

1 **Title: Behavioral plasticity allows ungulates to balance risk and reward following megafire**

2

3 **Authors: Kendall L. Calhoun<sup>1</sup>, Thomas Connor<sup>1</sup>, Kaitlyn M. Gaynor<sup>2</sup>,**

4 **Amy Van Scoyoc<sup>1</sup>, Alex McInturff<sup>3</sup>, Samantha E.S. Kreling<sup>3</sup>, Justin S. Brashares<sup>1</sup>**

5

6 **Key Words: megafire, movement ecology, black-tailed deer, resource selection functions,**

7 **hidden Markov models, behavioral plasticity**

8

9 <sup>1</sup>Department of Environmental, Science, Policy, and Management, University of California

10 Berkeley, 137 Mulford #3114, Berkeley, CA, 94720, USA

11 <sup>2</sup> Departments of Zoology & Botany, University of British Columbia, BC, Canada V6T 1Z4

12 <sup>3</sup>School of Environmental and Forest Sciences, University of Washington, Anderson Hall, Box

13 352100, Seattle, WA, 98195, USA

14

15 \*Corresponding Author: kendallcalhoun@berkeley.edu, 210 Wellman Hall, Berkeley, CA,

16 94720, USA

17

18

19

20

21

22

23

24 **Abstract**

25 Anthropogenic climate and land use change has accelerated the frequency of extreme climatic  
26 disturbances such as megafire. These megafires dramatically alter ecosystems and threaten the  
27 long-term conservation of economically and ecologically important species, including s. Recent  
28 work suggests that ungulate species may be able to adjust to the immediate effects of megafire  
29 by adjusting their movement and behavior, but whether these adjustments persist or change over  
30 time following these major disturbances is far less is understood. We take advantage of a rare  
31 research opportunity to examine how a dominant ungulate species, black-tailed deer (*Odocoileus*  
32 *hemionus columbianus*), adjusts its movement and behavior immediately following a megafire.  
33 We collected GPS data from 24 individual doe over the course of a year and fit these data to  
34 resource selection functions (RSFs) and hidden Markov movement models (HMMs) to assess  
35 whether and how deer alter habitat selection and behavioral decisions to adjust to novel  
36 landscape conditions following this megafire. We found compelling evidence of adaptive  
37 capacity across black-tailed deer following megafire, with deer modifying their habitat usage and  
38 behavior following megafire. Deer avoided exposed (chaparral) and severely burned areas  
39 immediately following megafire, but later altered these behaviors to eventually select for areas  
40 that burned at higher severities to potentially take advantage of enhanced forage in these  
41 recovering areas. These results suggest that despite their high site fidelity, this deer population,  
42 and similar ungulate species, can effectively navigate altered landscapes to track relatively  
43 sudden shifts in predation risk and resource availability. The successful adjustment of dominant  
44 ungulate species to extreme disturbances such as these could help facilitate resilience at broader  
45 ecological and trophic scales.

46

47       **1. Introduction**

48 Anthropogenically induced change in the 21st century continues to accelerate instances of  
49 extreme climatic disturbance around the globe (Stott, 2016). In fire-prone ecosystems, megafires,  
50 wildfires that surpass the size and severity of historical fires, have become increasingly prevalent  
51 (Linley et al., 2022). Fire has served an important ecological and evolutionary role in many of  
52 these ecosystems (McLauchlan et al., 2020), but climate and land use change have driven the  
53 occurrence of extremely large and severe wildfires, otherwise known as megafires. These  
54 megafires can dramatically affect ecosystems and the species that inhabit them (Nimmo et al.,  
55 2022). Though many wild animal species in these fire-prone ecosystems have adaptations to  
56 coexist with their historic fire regimes (Jones et al., 2020; Pausas & Parr, 2018), novel megafires  
57 may challenge, and even overwhelm, the adaptive capacity of these species.

58

59       Wildfire continues to be a key tool for stewarding ecosystems around the world (Fletcher  
60 et al., 2021; Boisramé et al., 2017), but recent megafires far exceed the size, severity, and  
61 intensity of these wildfires. By quickly altering landscapes, megafire may impact how some  
62 species are able to navigate and use habitat. High severity fires, defined as fires that burn the  
63 dominant vegetation type in an ecosystem (i.e. trees in woodlands) (Keeley, 2009), can remove  
64 important structural resources from landscapes (Steel et al., 2021) and even cause direct  
65 mortality (Jolly et al., 2022). Changes in structural cover in these systems may alter interspecies  
66 interactions, such as predator-prey dynamics, by exposing prey species or by directly impacting  
67 the hunting success of predators (Doherty et al., 2022). At the same time, these high severity  
68 fires may also remove important vegetative food resources (i.e., forbs, grasses, seeds, etc.) and in

69 turn directly impact herbivorous species (Rickbeil et al., 2017), which may go on to impact  
70 populations of species at higher trophic levels.

71

72 The capacity for species to effectively respond to these environmental changes caused by  
73 megafire may be closely tied to their ability to adapt and adjust to novel disturbance regimes.

74 Recent work has documented the role plasticity plays in governing the adaptive capacity of  
75 species to other forms of global change (Hammond et al., 2018; Riddell et al., 2018; Schell et al.,  
76 2018). For larger wildlife, plasticity in movement and behavior play a significant role in allowing  
77 individuals to adjust to changes in their local environments (Suraci et al., 2021; Gaynor et al.,  
78 2018). For fire specifically, larger wild animal species may partition their time across recently  
79 burned landscapes to take advantage of new resources or avoid risky areas (Nimmo et al. 2019).

80

81 Ungulates are dominant species in many fire-prone ecosystems around the world, and the  
82 way they respond to megafire events may go on to have important consequences for other  
83 species they interact with. Under historic fire regimes, several ungulate species adjusted their  
84 movement and habitat selection decisions to avoid or take advantage of recently burned areas  
85 (Roerick et al., 2019; Cherry et al., 2018). Past work has documented a “magnet effect” across  
86 several ungulate species, where species select moderately burned areas that have improved  
87 forage post-fire (Allred et al., 2011; Archibald et al., 2005). In more severe fire events, recent  
88 work also suggests that behavioral plasticity may grant some ungulate species a buffer to the  
89 short-term impacts of megafire (Kreling et al., 2021), but whether these adjustments continue to  
90 protect ungulate species in the longer-term following megafire remains to be seen. The short-  
91 and long-term responses of ungulates to severe fire may also be modulated by the seasonality of

92 fire events, with fires potentially increasing scarcity of rare vegetative resources during the dry  
93 seasons or limiting required resources during energetically costly periods of the year (i.e. spring  
94 breeding season) (Proffitt et al., 2019).

95  
96 In this study, we examine the long-term consequences of megafire on an ecologically and  
97 economically important Californian ungulate, the black-tailed deer (*Odocoileus hemionus*  
98 *columbianus*), at the Hopland Research and Extension Center. We use GPS-collar data collected  
99 from 24 deer across one year to observe how long changes in black-tailed deer movement and  
100 behavior persist following the 2018 Mendocino Complex fire, the largest wildfire in recorded  
101 Californian history at the time. We use resource-selection functions to examine black-tailed deer  
102 habitat selection following megafire across time to observe whether and when deer habitat  
103 selection returns to pre-fire conditions. In addition, we also use Hidden-Markov Movement  
104 models (Michelot et al., 2016) to assess how fine-scale behavioral decisions may have been  
105 affected by high severity fire.

106  
107 We predicted that deer would preferentially use habitat that burned at low severity  
108 immediately following the fire to avoid exposure. Conversely, we predicted black-tailed deer  
109 would select for areas that burned at moderate severity the following growing season due to their  
110 increased nutritional value. We predicted that changes in habitat selection would persist through  
111 the study (1-year post-fire). We anticipated that black-tailed deer would adjust their behavioral  
112 decisions to make quick, directed movements through severely burned areas, again to avoid  
113 being exposed, and that this would be apparent throughout the entire study period. An improved  
114 understanding of the long-term capacity of deer to effectively cope with dramatic landscape

115 change could help identify if further conservation interventions are needed for populations across  
116 the Western US following megafire, as well as for other ungulate populations around the world.

117

## 118 **2. Methods**

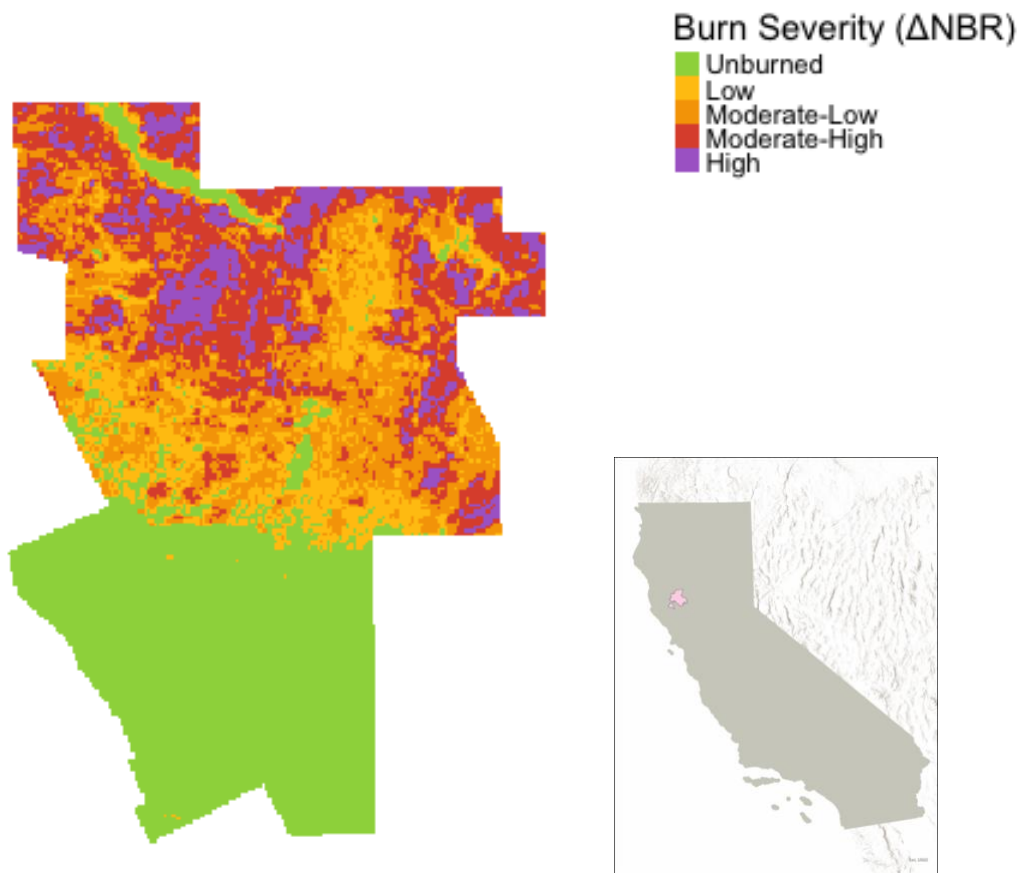
### 119 2.1 Study Site and Fire History

120 We conducted this study at the Hopland Research and Extension Center (Hopland hereafter) in  
121 Mendocino County of Northern California (5,300 acres, 39°00' N, 123°04' W). Hopland is  
122 composed of a diverse set of vegetation types including chaparral shrublands, oak woodland  
123 savannah, and open grassland. Hopland is characterized by a Mediterranean climate with cool,  
124 wet winters and warm dry summers. Hopland also operates as a working rangeland landscape,  
125 containing a sheep farming facility and several agricultural plots throughout the property.

