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1 Running head: Mechanisms of predation

2

3 **Building a mechanistic understanding of predation with GPS-based**  
4 **movement data**

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33 **Abstract**

34 Quantifying kill rates and sources of variation in kill rates remains an important challenge in  
35 linking predators to their prey. We address current approaches to using GPS-based movement  
36 data for quantifying key predation components of large carnivores. We review approaches to  
37 identify kill sites from GPS-movement data as a means to estimate kill rates and address  
38 advantages of using GPS-based data over past approaches. Despite considerable progress,  
39 modeling the probability that a cluster of GPS points is a kill site is no substitute for field visits  
40 but can guide our field efforts. Once kill sites are identified, time spent at a kill site (handling  
41 time) and time between kills (killing time) can be determined. We show how statistical models  
42 can be used to investigate the influence of factors such as animal characteristics (e.g., age, sex,  
43 group size) and landscape features on either handling time or killing efficiency. If we know the  
44 prey densities along paths to a kill, we can quantify the “attack success” parameter in functional  
45 response models directly. Problems remain in incorporating the behavioural complexity derived  
46 from GPS movement paths into functional response models, particularly in multi-prey systems,  
47 but we believe that exploring the details of GPS-movement data has put us on the right path.

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54 **1. INTRODUCTION**

55 The direct effects of predation on prey populations have been studied by understanding the  
56 numerical and functional response, i.e., changes in predator density and kill rates as a function of  
57 prey density (Solomon 1949). Quantifying kill rates for estimating functional response curves  
58 remains an important challenge in linking predators to their prey. High variation around  
59 empirically derived functional response models constrains our ability to specify model form  
60 (*sensu* Holling 1959) and therefore limits our ability to model population-level interactions (Dale  
61 *et al.* 1994; Marshal & Boutin 1999; Vucetich *et al.* 2002). More mechanistic rather than  
62 statistical curve-fitting perspectives of predation processes are needed to resolve the current  
63 debates about the nature of functional responses (Abrams & Ginzburg 2000). Progress towards  
64 understanding the functional response of large carnivores has lagged behind that for large  
65 herbivores (see Spalinger & Hobbs 1992). This may be, in part, because of their secretive nature  
66 and wide-ranging movements, but also the relatively long temporal scale over which  
67 observations are needed to obtain kill rates. The advent of global positioning system (GPS)  
68 technology in wildlife studies has enhanced opportunities to examine movement behaviours of  
69 carnivores that reflect spatial processes in predation. The use of GPS technology can provide not  
70 only cost-efficient and often more precise estimates of kill rates, but can lead to a better  
71 understanding of how variation in kill rates is related to both prey densities and landscape  
72 features that may influence predator search rate, prey detection, and prey vulnerability in  
73 naturally heterogeneous environments.

74 In this paper we address current approaches to using GPS-based movement data for  
75 quantifying kill rates and indicate how GPS data can be used to improve estimates of kill rates  
76 and their variances. Next, we briefly review Holling's disc equation (1959), which gives a

77 simple conceptual approach to viewing allocation of time along a GPS-movement path to key  
78 components of predation: handling time and killing time. We review approaches to identify kill  
79 sites from GPS-movement data and illustrate new approaches to determine what environmental  
80 (e.g., habitat features) or animal factors (e.g., age, sex, or group sizes) influence killing  
81 efficiency. Finally, we show how to estimate attack rates when prey densities are known and  
82 discuss further issues for linking these measures to functional responses. Our paper focuses on  
83 terrestrial large carnivores, in particular wolves (*Canis lupus*) and cougars (*Puma concolour*),  
84 because availability of GPS data are most abundant for these species due to their size and the  
85 demands of the initial generation of GPS collars. Technological advances in GPS units design  
86 will make these approaches accessible to a wider range of carnivore species in the near future  
87 (see Tomkiewicz *et al.* this volume), but the potential usefulness of GPS data may depend on the  
88 spatio-temporal dynamics in their predatory behaviours.

## 89 **2. GPS-BASED MOVEMENT ANALYSIS TO ESTIMATE KILL RATES**

90 To date the most common approach to estimating kill rates of carnivores has been to identify kill  
91 sites based on variety of methods (see below) over an extended monitoring period (Peterson  
92 1977; Dale *et al.* 1995; Hayes *et al.* 2000; Garrott *et al.* 2007). Counts of kills ( $P_K$ ) are divided  
93 by total observation time (T), and kill rates are expressed based on an individual, pack, or  
94 population-level basis, and a ratio estimator of the variation in  $P_K/T$  is derived (Hebblewhite *et al.*  
95 2005). In the past, ecologists have used radiotelemetry techniques in combination with snow-  
96 tracking, either from an airplane or on the ground, to estimate kill rates of carnivores (Haglund  
97 1966; Peterson 1977; Fuller 1989; Okarma *et al.* 1997, Jobin *et al.* 2000, Jedrzejewski *et al.*  
98 2002). These methods demand extensive field efforts, i.e., highly frequent and accurate  
99 telemetry locations, or long ground-tracking sequences by foot, especially for large predators

100 (Jedrzejewski *et al.* 2002). In snow-free periods, predators cannot be tracked readily back to  
101 kills. With aerial approaches only snapshots of their daily position during daylight is usually  
102 possible. Unfavorable weather or dense vegetation may limit or preclude aerial observation of  
103 radiocollared predators, their tracks, or remains of killed prey even during winter, introducing the  
104 potential for substantial bias.

