for each pack. The maximum count was more

303 subjective than the minimum count. Each time we encountered a pack we checked for the

304 presence of a collared wolf to estimate the proportion of wolves missed during our survey. This

305 method did not produce a sufficient sample to calculate a correction factor, but did provide an

306 approximate detection rate for the survey method.

307   Wolf recruitment was estimated only in the treatment area in 2010 and 2011 and was

308   contrasted between a high and a low moose density zone within the treatment area. Moose

309   density was 2.2-fold higher in the high zone (0.43 vs. 0.20/km^2, summer density). The objective

310   of this comparison was to determine if this difference in moose abundance was enough to

311   observe a response in wolf recruitment (*sensu* Messier 1985). To estimate recruitment, we

312   placed motion triggered cameras (Reconyx, Inc., Holmen, Wisconsin) within home ranges of

313   wolves that were monitored using GPS collars. We focused on three wolf packs with existing or

314   recent telemetry data, which allowed us to estimate the location of denning areas. We also

315   placed cameras along known travel routes that were near den sites. Three to four cameras

316   were placed within each territory, and were occasionally moved to help maximize detection of

317   wolves. Commercial wolf urine and gland lure (Kootenay Brand Lures, Kimberly, BC) was placed

318   near the cameras to slow wolf movements. Cameras were checked approximately once per

319   month and lures were refreshed during these checks. Our metric of recruitment was the

320   number of different pups recorded in the photographs, as a minimum estimate of the number

321   of pups in the pack.

322   **Caribou population trends, abundance, and recruitment**

323   Caribou abundance, adult survival and recruitment estimates were compared across

324   treatment and reference areas, and before and after the moose reduction was initiated.

325   Caribou censuses were conducted every two years on average, from March to early April when

326   they were high in the mountains and their tracks in open snowfields made them highly visible.

327   Caribou sightability was positively correlated with snowpack depth ($r_s = 0.96$, $p = 0.002$; Flaa

328   and McLellan 2000). When snow depth exceeds 300 cm at 1800 m a.s.l. (which occurs most

329   winters), sightability is > 90% (Serrouya et al. 2017). In the 1990s, a large sample of individuals

330   marked with radio collars allowed researchers to correct for missed animals and estimate

331   precision using program NOREMARK (details in Wittmer et al. 2005a). However, in years when

332   the radiomarked sample was low (i.e., after 2003), the number of caribou observed was used as

333   the estimate. In these years, caribou were not counted unless the snow depth reached 300 cm.

334   Caribou trend was quantified using the finite rate of change (Caughley 1977), also termed

335   lambda (λ).

336   Calves were classified as a percent of the population because it was difficult to obtain

337   adult sex ratios without undue harassment. Ungulate recruitment has high inter-annual

338   variability (Gaillard et al. 1998) so there is little reason to believe that serial autocorrelation is

339   important, and we grouped recruitment data before and after the treatment, again reducing

340   the need to correct for autocorrelation. We used a linear mixed-effects model (LME) to test

341   whether recruitment changed after the treatment, by creating a variable with two levels

342   (before, after), and evaluated this effect separately in the treatment and reference area.

343   Caribou subpopulation was specified as the random intercept. Recruitment was converted from

344   a proportion using the logit link for LME analyses. Because some populations declined

345   dramatically over the monitoring period, it may be appropriate to correct for population size

346   when estimating recruitment, so that estimates from populations with very few numbers carry

347   less weight. Therefore, we repeated the previous analysis but weighted the model by

348   population size.

349   **RESULTS**

350   **Moose abundance, trend, and survival**

351   The moose population in the treatment area declined by 71 % from 2003 when

352   increased hunting began to 2014 (λ_{annual} = 0.86; Fig. 3). The average winter density across the

353   treatment area declined from 1.58/km^2 to 0.44/km^2 (1650 to 466 moose). However, the

354   detectable decline likely began 1–2 years after the treatment was initiated (Fig. 3), so before-

355   after analyses were centered on 2004. The reference area also demonstrated a declining

356   moose trend, but the magnitude was much less than the treatment area. The CPUE data

357   revealed that the slope of decline was more than five times greater in the treatment compared

358   to the reference area (slopes were –6.88 [–9.02 to –4.68, 95% CI] compared to –1.32 [–2.46 to –

359   0.265]; Appendix 1). From 2003 to 2009, annual adult moose survival in the treatment area was

360   0.803 (0.688 to 0.895, N = 54) and 0.878 (0.727 to 0.972, N = 13) in the reference area (P =

361   0.18). Detailed mechanisms of the moose population decline in the treatment area were

362   presented in Serrouya et al. (2015b).