126

127 Figure 1 - Map of fire severity across the Hopland Research and Extension Center perimeter.

128 Fire severity was quantified as the Differenced Normalized Burn Ratio (dNBR).



129            In late July of 2018, the southern half of the Mendocino Complex Fire, the River Fire,  
 130 swept through the northern half of Hopland, burning approximately 3,400 acres (65%) of the  
 131 property. The whole complex fire burned 459,123 acres total and is currently the 3rd largest  
 132 wildfire in California’s recorded history (CALFIRE-FRAP, 2022). Fires in this region typically  
 133 burn frequently at relatively low severities in the more open woodland and grassland habitats and  
 134 more infrequently, but more severely in the dense shrubland chaparral habitats (Syphard and  
 135 Keeley, 2020). The River Fire burned a much larger contiguous area and much more severely  
 136 than recent fires within Hopland.

137

138

## 139 2.2 Monitoring Black-tailed Deer Movement and Home Range Estimation

140 We deployed GPS-collars (Vertex Plus and Lotek Iridium Track M) across 16 individual does  
141 between July 2018 and July 2019. These data were used opportunistically to observe the effects  
142 of megafire on deer movement and behavior. We programmed all collars to record GPS locations  
143 once per hour. Deer were captured using Clover traps and were manually restrained to place  
144 collars on, without the use of chemical immobilizers. We monitored deer remotely post-capture  
145 for multiple days to ensure that each deer remained healthy following capture and collaring.

146

147 In order to observe how deer movement and behavior changed over time following  
148 megafire, we subset the collected GPS data temporally into three time periods: just after the fire  
149 (August - October 2018), the first spring green up following the fire (March - May 2019), and  
150 one full year post-fire (August - October 2019) (Table 1). Within each time period, we only  
151 included individual deer that had at least 500 recorded GPS locations for analyses. We removed  
152 8 erroneous GPS locations that were greater than 2km from their consecutive points.

153

154 For each deer and within each study period, we used the two months of collected GPS  
155 data to estimate individual home range sizes. We used 95% Kernel Utilization Densities (KUD)  
156 in the adehabitatHR package in R to create these home ranges (Barker et al., 2019; Calenge,  
157 2006; R Core Team, 2013). Of the 16 unique individuals collared across these 3 time periods, 10  
158 individuals maintained their collars across 2 or more study periods, resulting in 26 study period-  
159 specific home ranges that overlapped the Mendocino Complex fire burn perimeter. To assess  
160 whether deer home range sizes continue to change following megafire, we used paired Welch's



161 unequal variance t-test to compare doe home range sizes 1) just after fire (“Recently Burned”), 2)  
162 the first spring following fire (“First Spring”), and 3) one full year post-fire (“1 Year Post Fire”).

163

### 164 2.3 Environmental Covariates

165 We compiled fire and other environmental covariates alongside deer movement data in order to  
166 compare black-tailed deer movement responses to megafire over time. We predicted that fire  
167 severity, predation risk, and vegetation type, and time since burning would be strong predictors  
168 of both deer habitat selection and deer movement decisions following megafire. Originally, we  
169 planned to include NDVI as a measure of forage availability across the landscape, we found  
170 measures of NDVI were highly correlated with measures of fire severity, our primary covariate  
171 of interest. Therefore, we defaulted to including fire severity and removing NDVI. To quantify  
172 fire severity on the landscape, we calculated the differenced Normalized Burn Ratio (NBR)  
173 collected via Sentinel-2 (Sentinel Hub, 2021) satellite imagery (10m resolution) from both before  
174 and after the fire. NBR was calculated using the following equations (Keeley, 2009):

$$175 \quad \Delta NBR = NBR_{prefire} - NBR_{postfire}$$

$$176 \quad NBR = \frac{\text{Near-infrared (NIR)} - \text{shortwave infrared (SWIR)}}{\text{Near-infrared (NIR)} + \text{shortwave}} \\ 177 \quad \text{infrared (SWIR)}$$

178

179 We also included a quadratic term for fire severity to examine whether deer may  
180 preferentially select for moderately burned areas that, according to the magnet effect, may  
181 eventually have more nutritious forage.

182

183 To account for predation risk across the landscape for this study, we included a high-  
184 resolution mountain lion habitat suitability map produced for the entire State by Dellinger et al.  
185 2020 in our analyses (Dellinger et al. 2020). Mountain lions are the primary predator of black-  
186 tailed deer in this system, and we use this habitat suitability map to serve as important proxy of  
187 potential predation risk for where deer may be more likely to encounter mountain lions across  
188 our study site.

189

190 Finally, the short and long-term effects of fire on deer habitat may be directly related to  
191 the dominant vegetation type of that habitat. For example, grassland ecosystems typically  
192 recover faster following fire relative to shrubland and woodland systems (Halofsky et al., 2011),  
193 which may lead deer to preferentially choose these areas in the time following megafire. We  
194 classified the study site into three broad land cover categories: woodland, shrubland (chaparral),  
195 and grassland. To do this, we hand digitized vegetation layers using high-resolution (<1 meter)  
196 aerial imagery from the National Agriculture Imagery Program (2014-2015). In 2015, we  
197 ground-truthed these digitizations by checking 50 randomly generated points across the study  
198 site to validate classifications (results were 98% accurate).

199 Each of these environmental rasters (fire severity, mountain lion habitat suitability  
200 predation risk, and vegetation cover were clipped to the property boundary of Hopland REC  
201 from which we limit the spatial bounds of our study.

202

## 203 2.5 Resource Selection Functions

204 We used Resource Selection Functions (RSFs) to assess black-tailed deer habitat selection across  
205 each time period. We modeled habitat selection for all time periods combined to improve

206 interpretability of model results. We included a random effect of “Deer ID” within our RSFs to  
207 account for individual differences in behavior and resource availability for each deer (individual  
208 deer retained their same “Deer ID” across time periods). For each GPS-point we generated 4  
209 additional random “non-use” points from within each deer’s estimated KUD home range. Non-  
210 use points were stratified by time period so that the number of non-use points had the same ratio  
211 across time periods as the true use points. We compared “use” and “non-use” GPS points using a  
212 logistic regression via the *lme4* package in R (, R Core Team, 2021; Bates et al., 2015).

213

214 We used an *a priori* hypothesis driven approach to select a model to describe deer habitat  
215 selection. We included fire severity, fire severity squared, predation risk, vegetation type  
216 (chaparral, woodland, or grassland), and time since burn as covariate predictors for this RSF. We  
217 used woodland as the reference vegetation category within these RSFs. We randomly sampled  
218 “time since burn” for each non-use point as a randomly selected date from its respective time  
219 period. Prior to modeling, we standardized each of the included covariates (mean = 0, standard  
220 deviation = 1).

221

222 To assess goodness of fit of the RSF model, we used the performance package in R  
223 (Lüdecke et al., 2021) to calculate marginal and conditional  $R^2$  values for the model and visually  
224 inspect overall model fitting.

225

## 226 2.6 Hidden Markov Movement Models

227 To assess how deer behavioral decisions were impacted by megafire, we fit a hidden Markov  
228 model (HMM) across all time periods combined within our study using the “moveHMM”

229 package within R (Michelot et al., 2016). The number of behavioral states to model must be  
230 chosen before fitting the hidden Markov model, but recent work highlights pitfalls in drawing  
231 inference from too many modeled states (Pohle et al., 2017). Therefore, we considered HMMs  
232 with 2 behavioral states (1 = resting, 2 = traveling) to increase interpretability and to specifically  
233 observe whether deer traveling behavior changes across landscape variables to potentially avoid  
234 perceived risks (exposure, predation risk, etc.). We used modeled step lengths (via von Mises  
235 distributions) and turning angles (via gamma distribution) between consecutive points of a  
236 particular animal's track to characterize these 2 behavioral states. We chose starting values for  
237 step lengths and turning angles following guidance from Michelot et al., 2017 (Michelot et al.,  
238 2017).

239

240 We used the Viterbi algorithm to predict and assign behavioral states to each GPS point  
241 and used these to create activity budgets (the proportion of each behavioral state) for deer within  
242 each time period (Langrock et al., 2012). We used a Chi-squared test to assess whether the  
243 proportions of the two behavioral states was significantly different across time periods. Finally,  
244 we fit the hidden Markov model with a set of *a priori* selected covariates (*Severity + Predation*  
245 *Risk + Time Since Burn + Vegetation Cover + Severity\*Time Since Burn*) to estimate how the  
246 probability of transitioning between behavioral states changes as a function of fire severity, time  
247 since burn, and other environmental factors.

248

249 We assessed goodness of fit for the HMM using pseudo-residuals drawn from the fit  
250 model. Pseudo-residuals of the step length parameter should be normally distributed given good  
251 model fit (Farhadinia et al., 2020; Patterson et al., 2009). Therefore, we visually inspected step

252 length pseudo residuals and used a Shapiro-Wilk normality test using a random subset of pseudo  
253 residual values (n = 1000).