105       When working with species such as wolves, these approaches frequently have been the only  
106 available to produce estimates of kill rate for large sized prey (Peterson 1977; Fuller & Keith  
107 1980; Huggard 1993; Dale *et al.* 1994; Okarma *et al.* 1997; Jobin *et al.* 2000; Bergman *et al.*  
108 2006; Nilsen *et al.* 2009). Despite the potential biases, the estimates have been considered  
109 reliable due to the assumed habit of some carnivore species to stay close to the killed carcasses  
110 of large prey species, e.g. ungulates (Peterson *et al.* 1984; Ballard *et al.* 1987; Hayes *et al.* 2000;  
111 Smith *et al.* 2004). For small and mid-sized prey species these approaches most likely have  
112 resulted in gross under-estimates of kill rate (Fuller 1989; Sand *et al.* 2005). Consequently, as  
113 GPS technology became available, it was clear that quantitative data on movement behaviour  
114 could be useful for identifying kill sites of prey made at any time of the day, season and year,  
115 with low manpower input (Hulbert 2001; Rodgers 2001) resulting in increased availability and  
116 reliability of information on kill rates (Sand *et al.* 2005).

117       Because GPS movement data provide more consistent and continual sequences for  
118 monitoring animals (Cagnacci *et al.* this issue; Frair *et al.* this issue), these data may minimize  
119 several past limitations. For example, when there are differences in the time carnivores spend  
120 handling prey, the number of days they are relocated using aerial telemetry will influence the  
121 probability of locating them on a kill (Mech 1977, Fuller & Keith 1980). In contrast, GPS data  
122 provides regular sampling intervals. Previous field-based methods often were able to sample

123 only 10-30% of the winter to estimate wolf kill rates. Because GPS collars can provide data  
124 from a greater proportion of the period of interest, they will provide more precise estimates of  
125 kill-rates because the variance in ratio-based estimators depends on the proportion of the  
126 sampling period (e.g., winter) during which kills are located (Hebblewhite *et al.* 2003). Several  
127 different approaches have been used to truncate the “predation period” (*sensu* Hayes *et al.* 2000)  
128 that defines the start and finish of ground tracking period (see Hebblewhite *et al.* 2003 for  
129 review). Although sampling rates may still differ when using GPS data, use of long, continuous  
130 sequences of GPS data likely will reduce the influence of these differences and may lead to  
131 standardization among approaches. Finally, with more consistent monitoring over time,  
132 heterogeneity in kill rates are more easily identified, and lead to stratification that can improve  
133 the precision of the estimate.

134         Despite these advantages, GPS data bring their own problems. Relocations of animals  
135 based on GPS collars may miss relocations due to habitat bias (Frair *et al.* 2004, Frair *et al.* this  
136 issue), and they may fail to identify kill sites by not identifying clusters of relocations or as a  
137 result of the uncertainty from statistical models that identify clusters as kill sites (e.g., Webb *et*  
138 *al.* 2008). As GPS data are used more commonly for defining kill rates, more thought about how  
139 to incorporate the error into predictions kill-rates will be required. Regardless, improved  
140 estimates of kill-rates will be possible simply because of the vast improvement in our ability to  
141 estimate kill-rates over longer periods than most traditional methods.

### 142 **3. GPS-MOVEMENT BEHAVIOUR: COMPONENTS OF PREDATION REVISITED**

143 From the perspective of time budgets, the total time measured in estimating kill rates can be  
144 viewed as two key behaviours that potentially can be distinguished in movement patterns: (1)  
145 time allocated to searching, capturing, and killing prey ( $T_K$ ) and (2) time devoted to handling

146 prey ( $T_H$ ) at a kill site. Allocation of time to this simple dichotomy of behaviours was described  
147 by Holling (1959) by the “disc equation”, where blindfolded human subjects (predators) tried to  
148 find and pick up small discs of sandpaper (prey) on a flat surface at different densities. This  
149 assumes that the number of prey captured and killed ( $P_K$ ) over the experiment ( $T$ ) decreases with  
150 prey density and increases the available time searching ( $T_s$ ) and the efficiency of searching or  
151 attack rate ( $a$ ) of the predator as:

$$152 \quad P_K = aT_s N \quad \text{Eq. 1}$$

153 Because  $T_s = T - T_h P_K$  where  $T_h$  is the handling time per prey, substituting this into Eq. 1 and  
154 rearranging we have the number prey killed over a period:

$$155 \quad \frac{P_K}{T} = \frac{aN}{1 + aT_h N} \quad \text{Eq. 2}$$

156 where  $P_K/T$  is considered the kill rate.

157 In large carnivores, sources of variation in handling times per prey ( $T_h$ ) have been related  
158 to prey size and biomass consumed, number of predators and age or sex composition of a feeding  
159 group, specialized handling behaviour like caching, digestive constraints, other large carnivores  
160 stealing their kill, and disturbance by humans (Hayes *et al.* 2000; Packard 2003; Zimmermann *et*  
161 *al.* 2007; MacNulty *et al.* 2009). On the other hand, search efficiency ( $s$ ) is the time necessary to  
162 find a prey and is a function of movement rate and the perceptual range of the animal, which is  
163 expressed as area searched per unit time ( $s = A_s/t$ ). Encounter rate with prey depends not only on  
164 search rate but on the density of prey ( $N$ ) and the ability of the predator to detect the prey ( $\delta$ ). If  
165 a predator spends  $T_s$  searching, the number of prey encountered is  $s\delta NT_s$ . Beyond encountering



166 a prey, a predator must decide to attack the prey (selection) and be efficient at killing the prey.  
167 The time devoted to these behaviours combined with search time we call killing time ( $T_K$ ) or  
168 time-to-kill. Most importantly, we distinguish  $T_K$  from the conventional estimate of kill rates  
169 ( $P_K/T$ ). Killing time, therefore, depends on  $s$ , probability of attack or prey selection ( $\alpha$ ), and  
170 prey vulnerability or kill success ( $v$ ), such that killing efficiency, or “attack success” now  
171 becomes  $a = s\delta\alpha v$ . Thus, the number of prey killed is  $P_K = aNT_K$ . It follows that the inverse in  
172 time to find and kill one prey ( $P_K = 1$ ) is linearly related to the prey density and the attack  
173 success ( $a$ ) as:

$$174 \quad \frac{1}{T_K} = aN \quad \text{Eq. 3}$$

175 (see McKenzie *et al.* 2009). If density of the prey is known for several  $T_K$ , then one can regress  
176  $1/T_K$  against density and the slope ( $a$ ) is an estimate of attack efficiency over the range of  
177 conditions in which the measurements were taken (Figure 1).

