

1 *Death comes for us all: an interplay of habitat selection, movement, and social behavior relate*  
2 *to cause specific mortality among grey wolves*

3

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

5

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12 **Abstract**

13 Avoiding death inflicts 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

30

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,

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

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 (Eberhard 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<sup>2</sup> 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<sup>2</sup> 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 (Blixenkron-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.



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

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

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
<i>Core</i>	ln(step length): Prop. forest	0.060	0.086	0.695	0.487
	ln(step length): Prop. open	0.246	0.090	2.730	<b>0.006</b>
	ln(step length): Prop. wet	0.126	0.088	1.431	0.152
<i>Movement</i>	ln(step length): COD human	-0.259	0.183	-1.418	0.156
	ln(step length): COD CDV	-0.379	0.151	-2.500	<b>0.012</b>
	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	<b>&lt;0.001</b>
	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	<b>0.007</b>
	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	<b>0.001</b>	
<i>Habitat</i>	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	<b>0.001</b>
	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	<b>0.031</b>
	ln(distance to road): ln(time to death): COD CDV	-0.019	0.033	-0.579	0.562
<i>Social</i>	ln(distance to NN): COD control	-1.272	0.148	-8.575	<b>&lt;0.001</b>
	ln(distance to NN): COD human	-2.062	0.389	-5.299	<b>&lt;0.001</b>
	ln(distance to NN): COD CDV	-1.257	0.333	-3.774	<b>&lt;0.001</b>
	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	<b>0.041</b>
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	

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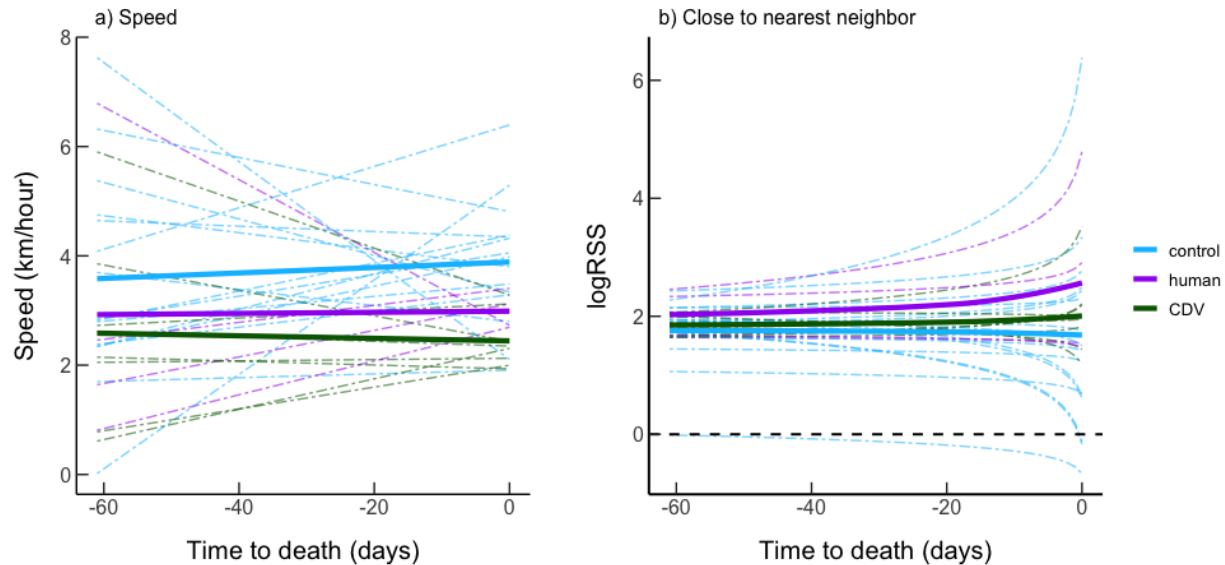
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As expected, control wolves did not significantly change their movement patterns, step length and turn angle, over time (Table 1, Fig. 1). Control wolves, however, increased their selection for open habitats as time passed, but showed no change in 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).



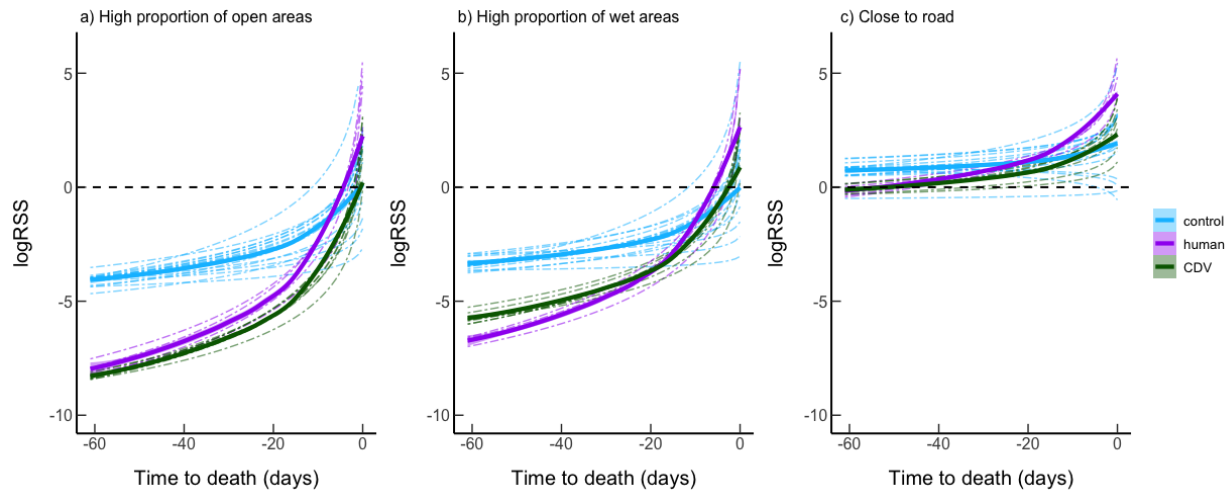
253 **Figure 1.** The change in a) speed and b) relative selection strength (RSS) for proximity (250m)  
254 to nearest packmate neighbors as wolves that survived (control), died due to humans, and died  
255 from CDV neared the end of the two-month period or death. The solid lines represent the  
256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

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

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).

## 297 **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



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

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.

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

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386

### 387 **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.

395

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