254

### 255 **3. Results**

#### 256 3.1 Home Range Comparison Across Seasons

257 The average deer home range size across all time periods was 0.90 km<sup>2</sup> (SD ± 0.49). Deer home  
258 range sizes across time periods varied. The average home range size was 0.94 km<sup>2</sup> (SD ± 0.45)  
259 during the “Recently Burned” period, 1.15 km<sup>2</sup> (SD ± 0.44) during the “First Spring” period, and  
260 0.38 km<sup>2</sup> (SD ± 0.14) during the “First Spring” time period, and X during the “1 Year Post Fire”  
261 time period (Table 1; Figure 2). We found no meaningful differences between deer home range  
262 sizes during the “Recently Burned” and “First Spring Period (t = -1.00, df = 17.08, p-value =  
263 0.33), but did find significant differences in deer home range sizes between the “Recently  
264 Burned” and “1 Year Post Fire” periods (t = 3.47, df = 10.05, p-value = 0.01), as well as between  
265 the “First Spring” and “1 Year Post Fire” periods (t = 5.25, df = 13.02, p-value = 0.0002).

266

267

268

269

270

271

272

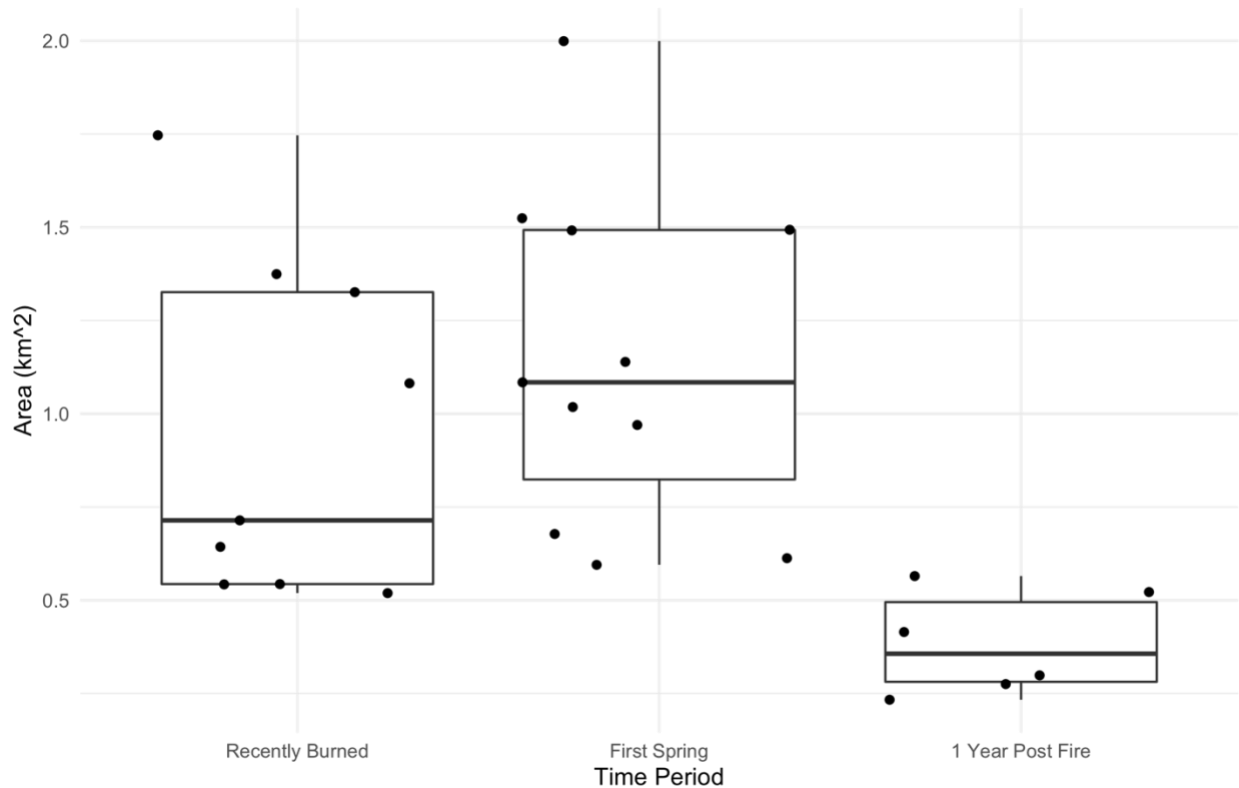
273

<b><i>Study Period</i></b>	<b><i>Dates</i></b>	<b><i>n (Number of Collared Deer)</i></b>	<b><i>Average Home Range Size (km<sup>2</sup>)</i></b>	<b><i>Home Range Size SD</i></b>
Recently Burned	August 1, 2018 – October 1, 2018	n = 9	0.94	±0.45
First Spring	March 1, 2018 – May 1, 2018	n = 11	1.15	±0.44
1 Year Post Fire	August 1, 2019 – October 1, 2019	n = 6	0.38	±0.14

274

275 Table 1 - Table of deer collaring efforts along with average home range size and standard  
276 deviations for each study period. Deer were opportunistically captured and collared across  
277 Hopland REC annual during the summer and fall. For the purposes of this study, collected deer  
278 movement data was subset to include deer whose home ranges overlapped with the Mendocino  
279 Complex Fire. Furthermore, we truncated deer movement data into 3 specific time periods to  
280 create “snapshots” of how deer habitat selection and behavior may be changing over time:  
281 “Recently Burned”, “First Spring” (the first spring following the wildfire), and “1 Year Post  
282 Fire”.

283



284

285 Figure 2 – Boxplot summaries of black-tailed deer (*O. hemionus columbianus*) home range size  
 286 estimation across time periods. Individual deer home ranges were estimated using 95% Kernel  
 287 Utilization Densities (KUD) in the adehabitatHR package in R (Calenge, 2006; R Core Team,  
 288 2013). Home range sizes across deer were summarized in the above plot for each of the study  
 289 periods of interest: Recently Burned, the first spring following wildfire, and 1 full year post fire  
 290 (from left to right).

291

### 292 3.2 Resource Selection Functions

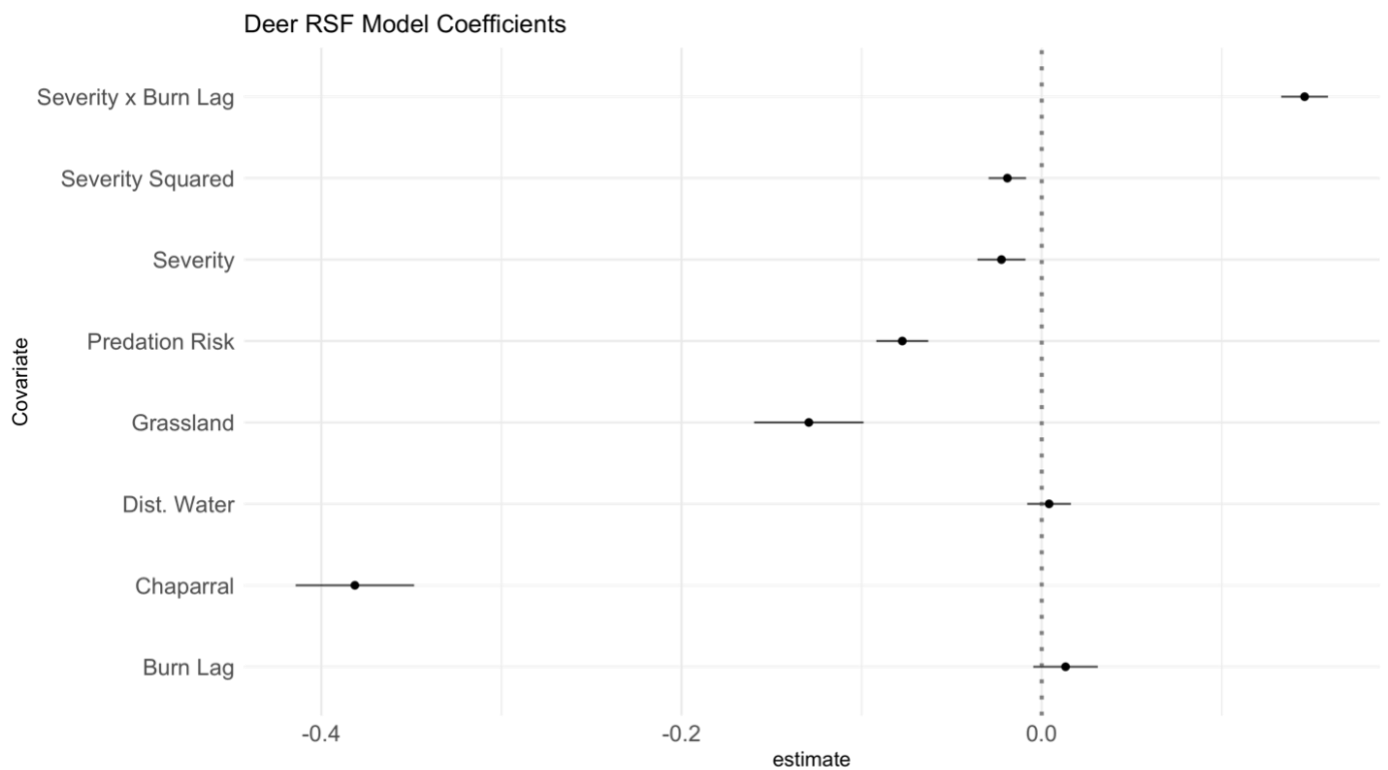
293 Overall, deer avoided areas that burned at both high and moderate (ie Severity Squared)  
 294 severities, as well as areas of high predation risk (Appendix 1 - Table S1.1). However, deer  
 295 habitat selection of fire burned areas appears to change over time as an interaction with time  
 296 since burn. During the “Recently Burned” time period, deer are more likely to avoid high

297 severity areas (Figure 3). Conversely, fire severity has little effect on deer habitat selection  
298 during the “First Spring” time period, and deer appear to select for higher severity burned areas  
299 during the final “1 Year Post Fire” period (Figure 4).

300

301 Deer showed a preference for woodland habitat and avoided both grassland and chaparral  
302 following the fire. Vegetation cover preferences appear to persist across burn severities (Figure  
303 S1.1) as well as over time.