178 ***FIGURE 1 SOMEWHERE HERE***

179 With GPS movement data, if kill sites can be identified, the time along a movement path  
180 can be partitioned into times at kill sites,  $T_h$ , and time along paths between kills,  $T_k$ , where  $T =$   
181  $\sum T_h + \sum T_k$  when killing and handling are exclusive. Mutual exclusion of killing and handling  
182 times may not hold for some carnivores or for herbivores that can process (e.g., chew) small prey  
183 as they continue to search (Spalinger & Hobbs 1992), but this is a reasonable assumption for  
184 large carnivores whose primary prey are also large and their consumption requires the predator to  
185 be in one place to process at least a portion of prey (Figure 2).

186

**FIGURE 2 SOMEWHERE HERE**

187           Prior to having GPS data, it was possible to locate kill sites by aerial or ground surveys  
188 and snow tracking and to obtain general kill rates,  $P_K$ , over periods of time (e.g.  $P_K/T$ , Peterson  
189 1977, Fuller 1989, Huggard 1993, Dale *et al.* 1995), but it was difficult or impossible to  
190 partition  $T$  into  $T_H$  and  $T_K$  directly. The value of partitioning movements into handling and  
191 killing behaviour using GPS data is that it (1) can indicate when a prey is killed, (2) provide an  
192 estimate of killing efficiency ( $1/T_K$ ), and when prey density is known an estimate of attack  
193 success ( $a$ ) for developing functional responses, and (3) permit us to examine factors influencing  
194 each process separately without confounding effects of the other behaviour. We submit that this  
195 will provide a clearer understanding of the variation in the observed relationships between kill  
196 rates and prey densities (Messier 1994; Marshall & Boutin 1999; Hayes *et al.* 2000), and lead to  
197 better models and predictions of the effects of predators on their prey among different areas. In  
198 the next sections, we review the state-of-the art in approaches to identifying kill sites and present  
199 new approaches to considering what influences killing time (time-to-kill) and when prey density  
200 is known, attack success for parameterizing functional responses.

201 **4. IDENTIFYING KILL EVENTS WITH GPS DATA: STATE-OF-THE-ART**

202 The link between GPS positions and kill-site detection is the analysis of the predator movement  
203 pattern: while the predator is handling the kill, it will stay at the same location over a longer time  
204 period than most non-foraging movements. High sampling frequency will result in a more  
205 distinct pattern of either consecutive, single positions that indicate movement or “clusters” of  
206 positions indicating non-movement. Several studies have shown that the majority of predation  
207 events occur during the night (Anderson & Lindzey 2003; Sand *et al.* 2005; Zimmermann *et al.*

208 2007), and this type of information can be extracted from GPS positions given they are sampled  
209 with adequate frequency.

210 Several approaches have been used to identify clusters of locations along movement  
211 paths that represent the time spent handling prey at a kill site. Anderson & Lindzey (2003) used  
212 a rule of  $\geq 2$  locations within 200 m within 6 days for cougars feeding on multiple prey types.  
213 Knopff *et al.* (2009) used the criterion of Anderson & Lindzey (2003) to define a cluster of  
214 cougar locations, but automated the process using an algorithm that is available from the authors.  
215 Sand *et al.* (2005) and Zimmermann *et al.* (2007) created circles defined by fixed radii (called  
216 “buffers”) around winter positions of wolves feeding primarily on moose (*Alces alces*) and  
217 defined locations with overlapping buffers as clusters, which were visited in the field. Webb *et*  
218 *al.* (2008) used a space-time permutation scan statistic (STPSS) originally developed to detect  
219 clusters of disease cases to identify clusters of GPS locations of wolves in winter.

220 Sampling frequency and fix rate bias are both important in identifying potential kill sites.  
221 Most approaches are based on randomly selecting a sequence of GPS positions of the predator  
222 obtained at relatively short fix intervals (e.g.,  $\leq 1$  hr) to ensure that all or the vast majority of kills  
223 made during the study period are found. Selection of a GPS fix interval is a trade-off between  
224 battery capacity (lifetime) of the GPS collar, and the ability to successfully identify kill sites. A  
225 fix interval needed to identify a certain proportion of the true number of kill sites can be assessed  
226 by rarifying the data (i.e., successively removing GPS-positions from the dataset, Sand *et al.*  
227 2005, Webb *et al.* 2008; Knopff *et al.* 2009). A detection of smaller-bodied prey is crucial to  
228 avoid biases in kill rate estimates towards larger prey and may require high position frequency  
229 (Sand *et al.* 2005; Webb *et al.* 2008; Knopff *et al.* 2009). Small prey such as rodents or neonate  
230 ungulates may, however, be consumed too quickly to be detected with a reasonable GPS-location

231 schedule. Further, optimal fix rate may need to be shorter for social carnivores than solitary (e.g.,  
232 wolves versus cougars) because many individuals may feed on the prey. Where fix rate bias  
233 exists (Hebblewhite *et al.* 2007), sampling rate should be evaluated with this error in mind (see  
234 Knopff *et al.* 2009).

