1   *Death comes for us all: an interplay of habitat selection, movement, and social behavior relate*

2   *to cause specific mortality among grey wolves*

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4   **Running title**: Pre-death behaviors change

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12   **Abstract**

13   Avoiding death infects biological processes, including behavior. Habitat selection, movement,

14   and sociality are highly flexible behaviors that influence the mortality risks and subsequent

15   fitness of individuals. In the Anthropocene, animals are experiencing increased risks from direct

16   human causes and increased spread of infectious diseases. Using integrated step selection

17   analysis, we tested how the habitat selection, movement, and social behaviors of grey wolves

18   vary as an individual dies due to humans or canine distemper virus (CDV) and how those

19   behaviors may vary in the lead up to death. Behaviors that changed prior to death were strongly

20   related to how an animal eventually died. Wolves killed by humans moved slower than wolves

21   that survived and selected to be nearer roads closer in time to their death. Wolves that died due to

22   CDV moved progressively slower as they neared death and reduced their avoidance of wet

23   habitats. All animals, regardless of dying or not maintained strong selection to be near packmates

24   across time, which seemingly contributed to disease dynamics in the packs that became infected

25   with CDV. Habitat selection, movement, and sociality interact to put individuals and groups at

26   greater risks, influencing their cause-specific mortality.

27

28   **Keywords:** *Canis lupus*, anthropogenic disturbance, disease, integrated step selection analysis,

29   animal behavior, canine distemper virus

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31   **Lay Summary:**

32   Not much is known about behaviors prior to death in wild animals. Grey wolves killed by

33   humans selected to be in riskier areas increasingly prior to their deaths. Wolves that died due to

34   disease moved slower and changed their habitat selection to be in areas with more water as they

35   became sicker. Sick wolves also continued to select for packmates, increasing the chances that

36   the whole pack would succumb to the disease.

37   **Introduction**

38   Death comes for us all and fundamentally shapes behavior as animals attempt to survive in

39   environments composed of risks. Mortality drives demography, and to mitigate this risk animals

40   modulate their behaviors. Fine-scale behaviors, such as habitat selection, movement, and

41   sociality, are flexible in many animal species, and animals have evolved to adjust their

42   behavioral responses to minimize long-term and short-term risks. Some of the most common

43   causes of death to large, highly mobile animals are humans – ranging from hunting to vehicle

44   collisions – and disease (Farias et al. 2005; M.H. Murray and St Clair 2015; Wynn-Grant et al.

45   2018). Anthropogenic risks have become inescapable as the wildlife-human interface expands

46   (Sih et al. 2010; Skelhorn et al. 2011; Haswell et al. 2017). Many predators alter their behaviors

47   to avoid the long-term impacts of anthropogenic disturbance by minimizing human-wildlife

48   conflict both spatially and temporally (Broekhuis et al. 2019; Nickel et al. 2019). With increasing

49   human disturbance, the risk of disease outbreaks also grows, which may induce behavioral

50   change, or sickness behaviors (Weary et al. 2009; Becker et al. 2020). Being ill creates short-

51   term risks that lead to temporary changes in behavior. Symptomatic animals often move less,

52   adjust their space use, and change their social patterns, particularly in more gregarious species

53   (Hart 2011). An individual's mortality is intertwined with habitat selection, movement, and

54   social behaviors (Webber and Vander Wal 2017), and here we test how these behaviors relate to

55   the specific cause of mortality in a social carnivore.

56   Habitat selection, where animals preferentially use different habitats in a non-random

57   manner, is one way animals can alter their behaviors that can have demographic consequences

58   (Morris 2003). Animals change their habitat selection based on the density of conspecifics,

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59   dynamic resource availability, and predation risks (McLoughlin et al. 2010; Avgar et al. 2020).

60   Selection of complex habitats by predators is associated with their higher mortality due to prey

61   availability or predation risk (Gigliotti et al. 2020). Many species adjust their habitat selection to

62   avoid human disturbance, particularly during the day when humans are most active (Martin et al.

63   2010; Gaynor et al. 2019 Feb 8). Humans frequently kill predators when they are near their

64   livestock or trapped/hunted as fur-bearer species, which are typically in open areas or along trails

65   (Recio et al. 2018). Sick animals also trade-off gaining easier access to food by selecting riskier

66   habitats that have human provisioning (M. Murray et al. 2015; M.H. Murray and St Clair 2017).

67   Movement behavior is necessary for variation in space use as habitat selection is possible

68   because of an individual's ability to travel between habitat types (Forester et al. 2007).