304



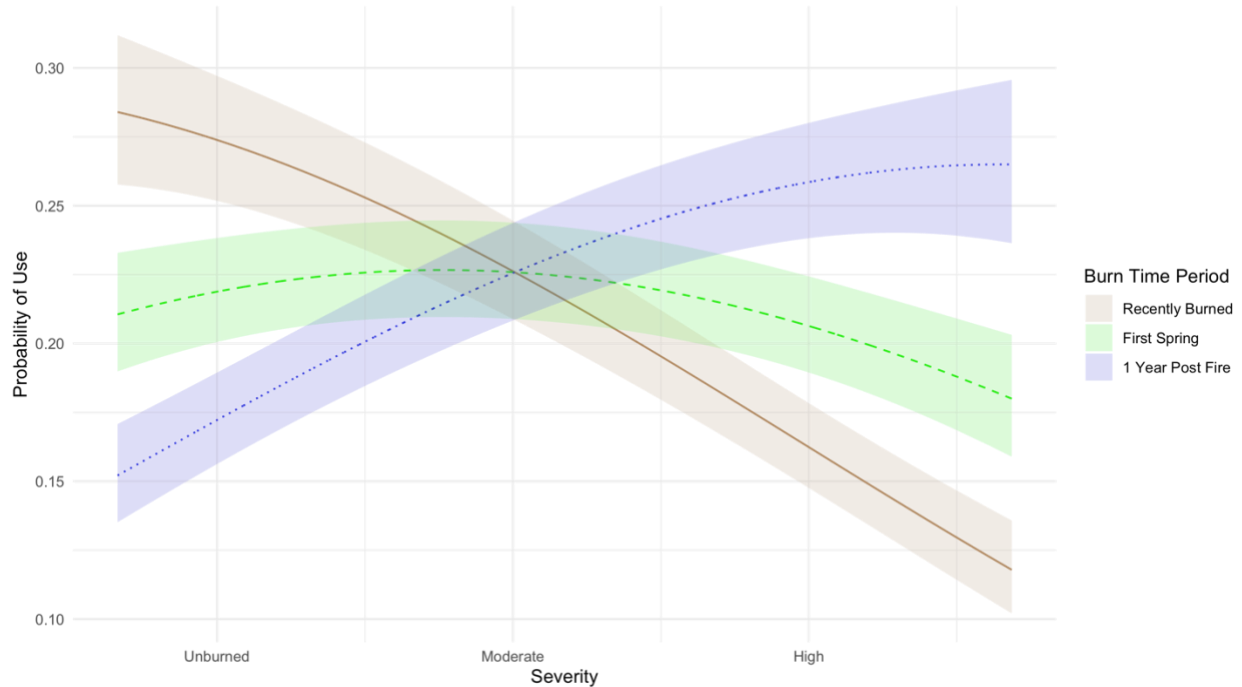
305

306

307 Figure 3 – Beta coefficients (and their associated standard error bars) for each covariate in the  
308 black-tailed deer (*O. hemionus columbianus*) Resource Selection Function model.

309





310

311 Figure 4 – RSF response curve of the effects of fire severity and Time Since Burn on black-  
 312 tailed deer (*O. hemionus columbianus*) habitat selection. To visualize the interaction, we used the  
 313 midpoint date of each time period to represent a categorical “Time Since Burn” variable in the  
 314 plot.

315

### 316 3.3 Hidden Markov Model Results

317 We used the Hidden Markov Model to fit the deer trek data into 1 of 2 states: Resting or  
 318 Traveling. State 1 (Resting) was characterized by shorter mean step lengths (mean = 16.47 ( $\pm$   
 319 0.67), SD = 13.72 meters ( $\pm$  0.71)) and wider turning angles between points (mean = -3.11  
 320 radians ( $\pm$  0.07), concentration = 0.39 ( $\pm$  0.03)). State 2 (Traveling) had long step lengths (mean =  
 321 120.83 meters ( $\pm$  2.66), SD = 107.53 meters ( $\pm$  1.78)) and smaller turning angles between GPS  
 322 fixes (mean = -0.03 ( $\pm$  0.07), concentration = 0.31 ( $\pm$  0.03)) (Table 2). We found a significant  
 323 difference in the composition of behavioral states between time periods, with deer spending a

324 greater proportion of time traveling than resting immediately following fire and during the first  
 325 spring ( $\chi^2 = 282.48$ ,  $df = 2$ ,  $p\text{-value} < 0.001$ ) (Appendix S1 – Figure S1.3).

326

<b>Behavioral State Parameters</b>		
	<i>State 1 (Resting)</i>	<i>State 2 (Traveling)</i>
Step Mean (m)	16.48 (15.84, 17.15)	120.83 (118.17, 123.55)
Step SD (m)	13.72 (13.01, 14.46)	107.53 (105.75, 109.34)
Angle Mean (radians)	-3.11 (-3.18, -3.04)	-0.03 (-0.10, 0.04)
Angle Concentration	0.39 (0.36, 0.43)	0.31 (0.28, 0.33)
<b>Covariate Transition Probability Coefficients</b>		
<b>Covariate</b>	<i>Resting → Travel</i>	<i>Travel → Resting</i>
Intercept	0.12 (NA)	-1.51 (NA)
Severity	0.05 (0.001, 0.11) *	-0.13 (-0.18, -0.09) *
Time Since Burn	-0.15 (-0.20, -0.10) *	0.15 (0.10, 0.20) *
Predation Risk	-0.14 (-0.19, -0.08) *	-0.06 (-0.11, -0.01) *
Distance to Water	0.04 (-0.01, 0.09)	-0.002 (-0.05, 0.05)
Severity Squared	0.06 (0.01, 0.10) *	-0.019 (-0.06, 0.02)
Chaparral	-0.80 (NA)	0.14 (NA)
Woodland	-0.54 (NA)	0.67 (NA)
Grassland	-0.44 (NA)	0.30 (NA)
Severity * Time Since Burn	-0.01 (-0.07, 0.04)	0.14 (0.09, 0.19) *

327

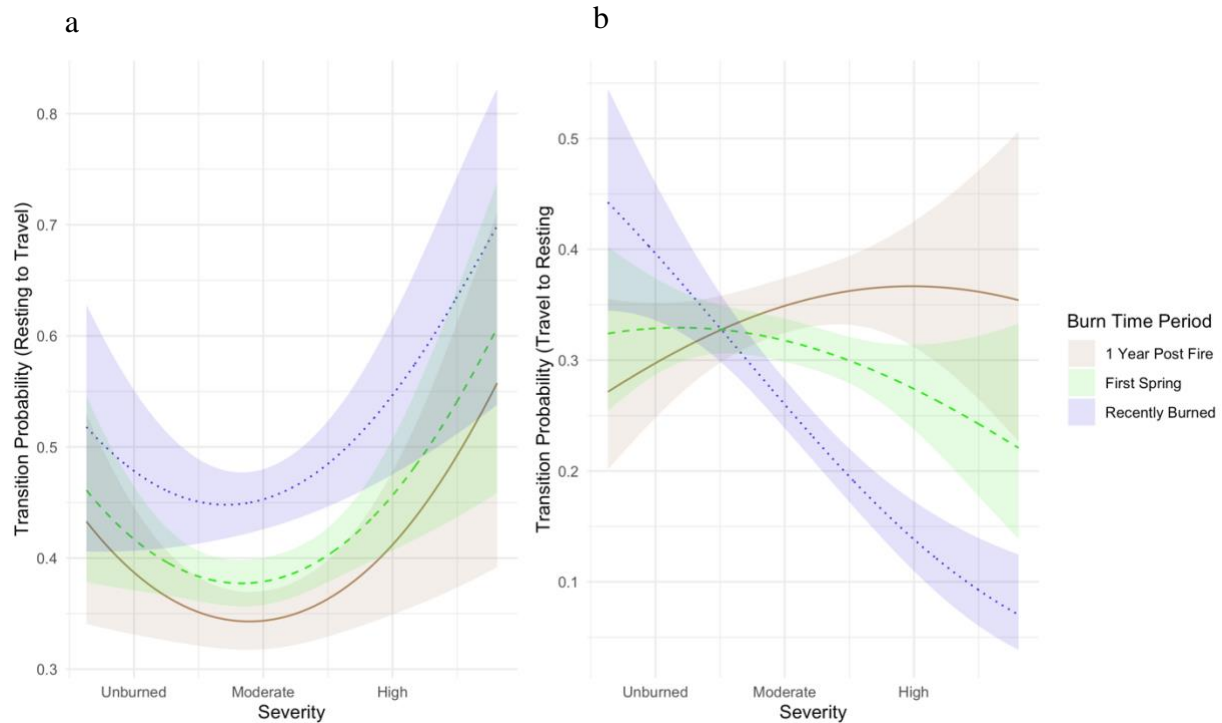
328 Table 2 – Estimated step lengths and turning angles for each modeled behavioral state (State 1 =  
329 resting and State 2 = traveling) produced from the Hidden Markov Model. Covariate regression  
330 coefficients for the transition probabilities between states are also listed. Significant predictors of  
331 behavioral transitions are marked with an asterisk (\*). Lower and upper confidence interval  
332 bounds are listed for behavioral state parameters and continuous regression coefficients  
333 (vegetation cover was categorical in the Hidden-Markov model).

334

335 Fire severity had a variable effect on deer behavioral states depending on the degree of  
336 severity, the amount of time that had passed since burn, and the type of vegetation the individual  
337 deer is moving through. Black-tailed deer were significantly more likely to transition towards  
338 making quick, directed movement in areas that burned at high severity, but only in the “Recently  
339 Burned” time period (mean = 0.14 ( $\pm$  0.05)). During this same time period, deer spent more time  
340 resting in woodland areas relative to other vegetation types (Appendix S1 – Figure S1.2).

341

342 Pseudo residuals drawn from the HMM suggested good model fit for the deer track data.  
343 Overall, plotted pseudo residuals had minimal autocorrelation (Appendix - Figure S1.4) and  
344 appeared normally distributed, except at the extreme ends of step lengths (Appendix S1 - Figure  
345 S1.5, Appendix S1 - Figure S1.6). We failed to reject the null hypothesis of the Shapiro-Wilks  
346 significance test ( $W = 0.99797$ ,  $p\text{-value} = 0.2728$ ), suggesting pseudo-residuals are drawn from a  
347 normal distribution.