235         Once a potential kill cluster is identified, it can be verified by a field visit. Coordinates of  
236 the positions or the centers of the clusters may be loaded into a hand-held GPS. Because GPS-  
237 locations are somewhat inaccurate (e.g., 5% of positions outside 114 m of true location, Webb *et*  
238 *al.* 2008; see also Frair *et al.* this volume), and because kill remains may be scattered around  
239 actual positions, a sufficiently large area in proximity to the selected positions should be  
240 searched thoroughly. Webb *et al.* (2008) showed that the geometric centers of selected clusters  
241 associated with kill sites were found within 200 m of actual kill locations. Investigation of single  
242 positions and tracking on snow revealed 9 out of 68 large-sized kills (13.2%) were outside  
243 clusters created by 100-m radii around hourly positions (Sand *et al.* 2005). During snow-free  
244 periods, detection of prey remains is even more difficult.

245         The time span between the kill event and researcher visit to the kill site is critical to  
246 detect a carcass, correctly verify the cause of death, and determine information like prey species,  
247 sex and age. To date, average time spans have ranged from approximately 8 - 9 days  
248 (Zimmermann *et al.* 2007, Sand *et al.* 2008) to 200 days (Anderson & Lindzey 2003). The latter  
249 project used 'store-on-board' collars on cougars that allowed access to data only upon retrieval  
250 of the collar. GPS-collars with remote data download via VHF, UHF, GSM or satellite link allow  
251 visitation of sites before decomposition and scavenging make field verification less reliable  
252 (Webb *et al.* 2008). The time span should be long enough so field personal will not interfere with  
253 the predator. Studies using GPS-based locations from wolves, for example, showed they rarely

254 spent more than 3-4 days on any type of kill (Sand *et al.* 2005; Webb *et al.* 2008), whereas  
255 cougars exhibited a much longer handling of prey (Knopff *et al.* 2009). The cheaper and less  
256 energy consuming store-on-board collars may be used to provide estimates of kill rates  
257 retrospectively provided that models have been developed for a particular predator-prey system  
258 and their accuracy evaluated.

259         Field efforts for visiting kill sites can be reduced or potentially even dropped if models  
260 based on movement can reliably predict the presence of a kill. A successful model should be able  
261 to distinguish kill sites from non-kill sites and preferably even distinguish between different prey  
262 sizes (e.g., Webb *et al.* 2008). Model building should include a minimum of three steps: (1)  
263 inspection of GPS-data at known kill and non-kill sites to identify spatial, temporal or location  
264 features that might differentiate between such sites, (2) comparisons of alternative statistical  
265 models to predict kill locations following model selection procedures, and (3) validation of the  
266 best model by applying it to new or withheld datasets for which the true number of kill sites is  
267 known. A full discussion of statistical models with GPS sequence data is beyond the scope of  
268 this paper. We highlight models used for kill rate estimation to date and refer the reader to other  
269 contributions in this volume (Fieberg *et al.* this issue; Smouse *et al.* this issue).

270         Modeling approaches have included binomial logistic regression to predict presence or  
271 absence of large kills at GPS-location clusters (Andersen & Lindzey 2003; Zimmermann *et al.*  
272 2007), two-step binomial and multinomial logistic regression to estimate the chances of a site to  
273 contain a large- or small-bodied kill, or no kill (Webb *et al.* 2008; Knopff *et al.* 2009), and  
274 hidden Markov models to distinguish among kill, bed, and transit locations (Franke *et al.* 2006).  
275 Variables included in these models ranged from cluster dimensions including the number of  
276 continuous or discontinuous locations at the cluster and geometric cluster dimensions, time of

277 day, individual and pack characteristics like sex, age, and number of associated animals,  
278 characteristics of movements such as distance traveled, turn angles and travel rates, and  
279 environmental variables such as metrics of terrain ruggedness, human disturbance and vegetation  
280 cover (Franke *et al.* 2006; Zimmermann *et al.* 2007; Webb *et al.* 2008; Knopff *et al.* 2009).  
281 Random effects models also may include variation among individuals, study periods, and/or  
282 study areas (Zimmermann *et al.* 2007).

283         Validation of the predictions of the models, based on either independent data sets or k-  
284 fold cross validation approaches (Zimmermann *et al.* 2007; Webb *et al.* 2008; Knopff *et al.*  
285 2009), showed that a range of error existed depending on particulars of the clustering rules,  
286 sampling frequency, prey composition and sizes, and hunting behaviours of the species under  
287 study. Specification of omission error (identifying a kill site as a non-kill site) and commission  
288 error (identifying a non-kill site as a kill site; Webb *et al.* 2008; Knopff *et al.* 2009) will further  
289 help to evaluate model performance. As recommended by a number of authors, an  
290 understanding of these errors may help guide field efforts needed to obtain kill rates with a  
291 certain precision and accuracy. For example, in the case of a multi-prey system in Alberta, the  
292 greatest effort would be required to distinguish wolf kill sites of deer (*Odocoileus hemionus*, *O.*  
293 *virginianus*) from non-kill sites (Webb *et al.* 2008), whereas in Scandinavia differentiating  
294 between sites containing wolf-killed moose and non-kill sites or sites with small prey other than  
295 moose will be important.

296         Initial models have suggested that variability in factors influencing predator behaviour at  
297 kill sites are likely to be species and system specific because of differences in prey items, the  
298 types of other predators present, and amount of human disturbance. For example, solitary living  
299 cougars seem to express high site fidelity and relatively long handling times of prey resulting in a

300 high detection rate of killed prey (Anderson & Lindzey 2003; Knopff *et al.* 2009). In contrast,  
301 group-living wolves tend to have shorter handling times because large packs consume prey  
302 rapidly, and show a less distinct behaviour at kill sites ultimately resulting in lower detection  
303 rates of prey killed (Sand *et al.* 2005; Zimmermann *et al.* 2007, Webb *et al.* 2008). Similarly,  
304 prey- and predator population density, habitat type/quality, and stochastic events such as  
305 disturbance by humans or other predator species may influence variance in the behaviour of  
306 predators at kill sites. Very high local prey densities may result in excessive killing of  
307 individuals that may not be completely consumed (i.e., partial prey consumption). Zimmermann  
308 *et al.* (2007) observed large variation in the time wolves spent handling moose carcasses and  
309 discussed human disturbance, scavenging, and social organization of the re-colonizing wolf  
310 population as possible reasons. At the same time, emerging patterns suggest it may be too  
311 difficult to identify some smaller prey (e.g., deer) because of the short handling duration. For  
312 example, Webb *et al.* (2008) could identify 100% of the large-bodied prey, but only 40% of the  
313 smaller prey, and the same pattern emerged from the hidden Markov modeling technique  
314 (Franke *et al.* 2006). In contrast, other studies on wolves did not find any differences in the time  
315 for handling large and mid-sized/small prey as exemplified by adult and juvenile moose during  
316 both winter (Sand *et al.* 2005) and summer (Sand *et al.* 2008).