363

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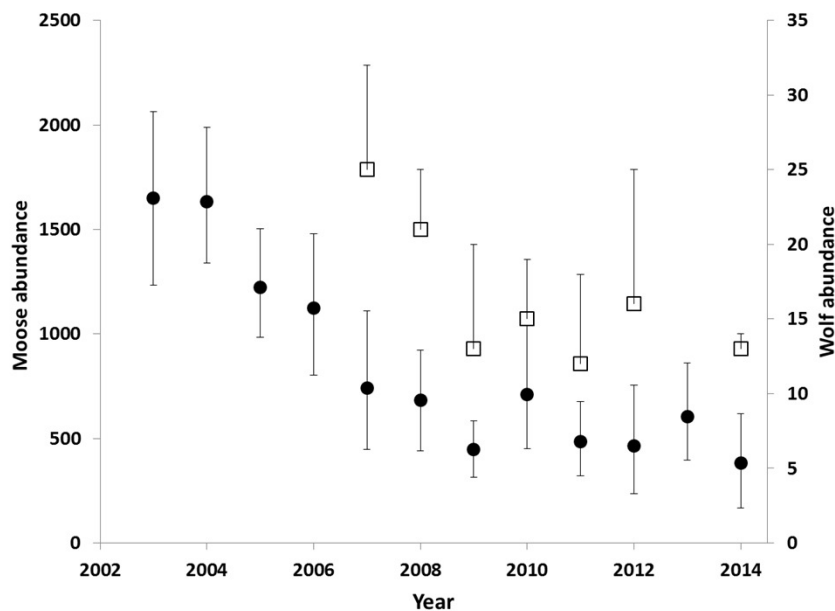
365   **Figure 3**. Moose (circles) and wolf (squares) abundance in the treatment area. Error bars for the
366   moose estimates represent 90% CIs. The upper error bar for the wolf estimate show the
367   maximum estimate, including a buffer around the treatment area. The square represents a
368   minimum estimate. Between 1994 and 2003 the moose population was estimated to have
369   doubled (Serrouya et al. 2011). Data updated from Serrouya et al. (2015a).

370

371   **Wolf dynamics**

372   From 2004 – 2010, 63 different wolves were captured on 82 separate occasions. Five

373   wolves were not located after capture and collar failure was suspected (they were GPS collars)

374   so were excluded from analyses. Therefore, 58 wolves were available for survival and dispersal

375   analyses; 34 in the treatment area and 24 in the reference area, with the sex ratio evenly split

376   in both areas. This sampling covered 32.4 monitoring years in the treatment, and 22.2 years in

377   the reference area. There were 12 mortalities of wolves collared in the treatment area. One

378   died after dispersing and was not monitored during the intervening period so it was right

379   censored. Another was a management removal and was also right censored. Eight of 34

380   (23.5%) wolves dispersed from the treatment area, compared to 2 of 24 (8.3%) in the reference

381   area. If the larger buffer (61.3 km) is considered, then the number of confirmed dispersers

382   from the treatment is reduced from 8 to 7. One additional wolf left the treatment area by

383   crossing west over the Monashee Mountains, but then shed its collar. Because it was only 10

384   km from the edge of the treatment area it was not counted as a disperser. However, this wolf

385   was likely eating little based on kill rate estimates (Serrouya 2013), and may have crossed the

386   mountains in search of higher moose abundance and could be considered a disperser. If

387   potential dispersers are included (those whose radio signals were lost unexpectedly), then 13 of

388   34 (38.2%) and 6 of 24 (25%) wolves dispersed from the treatment and reference areas,

389   respectively. These dispersal values are presented as annual rates in Table 2.

390   In the reference area there were eight mortalities, including two wolves that dispersed

391   prior to dying (and were right censored for mortality estimation), and no other dispersals were

392   recorded. Thus, in total, eight animals either dispersed or died from the reference area. Survival

393   rates for the two areas were similar (0.726 [0.58 – 0.85] vs. 0.757 [0.56 – 0.92]; Table 2). In the

394   treatment area, two wolves from separate packs starved and one was killed by other wolves.

395   Two non-collared wolves from different packs were also found to have starved in the treatment

396   area. One was a pup found at the den site of the collared female that had starved. The other

397   was a subordinate male that starved weeks after its collared pack-mate starved. Human-caused

398   mortality rates (road kills, trapping and hunting) summed to 0.243 in the reference area but

399   0.129 in the treatment area (Table 2).

400   There was a minimum of 25 wolves in the treatment area in 2007, but evidence from

401   the integrated count suggests that 32 individuals was more likely and was considered the

402   maximum estimate for that year (Fig. 3). Populations were lower and stable from 2009 to 2014,

403   with 2014 having the lowest maximum estimate (14). From 2008 – 2012, all collared packs (n =

404   7) were detected during the survey (no collars were on air in 2014).

405   Wolf recruitment was higher in the high moose density zone in both 2010 and 2011

406   (Table 3). Sample sizes were small however (one pack in the high and two packs in the low

407   zone), so no statistics were performed. In 2011, photos from the end of September suggested

408   that the eight pups seen in July for the pack in the high density zone were reduced to four pups.