69   Movement is mechanistically determined by the internal states, motions, and navigation

70   capabilities of individuals (Nathan et al. 2008), all of which are dynamic and can be altered

71   depending on risks (Knowlton and Graham 2010). For example, mule deer (*Odocoileus*

72   *hemionus*) that migrated along central, high-use routes had much greater survival than those that

73   traveled more peripheral routes (Sawyer et al. 2019). Individuals migrating along the periphery

74   were depredated more often than individuals travelling more centrally or in bigger groups

75   (Sawyer et al. 2019). Moreover, many species tend to move faster in anthropogenic areas to

76   avoid risks from humans (Tucker et al. 2018). Diseased or injured banded mongooses (*Mungos*

77   *mungo*) are less active, move less, and delay dispersal (Fairbanks, Hawley, and Alexander

78   2014a; Fairbanks, Hawley, and Alexander 2014b). Successfully delaying dispersal when

79   recovering from injury or illness can enables the individual to avoid death and maintain

80   reproductive opportunities that may have been lost if they did not alter their behavior (Boydston

81   et al. 2005; Altizer et al. 2011). Dispersal, for example, demonstrates how animals cannot

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82   preferentially use different areas without movement and results in fitness consequences ranging

83   from obtaining enough nutrients to survive to reproductive opportunities to mitigating more

84   direct mortality risks.

85   Variations in sociality can also have important fitness ramifications (J.B. Silk 2007). It is

86   well established in many primate species that being more social generally improves fitness, but

87   there is growing evidence for longevity being negatively influenced by sociality in certain

88   situations (reviewed in Thompson 2019 Mar 21). Being social can also counteract negative

89   effects of stress (Kikusui et al. 2006), predation and fluctuating environments (Guindre-Parker

90   and Rubenstein 2020), yet social behavior can be costly in terms of competition and disease risk

91   (Eberhard1975 1975). In response to this sociality trade-off, individuals can behave in a manner

92   that improves their individual fitness, as in healthy house finches (*Carpodacus mexicanus*)

93   actively avoiding sick individuals (Zylberberg et al. 2012). In addition, individuals can exhibit

94   behaviors that improve inclusive fitness through acting in the interest of the group (Cantor et al.

95   2020). For example, several species of insects demonstrated self-imposed social isolation from

96   the colony when they were near death to mitigate disease risks to the colony (Heinze and Walter

97   2010; Geffre et al. 2020). However, in social mammals, social isolation is more subtle to observe

98   because the alternations to social interactions occur at a fine scale, such as decreasing physical

99   contact. These adjustments confer the same benefits to their social groups, by maintaining or

100   improving inclusive fitness (Buck et al. 2018; Shakhar 2019). In social species in particular,

101   social behavior is linked to habitat selection and movement behavior as individuals navigate both

102   their social and spatial environments and associated risks (Webber and Vander Wal 2017; He et

103   al. 2019).

104   Wolves (*Canis lupus*) are a highly mobile social species that are exposed to increasing

105   mortality risks (D.L. Murray et al. 2010; Sidorovich et al. 2017; Joly et al. 2019; Hebblewhite

106   and Whittington 2020). Wolf habitat selection, movement, and social behaviors are highly

107   flexible both throughout the year and in response to rapid environmental change and

108   disturbances (Houle et al. 2010; Mancinelli et al. 2019). Humans frequently kill predators in

109   general, and wolves in particular, when they occur near livestock or as fur-bearer species,

110   typically in open areas or along trails (Theuerkauf 2009). There is evidence that wolves respond

111   to this risk by moving faster in open areas and near human development (Recio et al. 2018).

112   Furthermore, as wolves increasingly use anthropogenic areas, they are at greater risk of

113   contracting diseases such as canine distemper virus (CDV) that frequently occur as reservoirs in

114   urban-rural transition zones (Stronen, Sallows, et al. 2011; Prager et al. 2012; Beineke et al.

115   2015).

116   Here, we tested how movement, habitat selection, and sociality related to mortality

117   sources and change as individuals near death using data from GPS collared grey wolves. In the

118   months preceding death, we tested if movement, habitat selection, and sociality would vary

119   predictably, such that the individual's cause of death would be apparent. Specifically, we tested

120   how movement, habitat selection, and sociality vary prior to death from two types of mortality

121   sources: 1) humans – a long-term risk in the life of an individual and 2) disease – a relatively

122   short-term set of risks while an individual is symptomatic. Specifically, we hypothesized that

123   intrinsic behavioral qualities of individuals, consistent habitat selection, movement, or social

124   behavior patterns, put them at greater risk from humans compared to those that survived (Table

125   S1). Furthermore, we hypothesized that individuals change their habitat selection, movement,

126   and sociality behaviors due the extrinsic influences of disease (Table S1). Thus, we aim to

127   address how variation in habitat selection, movement, and sociality influences not only how an

128   individual dies but also have the potential to change as an animal nears the end of life.