317

## 318 **5. TIME-TO-KILL: NEW APPROACHES FOR GPS MOVEMENTS**

319

320 Once clusters of GPS-based locations has been identified as kill sites along a movement path, the  
321 time between kills ( $T_k$ ) can be determined (Figure 2). Delineating  $T_k$  depends on a decision rule  
322 for when  $T_k$  is initiated and when it ends. One approach is to define  $T_k$  as beginning at the time  
323 of the first recorded GPS location away from the kill site and ending at the first location at the

324 next kill site. Different approaches for allocating GPS fixes near a kill site to handling or killing  
325 behaviours may be developed, and frequency of sampling fixes is an important consideration in  
326 refining these rules, but no evaluations have been made to date. Once delineated, hypothesized  
327 mechanisms for what influences killing efficiency,  $T_k$ , such as age, sex, or social group size, prey  
328 density, or environmental characteristics along paths leading up to the kill, can be evaluated  
329 using several modeling approaches that provide somewhat different information and require  
330 meeting different assumptions. Further, where density of prey is known, an estimate of attack  
331 success ( $a$ ) is obtainable for the conditions under study.

332 We illustrate the modeling approaches using data from one GPS-collared wolf whose  
333 movements have been monitored for 19 kills in west-central Alberta, Canada in the winter of  
334 2005-2006. The wolf inhabited mountainous areas that were heavily forested (~60%) with  
335 clearcuts and open areas (~20%) dispersed through the area (see Webb *et al.* 2008 for details).  
336 Major ungulate prey included deer, elk (*Cervus elaphus*), moose, and wild horse (*Equus*  
337 *caballus*). Kill sites of the wolf were identified using 2-hr locations as described by Webb *et al.*  
338 (2008) with 60% of the potential clusters identified statistically visited in the field to verify the  
339 presence of a kill. Time between kills ( $T_K$ ) was defined as in Figure 2 based on the decision rule  
340 described above and averaged  $7.0 \pm 4.9$  (mean  $\pm$  SD) days (range 10 hrs to 15 days). Kill paths  
341 (the path between kill sites) were delineated using straight-lines that connected sequential 2-hr  
342 GPS fixes between kill sites. Along each of the 19 kill paths the following environmental  
343 covariates were estimated within a 500-m buffer around each 2-hr path segment (and averaged  
344 across segments for the entire kill path): density of ungulate prey, mean proportion of area that  
345 was forest, open meadow, or clearcut, mean elevation (m), terrain ruggedness (standard deviation  
346 of elevation), distance to forest edge (km), density of roads ( $\text{km}/\text{km}^2$ ), and density of other linear



347 features ( $\text{km}/\text{km}^2$ ) such as seismic lines and pipelines (McPhee 2009). Density of ungulate prey  
348 was derived from interpolated pellet group densities (based on counts along 372, 1-km transects)  
349 that we converted to animal numbers first based on the ratio of aerial moose counts to pellet  
350 counts, and for other prey based on the body weight ratios of moose to other prey assuming  
351 similar defecation rates in winter (Webb 2009). Because prey encounter rates also may be  
352 altered by prey aggregation (Fryxell *et al.* 2007; McLellan *et al.* 2010), a spatial index of prey  
353 patchiness based on the coefficient of variation in prey density across a 2-hr path segment was  
354 also derived. Finally, the average distance travelled between 2-hr GPS locations was recorded to  
355 indicate rate of search. We related the inverse of  $T_k$  to the above covariates using backward  
356 stepwise linear regression, and adjusted standard errors for autocorrelation using a Huber-White-  
357 Sandwich estimator in STATA (StataCorp LP, College Station, Texas, USA).

358         We found  $1/T_k$  was related only to prey density ( $\beta = 0.0055 \pm 0.0820$ ,  $P = 0.003$ ) and the  
359 extent of forest along the paths leading to the kill ( $\beta = -0.1427 \pm 0.0086$ ,  $P < 0.001$ ), indicating  
360 that it took longer to find prey in areas of low prey density and high forest cover ( $r^2_{\text{model}} = 0.92$ ,  $P$   
361  $< 0.001$ ). Forest extent and prey density were not closely related ( $r = 0.35$ ,  $P > 0.15$ ), and a  
362  $\log(\text{time})$  model did not improve model fit ( $r^2_{\text{model}} = 0.70$ ,  $P = 0.01$ ). These are reasonable results  
363 because it has been reported that prey detection is low in forested habitats (Mech *et al.* 1998;  
364 MacNulty *et al.* 2007). In fact, only after accounting for prey detectability (i.e., forest extent) we  
365 found a relationship between  $1/T_k$  and prey density. The relatively weak effect of prey density  
366 on  $1/T_k$  compared with landscape condition (i.e., forest cover) may result from the generally high  
367 deer density in this area or selection by wolves to hunt primarily in areas of high prey density  
368 (McPhee 2009). Further, we found no evidence for an interaction between prey density and  
369 forest extent revealing that detecting prey in forest cover did not depend on prey density. Recall

370 that the value of  $a$  is the slope of the line between  $N$  and  $1/T_k$ . Here, we estimated  $a = 0.0165 \pm$   
371  $0.0078$ , but the value varied with extent of forest cover along the path, which we have interpreted  
372 to be primarily an effect of prey detection.