409   Similarly, the pups seen from the Bigmouth and Red Rock packs earlier in the summer were

410   absent from photos in September that included adult wolves.

411

412 **Table 2**: Annual survival, mortality, and dispersal rates (95% CIs) for wolves in the treatment

413 and reference areas. Effective survival considers animals that dispersed to equal death from the

414 area. P-values were calculated based on a bootstrap comparison of the difference between the

415 two areas.

Parameter	Treatment	N	Reference	N	P-value
Survival	0.726 (0.58 − 0.85)	34	0.757 (0.56 − 0.92)	24	0.62
Road kill	0.024 (0 − 0.07)	1	0.082 (0 − 0.21)	2	0.78
Hunt / Trap	0.105 (0.02 − 0.21)	4	0.162 (0.04 − 0.33)	4	0.74
Starvation	0.063 (0 − 0.17)	2	0	0	NA
Predation	0.028 (0 − 0.09)	1	0	0	NA
Unknown	0.053 (0 − 0.13)	2	0	0	NA
Dispersal	0.221 (0.09 − 0.39)	8	0.087 (0 − 0.22)	2	0.08
Dispersal (max)[a]	0.333 (0.19 − 0.50)	13	0.239 (0.08 − 0.43)	6	0.20
Survival (effective)	0.513 (0.38 − 0.63)	34	0.586 (0.37 − 0.77)	24	0.73

416 [a]Maximum (max) dispersal considers any animal that disappeared while being monitored to be
417 a potential dispersal.
418
419

420 **Table 3**. Highest number recorded of pups in the treatment area during the summer months

421 using remote cameras in three different wolf territories within two zones of moose density.

422 Moose density was approximately 0.43/km^2 in the High zone (H) and 0.20/km^2 in the Low zone

423 (L) (summer density estimates).

Pack	Zone	Pups 2010	Pups 2011	No. cameras Sites	Trap Nights	Photos with wolves
Gothics	H	3	8	7	727	208
Bigmouth	L	1[b]	2	6	583	49
Red rock	L	0	1[a]	7	706	158

424 [a] This pup was not recorded in the camera traps but was observed alone while deploying a
425 camera trap along a logging road.
426 [b] This pup was found dead at the den site with its collared mother, which also appeared to
427 starve.
428

429 **Caribou abundance, recruitment and survival**

430   The two smaller caribou populations in the treatment area (Columbia South and Frisby-

431 Queest) continued to decline after the treatment was initiated (Fig. 4). The rate of decline

432   increased for Columbia South, and remained steady for Frisby-Queest (λ = 0.92 – 0.94). The

433   growth rate of the largest subpopulation in the treatment area, Columbia North, increased

434   following the moose reduction (Fig. 4), though that increase was primarily because of the 2013

435   estimate, with 32 additional animals compared to the 2011 estimate. In the reference area, the

436   smaller subpopulation (Groundhog) continued to decline, and the Wells Gray South

437   subpopulation initially appeared to stabilize but a marked reduction was observed in 2013 (Fig.

438   4). After moose were reduced, adult caribou survival increased from 0.784 to a high of 0.879 in

439   the treatment area (Columbia North subpopulation, pooled P-value = 0.11), but declined in the

440   reference area (Wells Gray subpopulation; P < 0.02; Table 4).

441

442

443   **Table 4**. Survival of radio-marked adult caribou in the treatment and reference area, both

444   before and after the treatment began (pre and post 2004, respectively). N is the number of

445   caribou monitored during the time period. For this comparison, the treatment area included

446   the Columbia North subpopulation, and the reference area was the Wells Gray subpopulation.

Treatment area				Reference area		
Time period	Survival		N	Time period	Survival	N
Before treatment						
1996–2002	0.793	(0.697–0.873)	40	1997–2004	0.868 (0.801–0.923)	39
2002–2004	0.784	(0.556–0.944)	17			
After treatment						
2004–2006	0.879	(0.731–1.0)	14	2004–2010	0.725 (0.531–0.851)	15
2006–2008	0.857	(0.676–1.0)	10			

447
448

449

450   There was no indication that caribou recruitment improved as a result of the treatment

451   (LME β_{before} = 0.456, SE = 0.32, p = 0.17, n = 30, 3 groups; Fig. 5). The predicted value of

452   recruitment was 15.5% (before) vs. 10.1% (after), and if the analysis was weighted by

453   population size then the values changed little, to 14.3 and 11.5%, respectively. Recruitment

454   improved in the reference area after the treatment began (LME β_{before} = −0.380, SE = 0.15, p =

455   0.02, n = 20, 2 groups; 13.1% (before) vs. 18.1 (after); Fig. 5), but when population size was

456   accounted for the difference was negligible (14.8% to 16.3%), and non-significant (p = 0.38)

457   likely because the high recruitment value (33%; Fig. 5) from Groundhog in 2011 was discounted

458   due to its much reduced population size (n = 9; Fig. 4).