129   **Methods**

130   *Study sites and subjects*

131   We studied two populations of wolves in in Manitoba, Canada: Riding Mountain National Park

132   (RMNP) and a provincial management unit, Game Hunting Area 26 (GHA 26). Riding Mountain

133   National Park (RMNP; 50°51′50″N 100°02′10″W) is a 2,969 km^2 protected area in southwestern

134   Manitoba. RMNP is located at the confluence of prairie grassland, aspen parkland and boreal

135   transition, creates a distinct edge with surrounding agricultural land. The RMNP wolf population

136   was estimated from aerial and snow track surveys at ~70 individuals 2016-2017. GHA 26 is an

137   ~7,200 km^2 unit located in southeastern Manitoba, bordered by Lake Winnipeg to the west and

138   the Manitoba-Ontario border to the east. The landscape is composed predominantly of coniferous

139   and mixed forests, interspersed with rock outcrops, rivers, lakes and bogs. The area is

140   predominantly public land, but also encompasses several communities as well as the Nopiming

141   and Manigotagan River Provincial Parks. The GHA 26 wolf population was estimated to be

142   ~140 wolves by aerial survey between 2014 and 2016.

143   *Wolf GPS collar data collection*

144   Between 2014 and 2018 wolves in both study areas were captured and fit with GPS telemetry

145   collars (Lotek Iridium TrackM 2D, Lotek Wireless Inc, Newmarket, ON, Canada; Sirtrack

146   Pinnacle G5C, Sirtrack Limited, Hawkes Bay, New Zealand; Followit Tellus Medium 2D,

147   Followit Sweden AB, Lindesberg, Sweden). In RMNP, a total of 25 wolves were captured and

148   collared in winter 2016 and 2017, and 38 wolves in GHA 26 in the winters of 2014-2018. All

149   captures followed Memorial University AUP 16-02-EV. GPS collar data was rarified to a 2-hour

150   relocation schedule to sample animals at an equal intensity for analyses.

151   In RMNP, 17 of our collared individuals had known causes of death: 40% disease

152   (CDV), 16% anthropogenic (trapping, poisoning, gunshot), and 12% conspecifics (injuries from

153   canids). In GHA 26, 10 of the collared individuals had known causes of death: 18%

154   anthropogenic, 5% disease (heartworm), and 3% drowning. If cause of death was not easily

155   determined in the field (i.e., bullet wound), the cause of death was determined by necropsy.

156   Necropsies were performed by the Assiniboine Park Zoo and Canadian Wildlife Health

157   Cooperative. We categorized death into two main overarching sources of mortality: humans and

158   CDV. As a control, we used 16 wolves that did not die and assigned them a random "death" date

159   that fell in the range of our observed death dates and compared their habitat selection,

160   movement, and social patterns in the time leading up to that date to wolves with verified death

161   dates. Henceforth, we call wolves that succumb to these mortality factors 1) control, 2) human-

162   killed, or 3) CDV wolves.

163   Canine distemper virus (CDV) is a disease common in carnivores that is very contagious,

164   mainly through direct contact with infected fluids (Ferry 1911). Untreated diseased animals

165   frequently lose motor control and become fevered and dehydrated within one month from

166   infection, so many animals seek out water and may eventually die submersed in water

167   (Blixenkrone-Møller et al. 1993; Rodeheffer et al. 2007; Zhao et al. 2015). Individuals usually

168   die within 2-4 weeks of infection (Loots et al. 2017). Thus, we limited our analyses to the two

169   months leading up to the death date such that control, human-killed, and CDV wolves had at

170   least 1 month of asymptomatic behaviors so we could examine changes over time.

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171   *Integrated step selection analysis*

172   We used integrated step selection analysis (iSSA) to test how habitat selection, movement, and

173   sociality may relate to death, and how these behaviors change at fine temporal scales as an

174   animal nears death. Movement processes are described by two covariates indicating speed and

175   directionality: 1) step length, the straight-line distance between two consecutive GPS locations,

176   and 2) turn angle, the angular deviation from the previous step to the next (Fortin et al. 2005;

177   Avgar et al. 2016). Here, random steps were drawn from theoretical distributions, using gamma

178   for step length (mean tentative shape = 0.398, scale = 2410) and von Mises for turn angle (mean

179   tentative kappa = 0.0957). To ascertain how cause of death related to these behaviors, each

180   variable was interacted with mortality source: control (n = 16), human (n = 4), or CDV (n = 8).

181   To examine how behaviors change leading up to death, we interacted variables of interest with

182   time to death (days). We used natural logs of time to death to standardize it with other variables.