349

350 Figure 5 – Behavioral state transition probabilities of black-tailed deer (*O. hemionus*  
 351 *columbianus*) across fire severity and time periods following fire. Predicted effects of fire  
 352 severity and time since burn on transition probabilities between behavioral states. Plot a) displays  
 353 the probability of transitioning from a resting state to a traveling state as severity increases across  
 354 the three time periods (“Recently Burned”, “First Spring” and “1 Year Post Fire”). Plot b)  
 355 displays the probability of transitioning from a traveling state to a resting state as severity  
 356 increases across the three same time periods. Note that y-axis scaling of plots a and b are  
 357 different.

358

#### 359 4. Discussion

360 Black-tailed deer habitat selection is influenced by landscape-scale impacts of megafire, but the  
 361 specific behavioral choices made by these animals varies with time following fire. As previous

362 work has outlined, estimated ungulate home ranges are larger following megafire, but this effect  
363 does not persist over time. We found that deer home range size was significantly smaller 1-year  
364 post-fire than home range sizes immediately following megafire (Figure 2). Deer habitat  
365 selection in response to megafire also appears to change over time following megafire. Directly  
366 following megafire, deer strongly avoided areas that burned at high severity, but this effect  
367 waned in the initial spring months following fire and inverts by the 1-year post-fire time period,  
368 with deer selecting for habitat that burned at higher severities instead (Figure 4). Similarly, deer  
369 were more likely to take quick, direct movements through high severity areas immediately  
370 following megafire, but this effect diminishes over the course of the year (Figure 5b). Our  
371 findings suggest that megafire may present the greatest threat to ungulate populations during and  
372 immediately following the fire event. However, black-tailed deer, and similar ungulate  
373 populations, may have some degree of behavioral plasticity to allow them to adjust their habitat  
374 usage and behavior following megafire to persist in dramatically converted landscapes, and  
375 eventually take advantage of the resulting resources that become available over time.

376

377 Fire severity had a profound influence on habitat selection and behavior over the course  
378 of the study, but the exact realized effect of severity on deer behavioral responses varied  
379 depending on other environmental factors. For example, severity by itself was an important  
380 predictor of deer habitat selection, but we found that the direction of selection (against high  
381 severity areas vs towards high severity areas) changed as an interaction with the amount of time  
382 that had passed since the fire burned. As observed in previous studies (Kreling et al., 2021),  
383 black-tailed deer avoided high severity burned areas in the immediate aftermath following the  
384 fire, potentially to avoid exposure to predators in cover-less areas or to select for areas with

385 higher forage availability. During the first spring green-up following megafire, however, we  
386 found that deer began to select for areas that burned at moderate severities (Figure 3). This may  
387 support the occurrence of a “magnet effect” as observed in several other ungulate studies where  
388 ungulate species preferentially choose to use recently burned areas that have enhanced forage  
389 (Raynor et al., 2015; Gureja and Owen-Smith, 2002). Finally, and contrary to our initial  
390 hypotheses, we found that deer actually selected for high severity burned areas during the final  
391 time period of the study (“1-Year Post-Fire”). We expected that the high severity burned areas  
392 would be depleted of resources for the duration of our study, but these results suggest that once  
393 these severely burned areas are able to recover, they may provide increased resources (Funk et  
394 al., 2016) to herbivorous species that are able to effectively track these recovering resources.

395

396 Deer movement behaviors in relation to fire also changed over the course of the study.  
397 Severity had a significant effect on deer behavioral states as well (Appendix S1 – Table S1.1),  
398 but we found that movement decisions varied significantly with the interaction between severity  
399 and the amount of time that had passed since fire. Initially following megafire, we found that  
400 deer were more likely to travel quickly (State 2) through severely burned areas and spent more  
401 time resting (State 1) in low severity and woodland areas. This strategy may optimize their  
402 ability to avoid spending too much time in riskier, exposed areas, and more time in the limited  
403 areas that contain food and shelter resources they require (Nimmo et al. 2019). Immediately  
404 following megafire, deer seem to be moving across larger areas (Figure 2) using frequent, travel-  
405 centered movements, all with far less available food to them. This potentially results in the  
406 decreased body condition of ungulates following megafire observed in recent studies (Kreling et  
407 al. 2021). However, this strategy does not appear to persist in the latter time periods of the study,

408 as the relationship between fire severity and the “travel” behavioral state diminishes over time  
409 and eventually flips by the 1-Year Post-fire time period. Black-tailed deer in this study appear to  
410 have great capacity for short-term behavioral plasticity to allow quick adjustments of their  
411 behavioral decisions as disturbance and recovery occur. The initial drawbacks of high site  
412 fidelity following megafire may be offset by the eventual regrowth of increased vegetative  
413 resources in burned areas that deer can take advantage of as time passes, facilitating their choice  
414 to remain in these areas following fire (Morrison et al., 2021).

415

416 Changes in deer habitat selection and behavior over time will likely depend on how and  
417 when vegetation cover recovers over time. We found that deer strongly selected for woodland  
418 habitat and, as expected, strongly selecting against chaparral habitat. Chaparral burns naturally at  
419 high severities, and these areas become very exposed following wildfire. Deer likely avoided  
420 these open areas to avoid conspicuous encounters with predators (Pierce et al., 2004). We did not  
421 find a relaxation in the avoidance of high predation risk areas over time following wildfire as  
422 anticipated, but predator avoidance may instead be represented by the selection against fire  
423 severity and/or certain vegetation type parameters within the model. Future work that utilizes  
424 concurrent movement data from both ungulates and their predators could help fill this gap by  
425 explicitly examining how predator-prey interactions change following megafire and elucidate  
426 whether and for how long these events amplify or diminish the intensity of these interactions  
427 (Doherty et al., 2022).

428

429 During this study, we observed a preference for burned areas by black-tailed deer in the  
430 latter time periods, potentially highlighting some of the benefits of returning wildfire to fire

431 adapted ecosystems. Whereas megafire is a more extreme example of fire disturbance, more  
432 moderate disturbances such as prescribed fire and/or managed wildfire are known to perform  
433 important ecological work in maintaining key ecosystem functioning for local communities  
434 (Sangha et al., 2021) and generating improved habitat and resources for wildlife (Connor et al.,  
435 2022), without the more deleterious impacts created initially by megafire. These managed  
436 wildfire approaches also serve an important function in reducing the incidence of megafire  
437 events by promoting landscape heterogeneity and reducing continuous fuel loads (Coppoletta et  
438 al., 2016; Stephens et al., 2014). Thus, utilizing fire management may simultaneously  
439 accomplish important wildlife conservation goals (habitat creation and maintenance) and wildfire  
440 management goals (megafire prevention) in similar fire-prone ecosystems.

441  
442 We found evidence to suggest deer are resilient to the impacts of megafire over the  
443 course of a relatively short, 1-year time scale, but more work is necessary to understand whether  
444 these initial responses translate into longer term resilience. The lagged effects of megafire may  
445 present more challenges to species by altering longer cycles in resource availability (Abella et  
446 al., 2015) as well as interspecies interactions (Nimmo et al., 2021). For example, in oak  
447 woodland savannas where acorn masting is a primary food resource for many herbivorous  
448 species (Schnurr et al., 2002; McShea et al., 1993), megafires that top-kill mature oak trees could  
449 dramatically alter the availability of these resources until oaks are able regenerate and begin  
450 masting again. These indirect impacts could have powerful effects on future population  
451 dynamics such as in fitness and reproduction across the previously burned landscape.

452

## 453 **5. Conclusion**



454 Climate change and climatic disturbances will likely have a more severe impact on species that  
455 are unable to adjust their behavior to accommodate sudden changes in their environments.  
456 Despite having naturally high site fidelity in the region of our study, we found that black-tailed  
457 deer have a great deal of adaptive capacity to change their movements and behavior to  
458 adequately respond to the impacts and eventual resources following megafire. This adaptive  
459 capacity may also buffer similar ungulate species from other types of acute disturbances.  
460 Resilience of these dominant ungulate species could help facilitate broader ecological resilience  
461 at higher environmental and trophic scales following such disturbances. We can assist this by  
462 using land and fire management to produce the benefits created by wildfire while simultaneously  
463 avoiding the immediate drawbacks of megafire on ungulates.

464

#### 465 **Literature Cited**

466 Abella, S. R., & Fornwalt, P. J. (2015). Ten years of vegetation assembly after a North American  
467 mega fire. *Global change biology*, 21(2), 789-802.

468 Adams, M. A. (2013). Mega-fires, tipping points and ecosystem services: Managing forests and  
469 woodlands in an uncertain future. *Forest Ecology and Management*, 294, 250–261.

470 <https://doi.org/10.1016/j.foreco.2012.11.039>

471 Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. (2011). Ungulate preference for  
472 burned patches reveals strength of fire-grazing interaction. *Ecology and*

473 *Evolution*, 1, 132–144. <https://doi.org/10.1002/ece3.12>

474 Archibald, S., Bond, W. J., Stock, W. D., & Fairbanks, D. H. K. (2005). Shaping the landscape:

475 Fire-grazer interactions in an African savanna. *Ecological Applications*, 15, 96–

476 109. <https://doi.org/10.1890/03-5210>

477 Barker, K. J., Mitchell, M. S., & Proffitt, K. M. (2019). Native forage mediates influence of  
478 irrigated agriculture on migratory behaviour of elk. *Journal of Animal Ecology*, 88(7),  
479 1100-1110.

480 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models  
481 using lme4. *Journal of Statistical Software*, 67, 1–48.

482 Boisramé, G., Thompson, S., Collins, B., & Stephens, S. (2017). Managed wildfire effects on  
483 forest resilience and water in the Sierra Nevada. *Ecosystems*, 20(4), 717-732.

484 CALFIRE-FRAP. (2022). Fire Perimeters. Retrieved from: [https://frap.fire.ca.gov/frap-](https://frap.fire.ca.gov/frap-projects/fire-perimeters/)  
485 [projects/fire-perimeters/](https://frap.fire.ca.gov/frap-projects/fire-perimeters/)

486 Calenge, C. (2006). adehabitatHR: A tool for the analysis of space and habitat use by animals.  
487 Ecological Modeling. R package version  
488 0.4.15. <https://CRAN.Rproject.org/package=adehabitatHR>

489 Cherry, M. J., Chandler, R. B., Garrison, E. P., Crawford, D. A., Kelly, B. D., Shindle, D. B., ...  
490 & Conner, L. M. (2018). Wildfire affects space use and movement of white-tailed deer in  
491 a tropical pyric landscape. *Forest Ecology and Management*, 409, 161-169.