373         Although a simple linear regression illustrates the relationship between  $1/T_k$  and prey  
374 density or landscape conditions, other approaches may offer more appropriate means of  
375 analyzing events in time because ordinary least squares regression assumes normally distributed  
376 errors (Cleves *et al.* 2002). Semi-parametric and parametric time to event models provide  
377 improved approaches. The Cox proportional hazard model (CPH), and to a lesser extent  
378 parametric proportional hazard (PPH) or accelerated failure time models (AFT), are familiar to  
379 users of telemetry data for survival analyses (DelGiudice *et al.* 2002, Murray 2006; Fieberg &  
380 DelGiudice 2009). We refer readers to more extensive treatises on these methods (Hosmer &  
381 Lemeshow 1999; Therneau & Grambsch 2000; Cleves *et al.* 2002; Kalbfleisch & Prentice 2002),  
382 and briefly illustrate here how they might be applied to analyzing  $T_k$ .

383         Both semi-parametric and parametric models can be used to explore the influence of  
384 covariates on times to events (i.e., kills). However, they make different assumptions about the  
385 baseline hazard functions, which may suit different predator-prey systems differently, and  
386 provide different information to a particular question. CPH model provides a relative assessment  
387 of covariate effects on the hazard of a failure (kill) at time  $t$ . Using this approach assumes the  
388 hazard ratio is constant across subjects (but see “frailty” options below), without making any  
389 assumption about the shape of the baseline hazard—it can be constant, increasing or decreasing.  
390 With CPH, the cumulative hazard curve can be visually inspected to reveal temporal patterns in  
391  $T_k$  as we illustrate below. Further, it has the flexibility of including single or multiple segments

392 (e.g., corresponding to 2-hr segments) along one kill path, and a shared frailty term, which is  
393 similar to including a random-effect that accounts for variation among individuals (Cleves *et al.*  
394 2002). Continuing with our example, we modeled  $T_k$  using CPH and found similar support for  
395 models including forest cover both with and without total prey density ( $\Delta AIC_c < 2.1$ ), although  
396 prey density was no longer statistically significant (Table 1a). Data fit the proportional hazard  
397 model based on a test of the Schoenfeld residuals ( $X^2 = 0.53, P = 0.76$ ). Plotting the cumulative  
398 baseline hazard indicated that the risk of killing increased slowly 3-5 days post-kill, increased  
399 moderately from 5-12 days post-kill, and increased dramatically thereafter (Figure 3). Figure 3  
400 does not depict the effects of covariates; however, the probability of a kill at time  $t$  was lower as  
401 forest cover in the animal's kill path increased and higher as the density of prey increased (Table  
402 1a).

403 Unlike the CPH, parametric time to event models specify *a priori* a distribution for the  
404 baseline hazard. The most common distributions include exponential, Weibull, log-normal, log-  
405 logistic, and gamma failure rates, all of which are log(time) parameterizations (Hosmer &  
406 Lemeshow 1999; Cleves *et al.* 2002). PPH and AFT models provide estimates of baseline  
407 hazard rates and coefficient effects that have different interpretations. AFT models directly  
408 describe the expected change in the time to event for every unit change in  $x_i$ , rather than  
409 describing the change in the likelihood or relative likelihood of an event occurring at time  $t$ , as is  
410 the case with the PPH and CPH models (Therneau & Grambsch 2000; Cleves *et al.* 2002).

411 Based on the shape of the cumulative hazard curve in Figure 3, we fit parametric models  
412 assuming a Weibull distribution to our data. Because regressions based on the Weibull

413 distribution have both a proportional hazard (Table c) and AFT (Table d) formulation, it is also  
414 useful for our illustration. The Weibull baseline hazard is given as:

$$415 \quad h_0(t) = pt^{p-1} \exp(\beta_0) \quad \text{Eq. 4}$$

416 and it has two parameters,  $p$  and  $\beta_0$ , where  $p$  is the shape parameter and  $\beta_0$  is the intercept. When  
417  $p = 1$ , the hazard rate is constant over time. Adding the effects of covariates, PPH takes the  
418 form:

$$419 \quad h(t | x_i) = pt^{p-1} \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2) \quad \text{Eq. 5}$$

420 For our example,  $p = 2.094$ , which was significantly different than 1 (Wald test,  $z = 4.02$ ,  $P <$   
421  $0.001$ ; coefficient estimates given in Table 1c). Thus, our visual interpretation

422 *FIGURE 3 ABOUT HERE*

423 based on the CPH was supported. We also found that hazard ratios of the CPH (Table 1a) and  
424 PPH (Table 1b) were similar, indicating a good fit to the assumed underlying baseline hazard  
425 (Cleves *et al.* 2002). Under a Weibull distribution, the AFT formulation provided different  
426 coefficients because of their interpretation, but they are related to the hazard ratio of the PPH by  
427  $\exp(-p\beta_{AFT})$ . In our example,  $T_k$  increased rapidly as forest cover exceeded 40% over the path  
428 and low prey density augmented the delay in time-to-kill a prey (Figure 4).

429 *FIGURE 4 ABOUT HERE*

430 Time to event models offer both opportunities and challenges to exploring predation  
431 processes. The CPH models are flexible in that the shape of the curve and the effect of  
432 covariates can be explored without making restrictive assumptions about the distributions of  
433 failure times. When enough is known to make reasonable assumptions about the baseline

434 hazard, quantifiable estimates of time-to-kill under different combinations of covariates can be  
435 estimated along with measures of uncertainty. This may permit comparisons in the efficiencies  
436 of killing among different wolves or in different landscapes. When movement data from more  
437 than one individual is available, frailty models, which accommodate heterogeneity among  
438 individual responses similar to random effects, can be employed for population-level  
439 assessments. Further, in multi-prey systems, when more than one prey type is killed, and type  
440 of prey at each kill is known, a competing-risk analysis (Lunn & McNeil 1995) might be used to  
441 determine whether  $T_k$  varies across prey species and is influenced similarly by covariates.