183   Thus, covariates interacted with time to death represented changes in behaviors, and the non-

184   interacted variables represented their intrinsic baseline behaviors.

185   Tracks, random steps, and covariates for each step were extracted using the 'amt'

186   package (Signer et al. 2019) in R v. 3.6.2 (R Core Team 2019). We fit our iSSA model using the

187   'glmmTMB' package (Brooks et al. 2017) using the mixed effects model approach with a

188   Poisson error distribution described in Muff et al. 2019 (). To ensure model convergence, we

189   only included individuals that had >1% availability of a covariate during this two-month period,

190   which has previously been shown to provide a robust representation of the habitat available to

191   individuals (Dickie et al. 2019). Thus, 28 wolves met our criteria for inclusion (RMNP = 14

192   wolves, GHA 26 = 14 wolves). To ascertain the coefficients of specific individuals in addition to

193   the population, we further included random effects for the slope of each variable for each

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194   individual (Muff et al. 2019). When there are a large number of GPS relocations, as we have

195   over our two month observation windows, as few as two animals are sufficient to obtain robust

196   habitat selection estimates (Street et al. 2021).

197   Our model included variables important to wolf space-use and pertinent to testing our

198   hypotheses. To account for general space-use behaviors known of wolves, we included natural

199   log (ln) of step length (modifier of the gamma shape parameter) alone and interacted the ln step

200   length with proportion of habitat type to account for how animals move differently (faster or

201   slower) through different habitat types. In addition, we included the cosine (cos) of turn angle

202   (von Mises concentration parameter) to describe an individual's deviation in directionality.

203   To address our hypotheses, we included covariates to represent 1) movement, 2) habitat

204   selection, and 3) social behaviors in the model. We expected human-killed wolves to have

205   greater speed and selection for human infrastructure as they neared death, but there is no reason

206   to expect them to demonstrate different selection for proximity to packmates compared to control

207   wolves (Theuerkauf 2009). We expected that wolves dying from CDV would decrease

208   movement speed, increase selection for wet habitats, and increase avoidance of packmates as

209   they neared the end of life.

210   Habitat selection was described by habitat type and distance from road. We defined

211   habitat using the 2015 Canada landcover map at a 30 m x 30 m scale, reclassified to forest, open,

212   and wet habitat types (Table S2). We then calculated the proportion of each habitat type within a

213   100 m buffer around GPS locations. We included ln distance to roads as an indicator of human

214   presence in the area. Lastly, we included distances to nearest neighbor from the same pack and

215   distance from pack boundary as social covariates. All distance variables were ln transformed

216   because we expect animals to have a stronger response to features when they are closer to them,

217   and that response would decay at an unknown rate.

218   We calculated nearest neighbor with a collar and the distance to that individual using the

219   'spatsoc' package in R (Robitaille et al. 2019 May 24). For each available point, we calculated

220   the distance to the same neighbor that was the observed nearest neighbor. Because the collared

221   wolves made many forays outside of pack boundaries, we conservatively determined pack

222   boundaries based on wolf behaviors determined by tracking and site investigation where we

223   determined that the wolves hunted, scavenged, or rested when the collars were deployed. We

224   employed kernel density estimations using the center points of these behavioral clusters to

225   approximate pack boundaries using the adehabitatHR package in R (Calenge 2006).

226   Furthermore, we ran a binomial regression to ascertain if they spent more time outside of their

227   pack boundary dependent on their eventual cause of death.

228   *Relative selection strength*

229   To determine the effect size of selection, we calculated relative selection strength (RSS) of each

230   selection covariate, i.e., forest, open, wet, distance to road, distance to nearest neighbor, and

231   distance to pack boundary (Avgar et al. 2017). Following the method presented in 'amt' to

232   calculate the logRSS, we compared the average habitats used to the range of habitats used, one

233   variable at a time (Signer et al. 2019). Specifically, we held habitat variables constant while time

234   to death varied from 61 to 0 days from death.

235   **Results**

236   General patterns emerged in the population's habitat selection behavior, wolves moved more in

237   open areas (Table 1) and showed higher relative selection strength (logRSS) for proximity to

238   their nearest packmate than they did habitat variables (Figs. 1 and 2). However, wolves

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239   demonstrated a wide range of individual variation in selecting for habitat types and the nearest

240   distances to packmates (Figs. 1 and 2).