492 Coppoletta, M., Merriam, K. E., & Collins, B. M. (2016). Post-fire vegetation and fuel  
493 development influences fire severity patterns in reburns. *Ecological applications*, 26(3),  
494 686-699.

495 Connor, T., Tripp, E., Tripp, B., Saxon, B. J., Camarena, J., Donahue, A., ... & Brashares, J.  
496 (2022). Karuk ecological fire management practices promote elk habitat in northern  
497 California. *Journal of Applied Ecology*.

498 Dellinger, J. A., Cristescu, B., Ewanyk, J., Gammons, D. J., Garcelon, D., Johnston, P., ... &

499 Torres, S. G. (2020). Using mountain lion habitat selection in management. *The Journal*  
500 *of Wildlife Management*, 84(2), 359-371.

501 Doherty, T. S., Geary, W. L., Jolly, C. J., Macdonald, K. J., Miritis, V., Watchorn, D. J., ... &  
502 Dickman, C. R. (2022). Fire as a driver and mediator of predator–prey  
503 interactions. *Biological Reviews*.

504 Farhadinia, M. S., Michelot, T., Johnson, P. J., Hunter, L. T., & Macdonald, D. W. (2020).  
505 Understanding decision making in a food-caching predator using hidden Markov  
506 models. *Movement ecology*, 8(1), 1-13.

507 Fletcher, M. S., Romano, A., Connor, S., Mariani, M., & Maezumi, S. Y. (2021). Catastrophic  
508 bushfires, indigenous fire knowledge and reframing science in Southeast  
509 Australia. *Fire*, 4(3), 61.

510 Funk, K. A., Koenig, W. D., & Knops, J. M. (2016). Fire effects on acorn production are  
511 consistent with the stored resource hypothesis for masting behavior. *Canadian Journal of*  
512 *Forest Research*, 46(1), 20-24.

513 Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of  
514 human disturbance on wildlife nocturnality. *Science*, 360(6394), 1232-1235.

515 Gureja, N., & Owen-Smith, N. (2002). Comparative use of burnt grassland by rare antelope  
516 species in a lowveld game ranch, South Africa. *South African Journal of Wildlife*  
517 *Research-24-month delayed open access*, 32(1), 31-38.

518 Halofsky, J. E., Donato, D. C., Hibbs, D. E., Campbell, J. L., Cannon, M. D., Fontaine, J. B., ...  
519 & Spies, T. A. (2011). Mixed-severity fire regimes: lessons and hypotheses from the  
520 Klamath-Siskiyou Ecoregion. *Ecosphere*, 2(4), 1-19.

521 Hammond, T. T., Palme, R., & Lacey, E. A. (2018). Ecological specialization, variability in

522 activity patterns and response to environmental change. *Biology Letters*, 14(6),  
523 20180115.

524 Jolly, C. J., Dickman, C. R., Doherty, T. S., van Eeden, L. M., Geary, W. L., Legge, S. M., ... &  
525 Nimmo, D. G. (2022). Animal mortality during fire. *Global Change Biology*, 28(6),  
526 2053-2065.

527 Jones, G. M., Kramer, H. A., Whitmore, S. A., Berigan, W. J., Tempel, D. J., Wood, C. M., ... &  
528 Peery, M. Z. (2020). Habitat selection by spotted owls after a megafire reflects their  
529 adaptation to historical frequent-fire regimes. *Landscape Ecology*, 35(5), 1199-1213.

530 Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: a brief review and suggested  
531 usage. *International journal of wildland fire*, 18(1), 116-126.

532 Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., & Morales, J. M. (2012).  
533 Flexible and practical modeling of animal telemetry data: hidden Markov models and  
534 extensions. *Ecology*, 93(11), 2336-2342.

535 Linley, G.D., Jolly, C.J., Doherty, T.S., Geary, W.L., Armenteras, D., Belcher, C.M., Bliege  
536 Bird, R., Duane, A., Fletcher, M.S., Giorgis, M.A. and Haslem, A., 2022. What do you  
537 mean, ‘megafire’? *Global Ecology and Biogeography*.

538 Lüdecke et al., (2021). performance: An R Package for Assessment, Comparison and Testing of  
539 Statistical Models. *Journal of Open Source Software*, 6(60), 3139.  
540 <https://doi.org/10.21105/joss.03139>

541 McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., ... &  
542 Watts, A. C. (2020). Fire as a fundamental ecological process: Research advances and  
543 frontiers. *Journal of Ecology*, 108(5), 2047-2069.

544 McShea, W. J., & Schwede, G. (1993). Variable acorn crops: responses of white-tailed deer and

545 other mast consumers. *Journal of Mammalogy*, 74(4), 999-1006.

546 Michelot, T., Langrock, R., Patterson, T.A. (2016). moveHMM: an R package  
547 for the statistical modelling of animal movement data using hidden Markov  
548 models. *Methods in Ecology and Evolution*, 7 (11), pp. 1308-1315.

549 Michelot, T., Langrock, R., Bestley, S., Jonsen, I. D., Photopoulou, T., & Patterson, T. A.  
550 (2017). Estimation and simulation of foraging trips in land-based marine  
551 predators. *Ecology*, 98(7), 1932-1944.

552 Morrison, T. A., Merkle, J. A., Hopcraft, J. G. C., Aikens, E. O., Beck, J. L., Boone, R. B., ... &  
553 Kauffman, M. J. (2021). Drivers of site fidelity in ungulates. *Journal of animal  
554 ecology*, 90(4), 955-966.

555 Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., ... &  
556 Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological  
557 Reviews*, 94(3), 981-998.

558 Nimmo, D. G., Carthey, A. J., Jolly, C. J., & Blumstein, D. T. (2021). Welcome to the Pyrocene:  
559 Animal survival in the age of megafire. *Global Change Biology*, 27(22), 5684-5693.

560 Nimmo, D. G., Andersen, A. N., Archibald, S., Boer, M. M., Brotons, L., Parr, C. L., & Tingley,  
561 M. W. (2022). Fire ecology for the 21st century. *Diversity and Distributions*, 28(3), 350-  
562 356.

563 Patterson TA, Basson M, Bravington MV, Gunn JS. Classifying movement behaviour in  
564 relation to environmental conditions using hidden Markov models. *J Anim Ecol.*  
565 2009;78:1113–23.

566 Pausas, J. G., & Parr, C. L. (2018). Towards an understanding of the evolutionary role of fire in  
567 animals. *Evolutionary Ecology*, 32(2), 113-125.

568 Pierce, B. M., Bowyer, R. T., & Bleich, V. C. (2004). Habitat selection by mule deer: forage  
569 benefits or risk of predation?. *The Journal of Wildlife Management*, 68(3), 533-541.

570 Pohle J, Langrock R, van Beest FM, Schmidt NM. Selecting the number of states in hidden  
571 Markov models: pragmatic solutions illustrated using animal movement. *J Agric Biol*  
572 *Environ Stat.* 2017;22:270–93 Springer.

573 Proffitt, K. M., DeVoe, J., Barker, K., Durham, R., Hayes, T., Hebblewhite, M., ... & Shamhart,  
574 J. (2019). A century of changing fire management alters ungulate forage in a wildfire-  
575 dominated landscape. *Forestry: An International Journal of Forest Research*, 92(5), 523-  
576 537.

577 Raynor, E. J., Joern, A., & Briggs, J. M. (2015). Bison foraging responds to fire frequency in  
578 nutritionally heterogeneous grassland. *Ecology*, 96(6), 1586-1597.

579 Rickbeil, G. J., Hermosilla, T., Coops, N. C., White, J. C., & Wulder, M. A. (2017). Barren-  
580 ground caribou (*Rangifer tarandus groenlandicus*) behaviour after recent fire events;  
581 integrating caribou telemetry data with Landsat fire detection techniques. *Global Change*  
582 *Biology*, 23(3), 1036-1047.

583 Riddell, E. A., Odom, J. P., Damm, J. D., & Sears, M. W. (2018). Plasticity reveals hidden  
584 resistance to extinction under climate change in the global hotspot of salamander  
585 diversity. *Science Advances*, 4(7), eaar5471.

586 Roerick, T. M., Cain III, J. W., & Gedir, J. V. (2019). Forest restoration, wildfire, and habitat  
587 selection by female mule deer. *Forest Ecology and Management*, 447, 169-179.

588 Sangha, K. K., Evans, J., Edwards, A., Russell-Smith, J., Fisher, R., Yates, C., & Costanza, R.  
589 (2021). Assessing the value of ecosystem services delivered by prescribed fire  
590 management in Australian tropical savannas. *Ecosystem Services*, 51, 101343.

591 Schell, C. J., Young, J. K., Lonsdorf, E. V., Santymire, R. M., & Mateo, J. M. (2018). Parental  
592 habituation to human disturbance over time reduces fear of humans in coyote  
593 offspring. *Ecology and Evolution*, 8(24), 12965-12980.

594 Schnurr, J. L., Ostfeld, R. S., & Canham, C. D. (2002). Direct and indirect effects of masting on  
595 rodent populations and tree seed survival. *Oikos*, 96(3), 402-410.

596 Sentinel Hub (2022). Modified Copernicus Sentinel Data. <https://www.sentinel-hub.com>

597 Steel, Z. L., Fogg, A. M., Burnett, R., Roberts, L. J., & Safford, H. D. (2022). When bigger isn't  
598 better—Implications of large high-severity wildfire patches for avian diversity and  
599 community composition. *Diversity and Distributions*, 28(3), 439-453.

600 Stott, P. (2016). How climate change affects extreme weather events. *Science*, 352(6293), 1517-  
601 1518.

602 Suraci, J. P., Gaynor, K. M., Allen, M. L., Alexander, P., Brashares, J. S., Cendejas-Zarelli, S., ...  
603 & Wilmers, C. C. (2021). Disturbance type and species life history predict mammal  
604 responses to humans. *Global change biology*, 27(16), 3718-3731.