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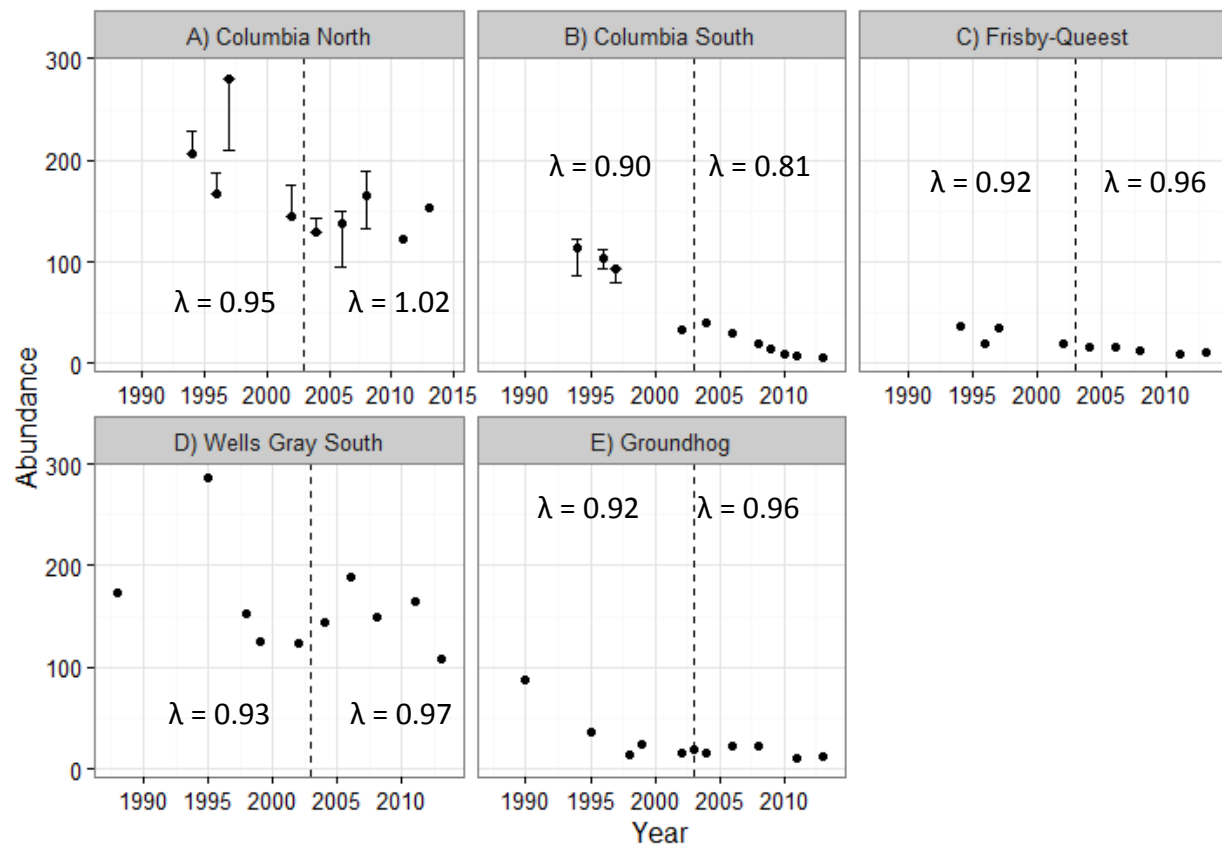
460
461   **Figure 4**. Caribou population estimates for five subpopulations, three in the treatment area (A

462   – C; top row) and two in the reference area (D, E; bottom row). Error bars are 95% CIs. The

463   dashed vertical line represents the beginning of the moose reduction treatment in 2003.

464   Lambda values to the left of the dashed line represent the years 1994 to 2004 whereas those to

465   the right of the line represent the years 2004 to 2013. Data updated from Wittmer et al.

466   (2005a).