241   **Table 1.** GLMM model output of fixed effects. Bolded p-values are significant at $\alpha = 0.05$ (n =
242   29 wolves). Highlighted variables were confirmed to be important with mean speed estimates or
243   relative selection strengths (RSSs) of individuals (blue = control, purple = human, green =
244   CDV).

component	term	estimate	SE	statistic	p-value
	(Intercept)	6.576	47.688	0.138	0.890
Core	ln(step length): Prop. forest	0.060	0.086	0.695	0.487
	ln(step length): Prop. open	0.246	0.090	2.730	**0.006**
	ln(step length): Prop. wet	0.126	0.088	1.431	0.152
Movement	ln(step length): COD human	-0.259	0.183	-1.418	0.156
	ln(step length): COD CDV	-0.379	0.151	-2.500	**0.012**
	cos(turn angle): COD control	0.023	0.088	0.263	0.792
	cos(turn angle): COD human	-0.099	0.149	-0.663	0.507
	cos(turn angle): COD CDV	-0.627	0.139	-4.524	**<0.001**
	ln(step length): ln(time to death): COD control	0.011	0.023	0.451	0.652
	ln(step length): ln(time to death): COD human	0.084	0.044	1.919	0.055
	ln(step length): ln(time to death): COD CDV	0.092	0.034	2.686	**0.007**
	cos(turn angle): ln(time to death): COD control	-0.044	0.025	-1.742	0.082
	cos(turn angle): ln(time to death): COD human	0.005	0.046	0.110	0.913
	cos(turn angle): ln(time to death): COD CDV	0.128	0.040	3.186	**0.001**
Habitat	Prop. forest: COD human	3.020	53.813	0.056	0.955
	Prop. forest: COD CDV	-0.805	93.412	-0.009	0.993
	Prop. open: COD human	0.012	53.815	0.000	1.000
	Prop. open: COD CDV	-0.792	93.441	-0.008	0.993
	Prop. wet: COD human	2.156	53.815	0.040	0.968
	Prop. wet: COD CDV	0.524	93.413	0.006	0.996
	ln(distance to road): COD control	-0.206	0.062	-3.304	**0.001**
	ln(distance to road): COD human	-0.068	0.117	-0.581	0.561
	ln(distance to road): COD CDV	0.030	0.117	0.257	0.797
	Prop. forest: ln(time to death): COD control	-1.262	14.080	-0.090	0.929
	Prop. forest: ln(time to death): COD human	-3.681	7.650	-0.481	0.630
	Prop. forest: ln(time to death): COD CDV	-2.332	23.742	-0.098	0.922
	Prop. open: ln(time to death): COD control	-1.702	14.081	-0.121	0.904
	Prop. open: ln(time to death): COD human	-3.287	7.650	-0.430	0.667
	Prop. open: ln(time to death): COD CDV	-3.091	23.751	-0.130	0.896
	Prop. wet: ln(time to death): COD control	-1.492	14.081	-0.106	0.916
	Prop. wet: ln(time to death): COD human	-3.532	7.651	-0.462	0.644

|					
	Prop. wet: ln(time to death): COD CDV	-2.666	23.742	-0.112	0.911
	ln(distance to road): ln(time to death): COD control	0.038	0.018	2.154	0.637
	ln(distance to road): ln(time to death): COD human	-0.016	0.033	-0.472	**0.031**
	ln(distance to road): ln(time to death): COD CDV	-0.019	0.033	-0.579	0.562
Social	ln(distance to NN): COD control	-1.272	0.148	-8.575	**<0.001**
	ln(distance to NN): COD human	-2.062	0.389	-5.299	**<0.001**
	ln(distance to NN): COD CDV	-1.257	0.333	-3.774	**<0.001**
	ln(distance to boundary): COD control	0.104	0.102	1.025	0.306
	ln(distance to boundary): COD human	-0.054	0.147	-0.367	0.714
	ln(distance to boundary): COD CDV	0.340	0.334	1.017	0.309
	ln(distance to NN): ln(time to death): COD control	0.016	0.042	0.378	0.706
	ln(distance to NN): ln(time to death): COD human	0.162	0.118	1.378	0.168
	ln(distance to NN): ln(time to death): COD CDV	0.157	0.093	1.689	0.091
	ln(distance to boundary): ln(time to death): COD control	0.113	0.055	2.045	**0.041**
	ln(distance to boundary): ln(time to death): COD human	0.025	0.090	0.279	0.780
	ln(distance to boundary): ln(time to death): COD CDV	0.009	0.111	0.084	0.933

As expected, control wolves did not significantly change their movement patterns, step length and turn angle, over time (Table 1, Fig. 1). Control wolves, however, increased their selection for open habitats as time passed, but showed no change in selection for the proportion of forest or wet habitats as time progressed (Table 1). Control wolves selected to be closer to roads than expected; this did not change over time (Table 1). Control wolves also selected to be closer to their nearest packmate than expected based on availability, and this pattern did not change over time (Table 1, Fig. 1).