605 Syphard, A. D., & Keeley, J. E. (2020). Mapping fire regime ecoregions in  
606 California. *International Journal of Wildland Fire*, 29(7), 595-601.

607

608

609

610

611

612

613

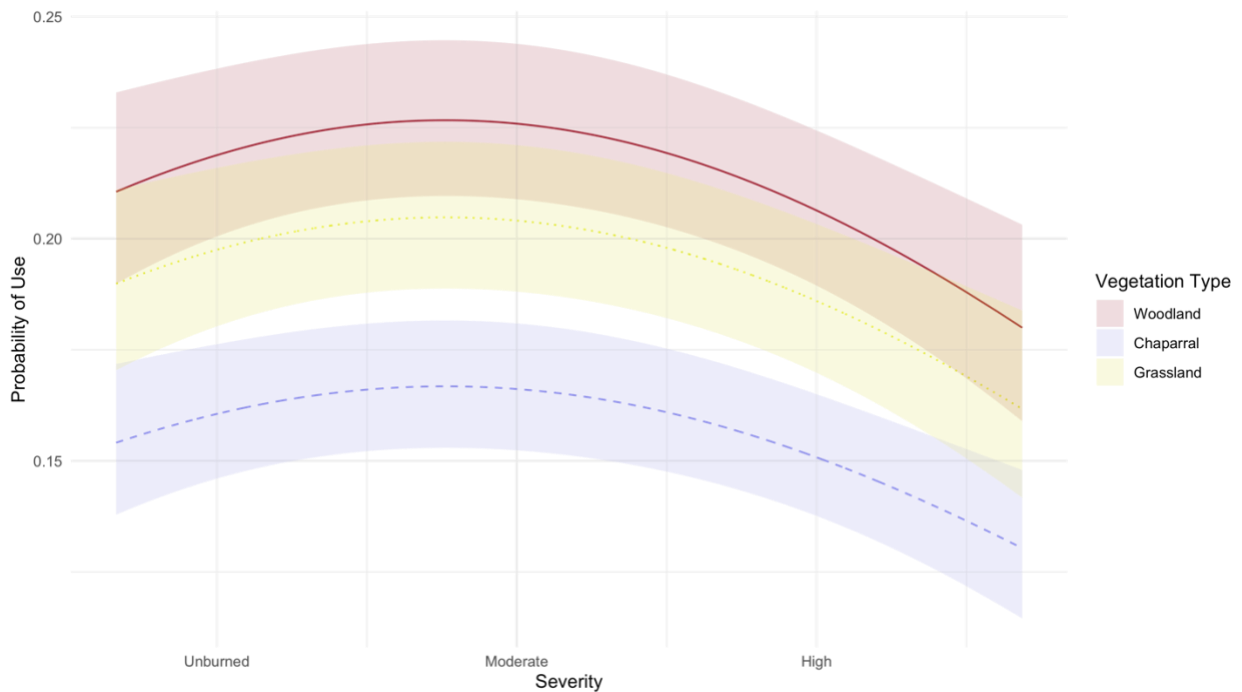
614 Appendix – S1 Additional Figures  
 615  
 616

Covariate	Beta Coefficient	Standard Error	p-Value
Intercept	-1.234	± 0.051	<0.001
Severity	-0.022	± 0.007	0.001
Severity Squared	-0.019	± 0.005	<0.001
Predation Risk	-0.077	± 0.007	<0.001
Chaparral	-0.381	± 0.017	<0.001
Grassland	-0.129	± 0.016	<0.001
Time Since Burn	0.013	± 0.009	0.147
Distance to Water	0.004	± 0.006	0.508
Severity * Time Since Burn	0.146	± 0.007	<0.001

617

618 Table 2 – Beta-coefficients, standard error and p-value estimates for each covariate of the black-  
 619 tailed deer (*O. hemionus columbianus*) resource selection function model.

620

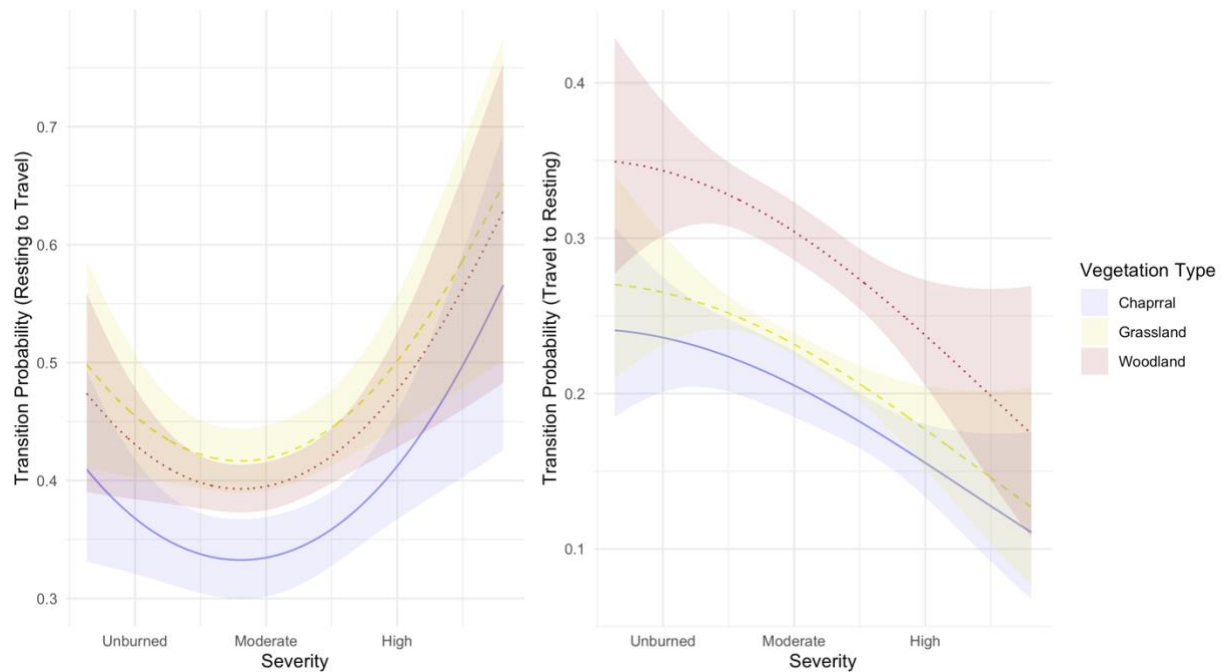


621

622 Figure S1.1 – RSF response plot of the effects of vegetation type and fire severity on black-tailed

623 deer (*O.hemionus columbianus*) habitat selection.

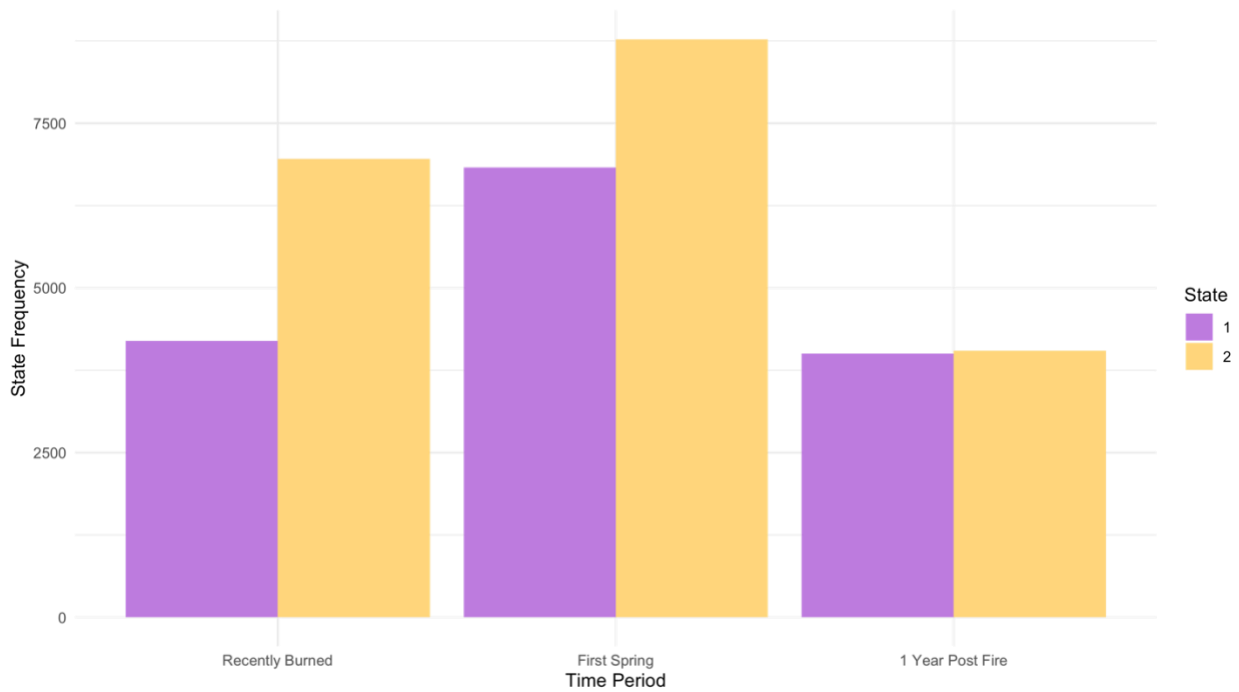




624  
 625 Figure S1.2 - Plotted behavioral state transition probabilities of black-tailed deer (*O. hemionus*  
 626 *columbianus*) across fire severity and across vegetation types. Predicted effects of fire severity  
 627 and time since burn on transition probabilities between behavioral states. Plot a) displays the  
 628 probability of transitioning from a resting state to a traveling state as severity increases across the  
 629 three vegetation types (“Woodland”, “Grassland” and “Chaparral”). Plot b) displays the  
 630 probability of transitioning from a traveling state to a resting state as severity increases across the  
 631 three same time periods. Note that y-axis scaling of plots a and b are different.

632  
 633  
 634  
 635  
 636  
 637  
 638  
 639  
 640  
 641  
 642  
 643  
 644

645



646

647

648 Figure S1.3 – Activity budgets for black-tailed deer (*O. hemionus columbianus*) during each time

649 period. Activity budgets show the proportion of each modeled behavioral state (State 1

650 = resting; State 2 = traveling). The proportion of time spent in each behavioral state changes over

651 time following fire.