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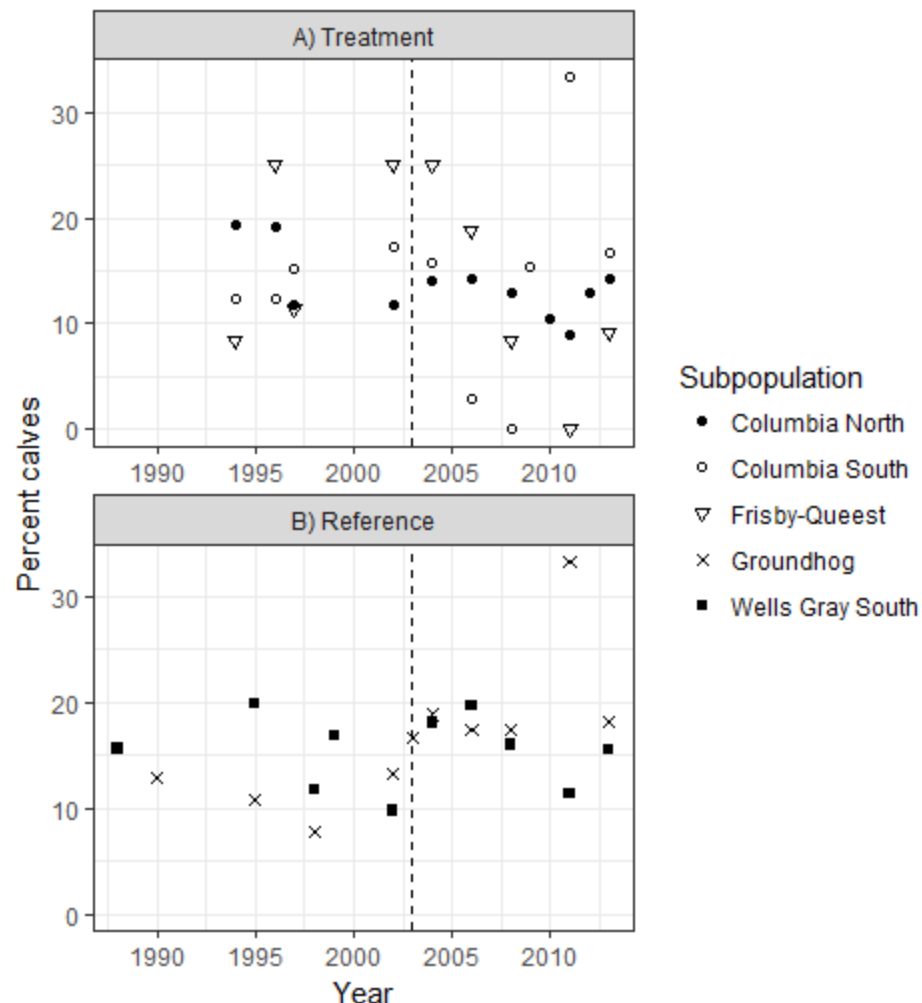
468
469 **Figure 5.** Caribou recruitment (% calves) within the treatment (A) and reference areas (B). The

470 vertical line represents when the moose reduction began in the treatment area. Symbols

471 represent separate subpopulations.

472

473 **DISCUSSION**

474   The primary hypothesis tested was that reducing moose abundance to an ecological

475 target would reduce the caribou's rate of decline. Within this hypothesis were three nested

476 hypotheses and predictions. The first of these was confirmed: moose were reduced using sport

477 hunting and two lines of evidence support this conclusion. First, the population declined at a

478 rate that was 5-fold greater than in a spatial reference area where the hunting kill was not

479 increased. Second, we contrasted the effects of hunting compared to predation and found that

480 both factors contributed to the decline, with the increased hunt initiating the depensatory

481 predation rate observed in the treatment area (Serrouya et al. 2015b). It may seem intuitive

482 that increasing hunting pressure on a large herbivore would reduce its abundance, particularly

483 with more females harvested. However, other North American cervids have been difficult to

484 control using sport hunting (Brown et al. 2000, McDonald et al. 2007, Simard et al. 2013)

485 because of poor access, urban refuges (Polfus and Krausman 2012), or high fecundity and

486 immigration rates. In one of the few other experimental attempts to reduce an overabundant

487 ungulate, Simard et al. (2013) found that white-tailed deer were not reduced in replicated 20-

488 km² treatments on a predator-free island. Moose are less fecund than white-tailed deer, which

489 may explain the discrepancy between the two systems. Furthermore, our treatment area was

490 300 times larger, with less chance of immigration because of the closure imposed by rugged

491 mountain ranges.

492   The second of the nested hypotheses was that wolves were primarily limited by moose

493 abundance, with the prediction that reducing moose would reduce wolf numbers. Ostensibly,

494 this hypothesis appears trivial because of established relationships between ungulate biomass

495 and wolf abundance (Fuller et al. 2003), but complimentary explanations have been proposed

496 related to the age or vulnerability of moose, or social constraints within wolf packs that limit

497 wolf abundance regardless of food availability (Messier 1994, Peterson et al. 1998, Hebblewhite

498 2013, Cubaynes et al. 2014). This hypothesis was also supported, because wolf numbers

499 declined following the moose reduction. The lack of wolf survey data prior to 2007 weakens this

500 conclusion, as does the absence of trend data of wolves in the reference area. Nonetheless, we

501 identified several mechanisms to explain the reduction in wolf abundance. First, the dispersal

502 rate was greater in the treatment area than the reference area, resulting in a relatively low

503 effective survival rate. At 0.51, the effective survival rate was lower than the minimum level

504 (0.64) required to maintain a stable wolf population (Fuller et al. 2003). These results mirror