13
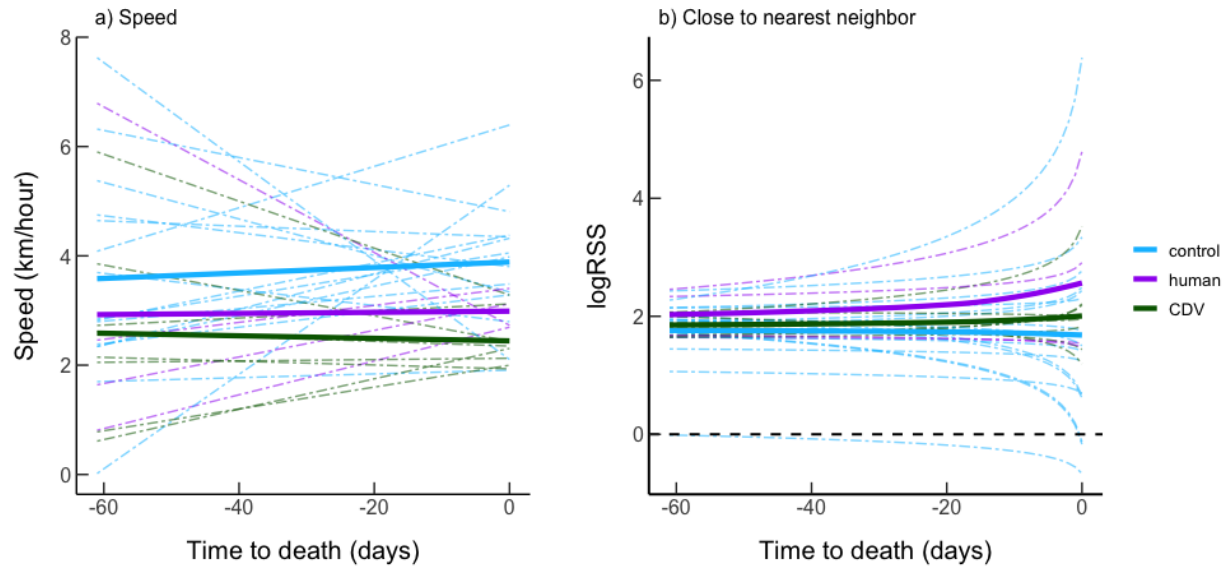
253
254 **Figure 1.** The change in a) speed and b) relative selection strength (RSS) for proximity (250m)
255 to nearest packmate neighbors as wolves that survived (control), died due to humans, and died
256 from CDV neared the end of the two-month period or death. The solid lines represent the
257 population trend with the filled area around the line indicating the 95% confidence intervals, and
258 dashed colored lines represent individual wolves. For the RSS, the black dashed horizontal line
259 indicates no response, above the line represents greater selection than expected, and below the
260 line indicates more avoidance of the habitat type than expected.
261

262   In comparison to the baseline behavior of control wolves, human-killed wolves did not

263 show differences in trajectory (cosTA), but they tended to move slower than control wolves

264 (Table 1, Fig. 1). Human-killed wolves did not differ in how they selected for forest, open, or

265 wet habitats compared to control wolves and did not respond to the proximity of roads (Table 1),

266 but they tended to select to be closer to roads right before death (Fig. 2). Human-killed wolves

267 also selected to be closer to their nearest packmate than expected (Fig. 1), but they did not show

268 a significant response to distance from pack boundary (Table 1). However, human-killed wolves

269 spent 21% of their time outside of their territory than in it compared to control wolves that spent

270 approximately 7% of their time outside of their territory ($\beta = 1.61$, $z = 0.7$, $p = 0.48$).

271 Furthermore, some of the behaviors of the human-killed wolves changed as they neared their

272 eventual death. The human-killed wolves tended to avoid open and wet areas less as they neared

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273   death (Table 1, Fig. 2), and they selected to be closer to roads near their death date (Fig. 2).