652

653

654

655

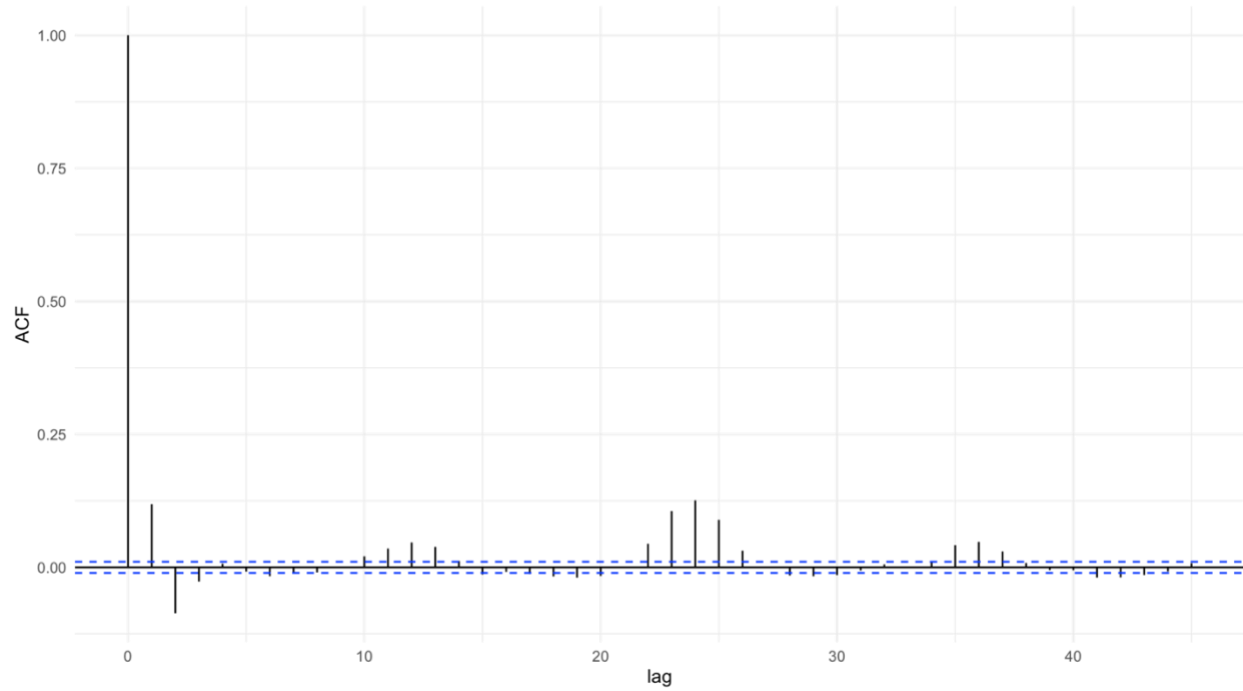
656

657

658

659

660



661

662 Figure S1.4 – ACF plot of step length residuals from the fit hidden-Markov model.

663

664

665

666

667

668

669

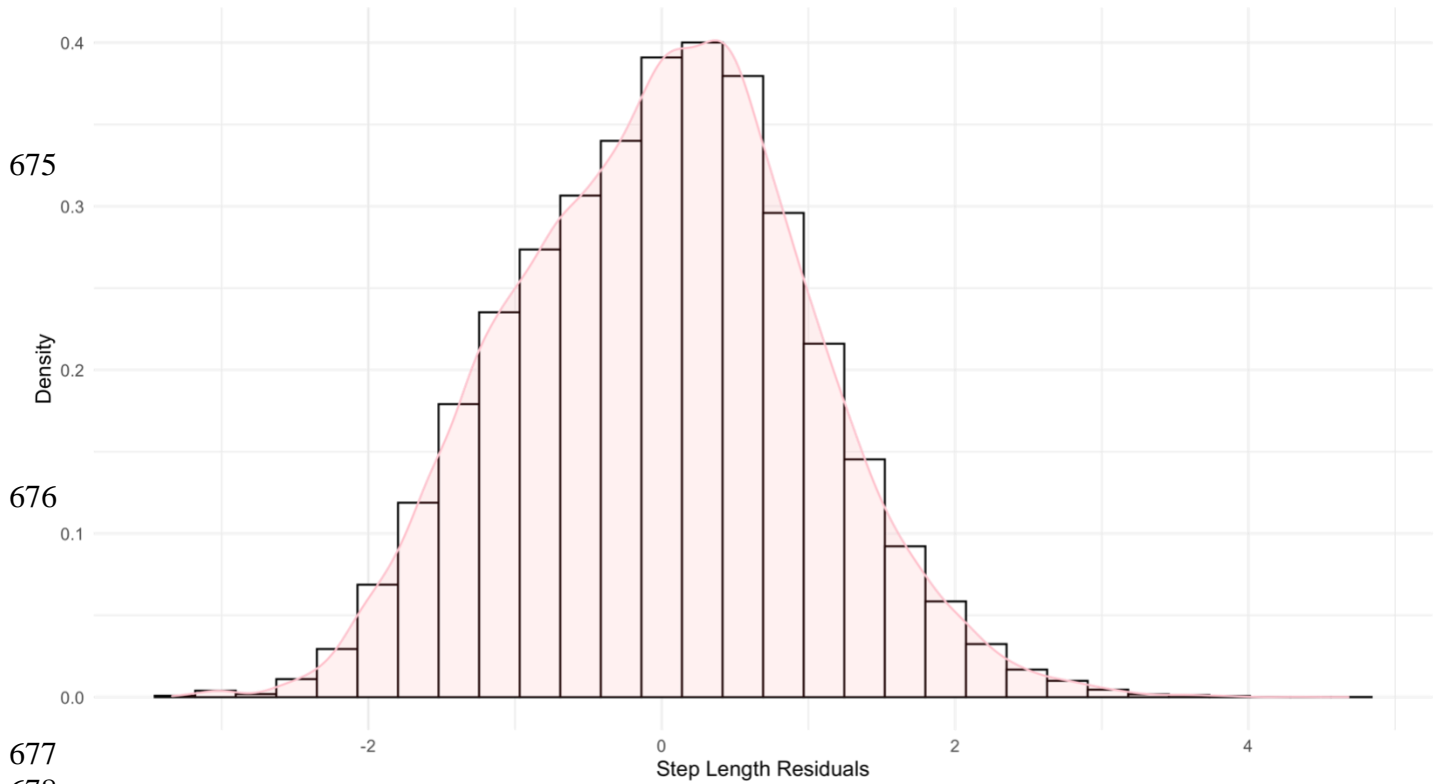
670

671

672

673

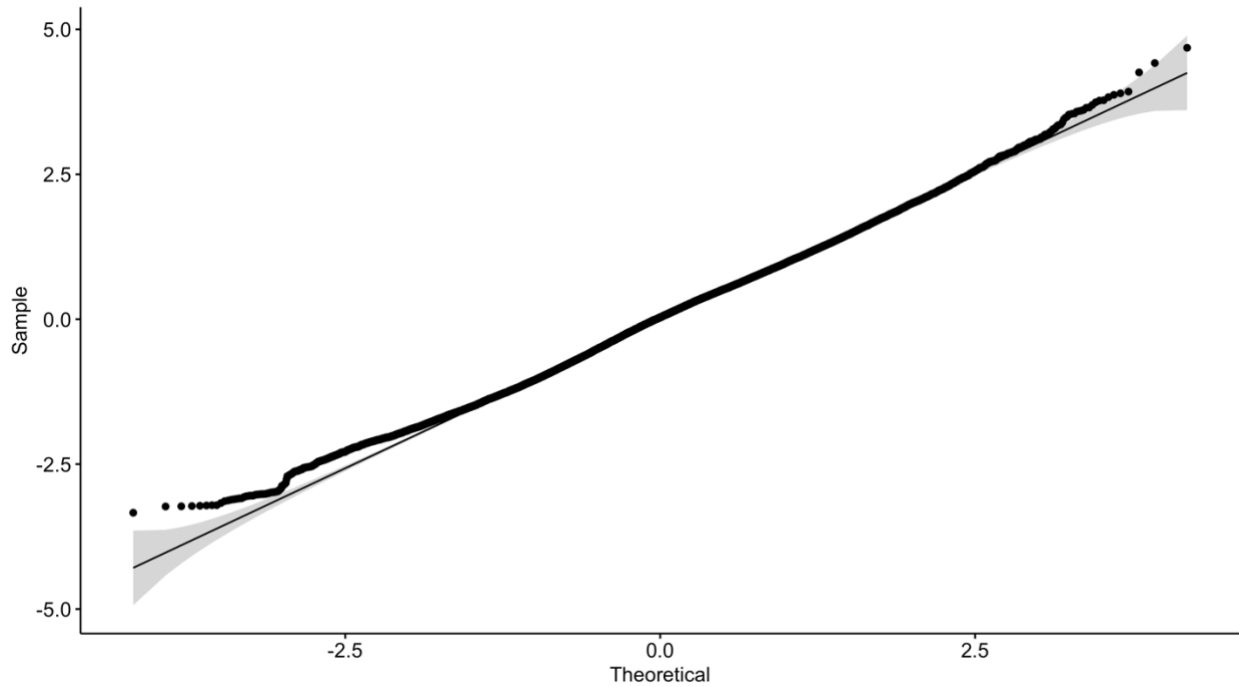
674



677  
678  
679 Figure S1.5 – Plotted histogram of step-length pseudo residuals from fit hidden Markov model.

680 We drew a random sample of pseudo-residuals from the fitted HMM to check goodness of fit of  
681 the model ( $n = 1000$ ). In cases of good model fit, pseudo residual step lengths should be  
682 normally distributed.

683  
684  
685  
686  
687



688  
689

690 Figure S1.6 – Quantile-Quantile (QQ) plot of step length pseudo residuals from the fit hidden  
691 Markov model. We drew a random sample of pseudo-residuals from the fitted HMM to check  
692 goodness of fit of the model ( $n = 1000$ ). Pseudo residuals for follow a linear line on the QQ-plot  
693 in cases of good model fit.

694  
695  
696  
697  
698