505 those of Steenweg (2011) who found dispersal to be the primary wolf vital rate affected by a

506 moose reduction treatment in the Parsnip area. The dispersal rate in our treatment area was

507 also greater than what was estimated by Webb et al. (2011), who reported an emigration rate

508 of 0.13 in a population in Alberta. Second, we found some evidence of reduced wolf

509 recruitment in areas with lower moose densities ($0.2/km^2$). Messier (1985) also found that at

510 moose densities $< 0.2/km^2$, wolves had difficulty recruiting pups. Third, wolf starvation was

511 recorded in the treatment area but not the reference area. Finally, analyses of wolf scat

512 contents showed that wolves were primarily supported by moose in this study area (Stotyn

513 2008, Serrouya 2013) so a reduction in wolf numbers is consistent with a reduction in their

514 major food source.

515   Although trappers removed wolves in the area, the overall trapping and hunting rate

516 (0.11) is low compared to other populations. In Alberta, Webb et al. (2011) estimated that a

517 harvest rate of 0.34 had no effect on the population trend of wolves. Few wolves were trapped

518 or hunted in the study area because the amount of snowfall confounds trap sets and thick

519 cover obscures visibility for hunting. Therefore, changes in wolf abundance can be attributed to

520 a reduction in food and not intensive human harvest.

521   The final hypothesis, that reduced wolf numbers would lessen the rate of caribou

522 decline relative to spatial and temporal contrasts, was partially supported. The three smallest

523 caribou populations continued to decline, regardless of whether they were in the treatment or

524 reference area. A number of mechanisms can negatively affect small populations including

525 environmental stochasticity and Allee effects (Allee 1931) resulting from predation, and both of

526 these processes have affected woodland caribou (Hebblewhite et al. 2010, McLellan et al.

527 2010). We acknowledge that only the largest of 3 subpopulations subjected to the moose

528 reduction demonstrate improved demographic trend. However, a parallel study in the Parsnip

529 region showed similar improvement to caribou populations when moose were experimentally

530 reduced (Steenweg 2011; Heard, D. unpublished data).

531   For the two largest subpopulations (Columbia North and Wells Gray), a modest increase

532 was observed in the treatment area (Columbia North) but a sharp decline in the reference area

533 (Wells Gray). It is tempting to conclude that the experiment was not a success because caribou

534 population growth was not immediate and pronounced in the treatment area. However, our

535 results are similar to other management actions intended to recover declining caribou herds. In

536 Alberta, 841 wolves were removed in a caribou range from 2005 to 2012 and resulted in

537 caribou λ increasing from 0.95 0.99 (Hervieux et al. 2014). Similarly, a moose reduction in the

538 Parsnip area resulted in λ of caribou increasing from 0.95 to 1.02 (Steenweg 2011; Heard, D.

539 unpublished data). These actions have not rapidly recovered caribou populations but the

540 resulting trends are an improvement over the alternative, continued population declines.

541 Formal caribou population comparisons from this study ended in 2013 because a maternity pen

542 (a pilot trial of *in situ* captive breeding designed to increase calf survival) was initiated in the

543 Columbia North subpopulation that year, which could confound results of the moose reduction.

544 However, the 2017 caribou census for Columbia North revealed a count of 147 caribou, still

545 higher than 2003, and 5 fewer than 2013, indicating at least stability from 2003 to 2017. The

546 population effect of the maternity pen pilot trial was likely negligible (estimated to have added

547 a net of 8 calves over 3 years; Legebokow and Serrouya 2017), meaning that 14 years of

548 population stability can likely be attributed to the moose reduction.

549 In our experiment, moose numbers were reduced using a change in hunting regulations,

550 addressing a more ultimate cause of the apparent competition problem, rather than direct wolf

551 control. Yet, because moose were not reduced to the target developed by Serrouya et al. (2011;

552 ~300 moose), or even to the lower range of the predicted target (lower 95% CI: 167 moose),

553 the caribou response was unlikely as strong as anticipated. Prior to the 1940s, moose were at

554 even lower densities than predicted by Serrouya et al. (2011) and may have been absent from

555 central and southern BC (Spalding 1990, Kay 1997, Santomauro et al. 2012). The precautionary

556 principle (Doak et al. 2008) would suggest reducing moose even lower than 300 to hold wolves

557 at lower numbers. Recent wolf densities in winter are *c*. 13/1000 km^2, which is above a target

558 developed by Bergerud and Elliot (1986), who found that caribou mortality was offset by

559 recruitment at the threshold of 6.5 wolves/1000 km^2. Prey switching by wolves from moose to

560 caribou could also be invoked to explain the lack of caribou population growth. However, an

561 analysis of wolf scats suggests that prey switching did not occur (Serrouya 2013), given that

562 moose were gradually reduced over 10 years. When prey are reduced suddenly, prey switching

563 becomes a greater risk (Serrouya et al. 2015a) and can exacerbate caribou declines.