274   Movement and social covariates did not change as they neared death (Table 1).

275
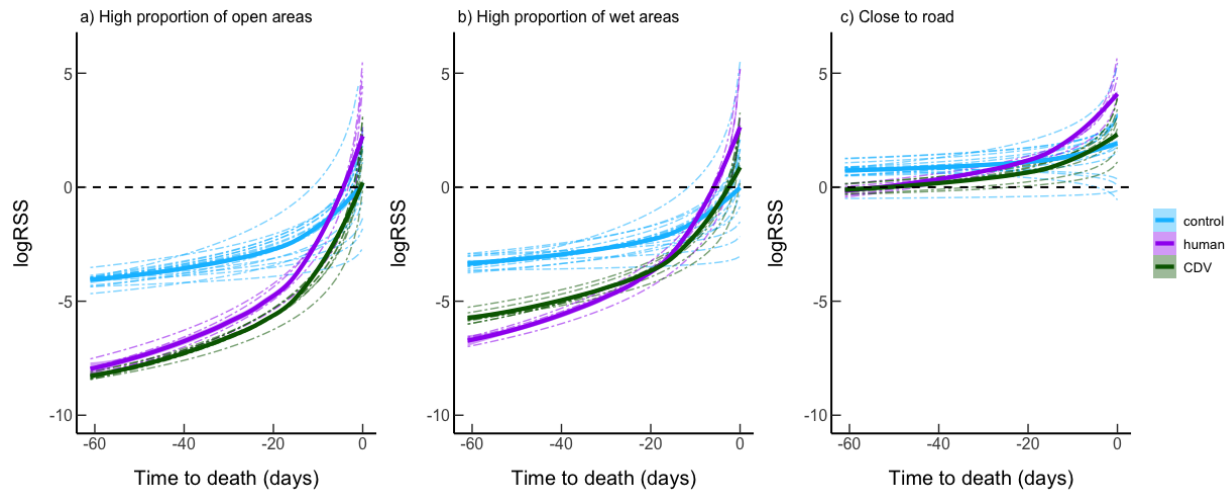
276
277   **Figure 2.** The change in relative selection strength (RSS) for a) high proportion (75% coverage)
278   open areas, b) high proportion wet areas, and c) and proximity (250m) to roads as wolves that
279   survived (control), died due to humans, and died from CDV neared the end of the two-month
280   period or death. The solid lines represent the population trend and dashed colored lines represent
281   individual wolves. The black dashed horizontal line indicates no response, above the line
282   represents greater selection than expected, and below the line indicates more avoidance of the
283   habitat type than expected.
284

285   Wolves that died from CDV generally moved and changed trajectory more than control

286   wolves (Table 1). The wolves that died from CDV showed no significant differences in baseline

287   response to any habitats compared to control wolves (Table 1). CDV wolves also showed no

288   significant response to road proximity (Table 1). Wolves that died from CDV showed the same

289   behavioral pattern as the human-killed wolves in selecting for be closer to their packmate and

290   showing no significant response to the distance from the territorial boundary (Table 1, Fig. 1).

291   They also spent approximately 5% of their time outside of the territory, not significantly

292   differing from control wolves ($\beta = 1.13$, $z = -0.6$, $p = 0.541$). CDV wolves also showed changes

293   in movement and habitat selection behavior as they neared their eventual deaths. CDV wolves

15

294   moved slower and changed direction more the closer they were to dying (Table 1, Fig. 1).

295   Furthermore, CDV wolves tended to avoid open and wet areas less as they neared death (Table 1,

296   Fig. 2). The social behavior of CDV wolves did not change over time (Table 1, Fig. 1).

Discussion

298   Our results highlight the interplay among habitat selection, movement, and social behaviors that

299   create and relate to how an individual lives and dies due to human and disease mortality risks.

300   Human-killed wolves did not demonstrate intrinsic, baseline, behaviors but changed their

301   behaviors that increased their risk of death (i.e., selection for roads). Wolves that died from CDV

302   also changed their behaviors as they were dying. Importantly, the increasing selection for open

303   areas and roads and their predilection to spend more time outside of their territorial boundaries

304   compared to control wolves contributed to the risk of death for human-killed wolves. Contrary to

305   our predictions, human-killed wolves were slower than control wolves. Wolves that died from

306   canine distemper virus (CDV) decreased speeds and tended to reduce their avoidance of wet

307   areas as they neared death, as predicted. However, they did not avoid packmates more than

308   control wolves and instead maintained strong selection to be near packmates. Thus, wolves that

309   died from human causes compared to CDV had distinctly different movement and habitat

310   selection patterns. Therefore, the interplay of behaviors provide insight into cause-specific

311   mortality and may help improve our understanding of population dynamics.