442         However, as with studying most ecological processes, issues of selecting scale of  
443 observation influences our view of the process. For our illustration we measured covariates at  
444 the scale of the entire path leading to a kill, but alternatively we could have used 2-hr segments  
445 along the path. Our interpretation that forest cover influenced time to encountering a prey by  
446 altering prey detection is reasonable at this scale, but characteristics of a 2-hr segment might be  
447 more informative on what specifically influenced the act of killing. For example, where a kill is  
448 located may differ from the characteristics where the predator encounters the prey because  
449 certain characteristics influence the act of killing more than encountering a prey (Hebblewhite *et*  
450 *al.* 2005). Time to event models developed on multiple records per path (e.g., each hr-segment  
451 along the path leading to a kill) may allow a better assessment of short-term processes. For  
452 example, using CPH models McPhee (2009) measured path features along each 2-hr segment of  
453 the path leading to a kill and found that hunting near oil and gas well sites influenced  $T_k$ , which  
454 was corroborated by kill site locations tending to occur further from well sites. Although  
455 sampling segments of movement paths can improve our understanding, sampling at too fine a  
456 movement scale also may degrade the signal. Multi-scale approaches to measuring covariates

457 back in time along movement paths may be necessary when the processes of predation (*sensu*  
458 Hebblewhite *et al.* 2005) work at different time scales. Further, if covariates are measured as  
459 varying in time along the path, prediction of the mean time-to-kill as illustrated in Figure 3  
460 becomes problematic because the expected  $T_k$  most commonly assumes fixed covariates in time.  
461 While obtaining estimates of time-to-kill is still possible, it remains mathematically difficult  
462 (Therneau & Grambsch 2000; Cleves *et al.* 2002) and methods of obtaining these estimates are  
463 not readily available in most statistical software packages.

## 464 **6. SUMMARY AND CONCLUSIONS**

465 Carnivore biologists that address how predators influence prey populations have focused  
466 predominately on understanding whether kill rates are most related to prey density alone (prey  
467 dependent) or to the ratio of the number of prey to the number of predators (ratio dependent)  
468 using statistical-curve fitting approaches to develop functional responses. Yet, empirical  
469 observations show high variation around both these relationships with little advancement gained  
470 in understanding the true nature of the interactions (Boutin 1992). Because of the size and  
471 weights of the first generation of GPS collars, large carnivore biologists are among the first to  
472 apply this technology to study movement behaviour of carnivores, which has led to a greater  
473 understanding of what movements reflect and for quantifying the processes of predation. For  
474 these far-ranging animals in particular, GPS technology has opened the door to obtaining  
475 sequences of animal locations at temporal extents and resolutions that previously were  
476 impossible or extremely difficult even with intensive field efforts. This has lead to improved  
477 precision in estimating kill rates.

478           At the same time, movement behaviour of large carnivores lend themselves to  
479 encapsulating basic predation processes. When predominance of biomass consumed by  
480 carnivores comes in relatively large, discrete packages it result in clustered movements patterns  
481 due to lengthy handling of prey. The large prey typically are dispersed and nonapparent (*sensu*  
482 Spalinger & Hobbs 1992) such that carnivores move relatively far in search of the next prey.  
483 This typically results in handling time at a kill site being exclusive of periods of search and  
484 killing. As a result, movement patterns particularly of large carnivores lend themselves to a  
485 dichotomy of simplified movement modes that can be distinguished with GPS locations and have  
486 relevance to key processes in the functional responses of predators -- handling time and killing  
487 time.

488           To date, analyses of GPS-based movement patterns of large carnivores have focused on  
489 identifying periods of handling time that identify kill sites, and the factors influencing handling  
490 time. Methods for identifying kill sites based on spatiotemporal patterns in the sequence of  
491 movement positions are evolving. As the approach is applied in more studies with a variety of  
492 species we will gain a better appreciation of how data sampling protocols and animal behaviour  
493 influence our ability to correctly distinguish a GPS-based kill site. At present, modeling the  
494 probability of a cluster being a kill site is no substitute for field visits but can guide our field  
495 efforts (Sand *et al.* 2005; Webb *et al.* 2008; Knopff *et al.* 2009). In the process, however, we  
496 have found we can identify factors related to handling time such as prey size, size of predator  
497 social groups, environmental site factors (e.g., snow), and disturbance by humans (Zimmermann  
498 *et al.* 2007; Webb *et al.* 2008).

499           Once kill sites are identified, the time-to-kill one prey ( $T_k$ ) can be determined as the time  
500 between kills. Similarly, we can identify animal characteristics and landscape factors along the  
501 movement path that influence  $T_k$  using time to event models. The most appropriate type of  
502 model is limited by the model's assumptions, but also depends on whether a probability of the  
503 event occurring at a specific time is of interest or the interest lies in how much the factor changes  
504 the actual time to event. Plotting the relative hazards due to variables that influence  $T_k$  on a map  
505 has the potential to be used as a metric of predation risk.  $T_k$  also is equivalent to  $1/aN$  from the  
506 typical Type II functional response (Holling 1959) and where prey densities are known an  
507 estimate of  $a$  is possible to derive. In this context  $a$  reflects not only searching for prey, but  
508 detecting, attacking, and killing the prey, which together reflects killing efficiency. Most  
509 functional response models have assumed  $a$  to be constant and unaffected by landscape factors,  
510 and these assumptions can now be tested. However, incorporating changes in social groupings  
511 that influence  $a$  and obtaining prey densities at relevant scales in both space and time are  
512 problematic. While we are not yet at the point of being able to incorporate the complexity  
513 derived from GPS movement paths into functional response models, particularly in multi-prey  
514 systems, exploring the details of GPS-movement data has put us on the right path.