564 In most ungulate systems adult survival is necessarily high (Gaillard et al. 1998), making

565 statistical comparisons (p < 0.05) difficult (McLellan et al. 1999, Hayes et al. 2003). This pattern

566 is also true of endangered species or low-density carnivores where large sample sizes are

567   challenging to obtain. However, in the ecological literature there is increasing emphasis placed

568   on stressing the magnitude of biological effects (Burnham and Anderson 2002). In our case,

569   there was a substantial increase in caribou adult survival in the treatment area (~ 8.5 units;

570   Table 4), enough to considerably affect population growth (DeCesare et al. 2012, Serrouya et al.

571   2017). The same pattern occurred for other vital rates such as moose survival (7.5 units lower in

572   the treatment area) and wolf dispersal (2.5 × greater in treatment area), with p-values

573   approaching statistical significance but the magnitude and direction of estimates supporting the

574   primary hypotheses in this study. Caribou recruitment appeared unaffected by the moose

575   reduction treatment, likely because bear predation, not wolves, is a major limitation on caribou

576   calves (Brockman et al. 2017). Furthermore, calf recruitment in ungulates is highly variable

577   (Gaillard et al. 1998) and affected by many factors including spring weather (Hegel et al. 2010),

578   so a reduction in wolves may be less likely to clearly affect this age class compared to adult

579   survival, which is relatively unaffected by abiotic factors (Gaillard et al. 1998).

580   Spatial and temporal variation in predation intensity has a major influence on

581   population dynamics (Creel and Winnie 2005). Predation on adult mountain caribou by wolves

582   or cougars shifts from predominantly wolves in northern areas to cougars in southern areas

583   (Wittmer et al. 2005a). Bears were the second highest source of mortality in each of the

584   southern and northern half of caribou range, but with both areas combined, they were the

585   primary source of mortality. Furthermore, bears are a major predator of woodland caribou

586   calves (Adams et al. 1995). McLellan (2011) and Mowat et al. (2013) found grizzly bear densities

587   inversely related to terrestrial meat in their diet and more closely linked to vegetative food,

588   mostly fruit production (McLellan 2015) and, grizzly bears appear to eat little meat in our study

589   area (Hobson et al. 2000). Because bear foraging is directed at vegetation, we did not expect a

590   numerical response of bears to the moose reduction treatment. Cougar abundance and diets

591   were monitored intermittently in the treatment area (Bird et al. 2010) using GPS cluster

592   analyses (Anderson and Lindzey 2003, Knopff et al. 2009), with moose comprising 5 – 43% of

593   individual cougar diets (Bird et al. 2010). Cougar predation on caribou began following the peak

594   and collapse of deer populations (Serrouya et al. 2015a). After this dynamic, cougar numbers

595   declined and wolf predation on caribou increased (Stotyn 2008). These examples illustrate how

596   conclusions drawn from landscape-level field experiments must consider how limiting factors

597   change, often unpredictably, over space and time (Doak et al. 2008). Nonetheless, by

598   combining what was observed in this and other case studies (Courchamp et al. 2003, Wittmer

599   et al. 2013), some generalities are supported. In the context of apparent competition, high but

600   especially fluctuating populations of primary prey can enhance extinction risk for rare prey

601   (Serrouya et al. 2015a). Maintaining lower and thus more stable populations of primary prey is

602   expected to reduce predator switching and help maintain predators at low numbers (Serrouya

603   et al. 2015a). This generality is likely applicable to other caribou systems where moose are not

604   the dominant ungulate biomass, but where other ungulates are expanding because of changing

605   land uses and climates.

606   Wolves are highly mobile and fecund, so if their primary prey remain abundant during a

607   period of wolf control, ingress occurs rapidly (Ballard et al. 1987, Hayes et al. 2003, Mosnier et

608   al. 2008). Therefore, at least an 80 % annual reduction in wolf abundance is required to elicit a

609   response in ungulate population growth (Hayes et al. 2003). However, if wolf control were to

610   be implemented concurrently with primary prey reduction, it would likely have to be less

611   intensive and less continuous relative to other areas where primary prey was not reduced (e.g.,

612   Yukon: Hayes et al. 2003; Quebec: Mosnier et al. 2008; Alaska: Gasaway et al. 1992; British

613   Columbia: Bergerud and Elliott 1998; Alberta: Hervieux et al. 2014).

614   In addition to this study, we are aware of three other attempts to reduce apparent

615   competition by reducing primary prey: 1) the Parsnip study; 2) a study where 25000 domestic

616   sheep were reduced to 2000 to try and recover endangered huemul deer (*Hippocamelus*

617   *bisulcus)* in Patagonia (Wittmer et al. 2013a,b); and, 3) the removal of feral pigs to recover the

618   island fox (*Urocyon littoralis*) on the Channel Islands of California (Courchamp et al. 2003),