312   Movement and habitat selection behaviors have a synergistic effect so that animals are at

313   greater anthropogenic risk before they die (Lamb et al. 2020). Human-killed wolves selected for

314   habitats where they were at greater risk, consistently moving slower and being more frequently

315   outside of their pack boundary and increasingly selecting for roads before they died. These

316   patterns of selection differed from wolves in our study that were not killed by humans and from

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317   general population trends in other predator species. Most notably, carnivores in boreal regions

318   generally select for forested areas and avoid anthropogenic disturbance (Lesmerises et al. 2012;

319   Recio et al. 2019). In many species ranging from predators to prey, variation in consistent

320   individual movement and habitat selection patterns put individuals at greater risk of human

321   caused mortality (M.H. Murray and St Clair 2017; Sawyer et al. 2019). Apex predators move

322   faster in developed areas (Buderman et al. 2018) but tend to slow down and move more

323   cautiously when they hear humans (Suraci et al. 2019). Human-killed wolves may be doing the

324   same as they moved slower than the control wolves and spent time in human-dominated areas

325   near roads. Selecting to be in riskier situations may be a byproduct of life-stage, as the human-

326   killed wolves were all estimated to be 1-2 years old, approximately the age of dispersal (Stronen,

327   Schumaker, et al. 2011). Dispersal is a risky time across species, and the wolves here showed

328   similar movement patterns to other dispersing carnivores (Bartoń et al. 2019; Herrero et al.

329   2020). Individuals that avoid being killed by humans may learn to better navigate their

330   environment to avoid risky situations (Greenberg and Holekamp 2017). Thus, we see that

331   movement and where individuals select to move synergistically create risky situations that lead

332   to death by humans.

333   Behavioral responses to disease in particular demonstrated the connections between

334   habitat selection, movement, and social behavior that put individuals at greater risk. Individual

335   wolves that died from CDV contributed to a tragedy of the pack; they maintain their social bonds

336   with their packmates to the detriment of the survival of other individuals in the pack. In our

337   study, most packs died off due to CDV. One pack had three collared wolves die from CDV over

338   the course of a month affecting the pack's movement for at least two months. Although the risks

339   that arise while infected with CDV may be short-term at the individual level, it has the potential

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340   to be more long-term at the pack level where serial infection affects the movements and habitat

341   selection of a pack for months. The social tendency to be close to packmates regardless of illness

342   could influence the inclusive fitness of the group and facilitate continuation of the disease in the

343   population when the whole pack does not disappear. The effects of sickness seem to depend on

344   the type of social interaction. Vampire bats do not change their spatial association behaviors

345   when immune-challenged, but they did decrease their number of grooming partners, likely due to

346   lethargy (Stockmaier et al. 2020 Feb 28). As wolves slow down when they are ill, they likely

347   change their direct social interactions in ways that could not be detected with relocation data.

348   However, the fact that wolves do not change their spatial association patterns indicates that the

349   direct and indirect fitness benefits of social cohesion likely remain greater than the benefits of

350   preventing infecting packmates.

351   Due to the difficulty of knowing when an animal is going to die and observing it, GPS

352   collar data is useful for quantifying end-of-life behaviors. Behavior-based models have

353   successfully predicted survivorship in population-level models (Stillman et al. 2000), but it is

354   less well understood how individual-level dynamics create those population-level responses.

355   Individual habitat selection, movement, and social behavior are behaviors that can be measured

356   remotely via GPS collars and even camera trapping (Caravaggi et al. 2017). We demonstrate that

357   these behaviors relate to cause-specific mortality. In the future, it would help to pair detailed

358   behavioral observation with movement data to gain more fine-scale insights to disease spread.

359   Furthermore, these remotely measured movement and habitat selection data not only indicate

360   that an animal is dying; they can alert managers to potential risks in the environment such as

361   poisoned carcasses, improper disposal sites, and illegal trapping in our research areas.

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362   The interconnections of habitat selection, movement, and social behavior have individual

363   and population level repercussions (Albery et al. 2020). Here, we relate the interaction of these

364   behaviors to cause-specific mortality after death. Humans harvesting carnivores and CDV

365   outbreaks are both linked to major demographic changes (Cleaveland et al. 2007; Lamb et al.

366   2020). Thus, fine-scale movement behaviors that are both the cause and consequence of dying

367   are an important factor to consider in conservation and management plans. For instance, scaling

368   up from the individual-level findings here we can get better estimates of the cause of mortality

369   within populations. Furthermore, if management calls for an intervention to control a CDV

370   outbreak, they will have to target members of pack to give a vaccine to stop the spread within the

371   pack once it reaches them (M.J. Silk et al. 2017). Overall, we see that individual-level patterns in

372   the interplay of habitat selection, movement, and social behaviors related to cause-specific

373   mortality from long- and short-term risks.

374

Acknowledgements

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386

Data Availability

388   Data and code will be made available upon publication on Zenodo and GitHub.

389

390   **Competing Interest:** The authors declare no conflict of interest

391

392   **Author Contributions:** JWT, CMP, and EVW conceptualized the idea and study design. CMP,

393   KAK, DLJD, and SZS collected the field data. JWT ran the analyses and drafted the article. All

394   authors critically revised the article and gave final approval for publication.

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