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663

664 Figure captions

665 Figure 1. The relationship between time-to-kill ( $T_k$ ), defined as the time between the first GPS  
666 location after leaving a kill site and the first GPS location at the next kill site. Note the units of  
667 y-axis have been inverted to reflect inverse of time-to-kill:  $1/T_k = aN$  in this simple form.

668 Figure. 2. Illustration of the time-to-kill ( $T_k$ ) derived from GPS-based location data where  
669 clusters of locations indicate time spent at a kill site (the handling time,  $T_h$ ) and the dashed line is  
670 the path of the animal between kills (the kill path).  $T_k$  is defined as the time between the last  
671 GPS location at a kill site or first location after leaving a kill site and the first location at the kill  
672 site.

673 Figure 3. Cumulative baseline hazard for time-to-kill prey along a wolf hunting path based on a  
674 Cox proportional hazard model using data from 19 wolf kill events during winter 2005-2006 in  
675 west central Alberta, Canada.

676 Figure 4. Predicted mean time-to-kill of a wolf in areas of various forest extent at high ( $4/\text{km}^2$ )  
677 and low ( $2/\text{km}^2$ ) total prey densities in central west Alberta. Estimates are based on accelerated  
678 failure time models assuming a baseline hazard following a Weibull distribution.

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Table 1. Hazard ratio and  $\beta$  coefficients of time to event models for the extent of forest cover (proportion of area) and total ungulate prey ( $\#/km^2$ ) along 2-hr GPS-paths of a wolf ( $n = 19$ ) that were related to time-to-kill ( $T_K$ ). Time-to-kill was defined as the time between the first GPS location after leaving a kill site and the first GPS location at a kill site. Total prey include only ungulate prey.

Model	$\beta$ or HR	SE	<i>P</i>
(a) <u>Cox proportional hazard</u> : hazard ratio			
Forest extent ( $ha/km^2$ )	0.000022	0.000092	0.008
Total prey ( $\#/km^2$ )	1.3500	0.4530	0.37
(b) <u>Parametric proportional hazard, Weibull</u> : hazard ratio			
Forest extent ( $ha/km^2$ )	0.000023	0.000058	< 0.001
Total prey ( $\#/km^2$ )	1.3260	0.4038	0.35
(c) <u>Parametric proportional hazard, Weibull</u> : $\beta$ coefficients			
Forest extent ( $ha/km^2$ )	-10.6730	2.5110	< 0.001
Total prey ( $\#/km^2$ )	0.2826	0.3043	0.30
Intercept	-5.4480	1.6713	0.001
(d) <u>Accelerated failure time, Weibull</u> : $\beta$ coefficients			
Forest extent ( $ha/km^2$ )	5.0960	0.6678	< 0.001
Total prey ( $\#/km^2$ )	-0.1349	0.1444	0.35
Intercept	2.6016	0.6530	< 0.001

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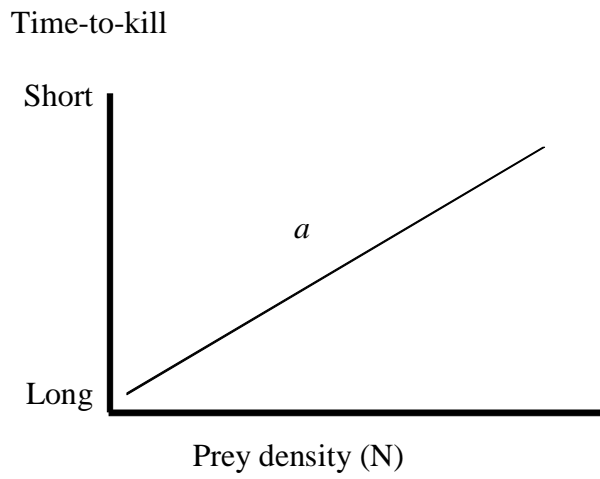
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689 Figure 1.

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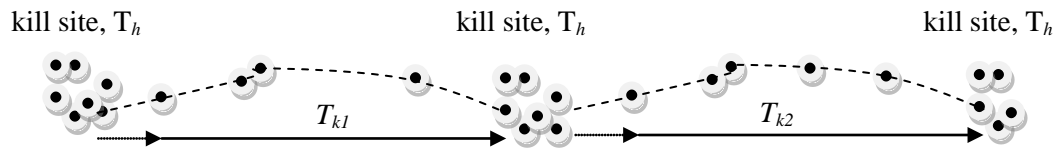
714 Figure 2.

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739 Figure 3.

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CPH Cumulative  
baseline hazard

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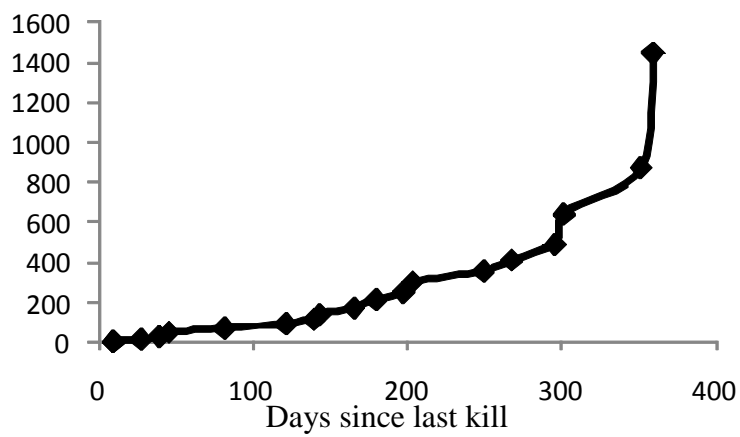
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764 Figure 4

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