619   although periodic predator removal of golden eagles (*Aquila chrysaetos*) also occurred in that

620   case. In a fourth study, a serendipitous experiment occurred when extensive poaching of

621   African buffalo (*Syncerus caffer*) was linked to reduced lion (*Panthera leo*) numbers, resulting in

622   a pronounced increase of impala (*Aepyceros melampus*; Sinclair 1995). In the Parsnip study,

623   results were similar to ours, with high wolf dispersal rates, and the caribou population

624   stabilized. In the case of huemul, their decline was exacerbated as a result of increased

625 predation by foxes (*Lycalopex culpaeus*) and pumas (*Puma concolor*), likely resulting from the

626 abrupt decline in sheep and predators switching to huemul. The results of these manipulations

627 suggest inconsistent responses to reducing primary prey as a recovery tool for species affected

628 by apparent competition. This conclusion will complicate the decision-making process for

629 management agencies, but evidence suggests that this approach should be considered when

630 used in concert with tools that address other proximate and ultimate limiting factors.

631 Historical accounts (Spalding 2000, Seip 1992) suggest that mountain caribou were once

632 at least an order of magnitude more abundant than they are today. During this period of

633 caribou abundance, it is possible that the trophic interactions were reversed, and moose were

634 the victim of apparent competition with wolf predation and harvest by First Nations (Kay 1997)

635 keeping them at low numbers. Extensive wolf control using poison and bounties occurred from

636 1906 – 1962 throughout BC (McLellan 2010), and this along with climate and ecosystem change

637 made it possible for moose to expand into southern BC. It is becoming increasingly evident that

638 returning to the caribou-dominated system will require exceeding the biological population

639 targets proposed by Bergerud and Elliot (1986) and Serrouya et al. (2011). Random processes

640 associated with small populations, and Allee effects due to predation (McLellan et al. 2010,

641 Armstrong and Wittmer 2011) will make it increasingly difficult to recover mountain caribou

642 populations. However, an emerging pattern is that single management actions may halt

643 declines, but multiple actions that address several limiting factors simultaneously will be

644 required to achieve population growth (Serrouya 2013, Boutin and Merrill 2015).

645

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654   this project.

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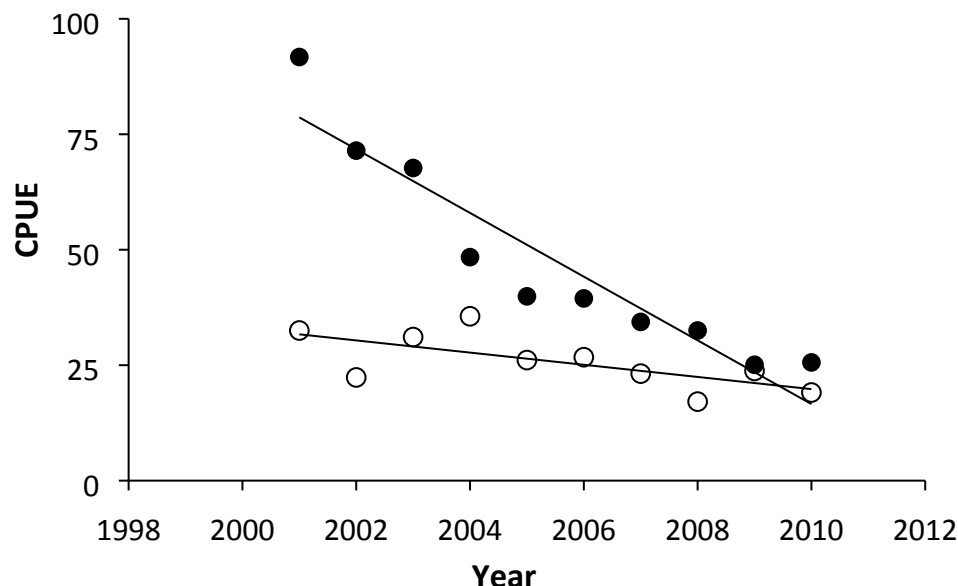
895   APPENDIX 1. MOOSE POPULATION TREND COMPARISON BETWEEN THE TREATMENT AND REFERENCE

896   AREAS.

897
898   **Figure Al:** The slope of decline was more than five times greater in the treatment (solid circles)

899   compared to the reference area (open circles; slopes were –6.88 [–9.02 to –4.68] compared to

900   –1.32 [–2.46 to –0.26] for the respective treatment and reference areas; 1000 bootstrapped

901   iterations). The slopes estimated here are slightly different from Serrouya et al. (2015b)

902   because the reference area was larger to accommodate the wolf ranges and caribou

903   subpopulations. Nonetheless, the ratio of the slopes between the two areas (i.e. comparing the

904   magnitude of change between the treatment and reference) was similar when the smaller or

905   larger reference area was compared to the treatment area.

906

907

908