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Does wildlife resource selection accurately inform corridor conservation?

Running Title: Wildlife corridors and resource selection

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SUMMARY

1. Evaluating landscape connectivity and identifying/protecting corridors for animal movement have become central challenges in applied ecology and conservation. Currently, resource selection analyses are widely used to focus corridor planning where animal movement is predicted to occur. An animal's behavioural state (e.g., foraging, dispersing) is a significant determinant of resource selection patterns, yet has largely been ignored in connectivity assessments.

2. We review sixteen years of connectivity studies employing resource selection analysis to evaluate how researchers have incorporated animal behaviour into corridor planning, and highlight promising new approaches for identifying wildlife corridors. To illustrate the importance of behavioural information in such analyses, we present an empirical case study to test behaviour-specific predictions of connectivity with long-distance dispersal movements of African wild dogs (*Lycaon pictus*). We conclude by recommending strategies for developing more realistic connectivity models for future conservation efforts.

3. Our review indicates that most connectivity studies conflate resource selection with connectivity requirements, which may result in misleading estimates of landscape resistance, and lack validation of proposed connectivity models with movement data.

4. Our case study shows that including only directed-movement behaviour when measuring resource selection reveals markedly different, and more accurate, connectivity estimates than a model measuring resource selection independent of behavioural state.

5. *Synthesis and applications*. Our results suggest that resource selection analyses that fail to consider behaviour may be insufficient in targeting movement pathways for corridor

24   protection. This failure may result in misidentification of wildlife corridors and

25   misallocation of limited conservation resources. Our findings underscore the need for

26   considering patterns of animal movement in appropriate behavioural contexts to ensure

27   the effective application of resource selection analyses for corridor planning.

28

29 **KEYWORDS**: behavioural state, conservation planning, corridor ecology, dispersal, landscape

30 connectivity, landscape resistance, movement ecology, resource selection, step selection

31

32 **INTRODUCTION**

33 Connectivity, i.e., the degree to which a landscape facilitates or impedes movement between

34 resources or habitats (Taylor *et al.* 1993), is a key aspect of land management for the

35 conservation of species and communities. Connectivity influences demography (Clobert *et al.*

36 2001), promotes dispersal and colonization (Hanski 1998), maintains genetic diversity (Hendrick

37 2005), increases a species' ability to respond to perturbations and changing climates (Heller &

38 Zavaleta 2009), and supports long term persistence in heterogeneous landscapes (Vasudev *et al.*

39 2015). Consequently, increasing landscape connectivity has been identified as a fundamental

40 strategy for mitigating impacts of climate change on biodiversity (Heller & Zavaleta 2009).

41

42 The identification and protection of wildlife corridors, i.e., land allowing movement of focal

43 species between two or more habitat areas (Beier et al. 2008), has become a critical tool for the

44 maintenance of landscape connectivity (Gilbert-Norton *et al.* 2010). As a response to global

45 concerns about habitat fragmentation, climate change, and loss of landscape connectivity,

46 establishment of wildlife corridors has accelerated in the last decade and half. Today, studies

47   aimed at evaluating connectivity and determining where to establish corridors have become

48   central to conservation science and practice (Beier, Majka & Spencer 2008; Beier *et al.* 2011;

49   Rudnick *et al.* 2012).

50

51   Here, we systematically review sixteen years of studies using wildlife resource selection to

52   estimate landscape connectivity and highlight promising new approaches for identifying wildlife

53   corridors. We argue that failure to assess resource selection in appropriate behavioural contexts

54   may lead to misidentification of wildlife corridors and misallocation of limited conservation

55   resources.

56

57   *Methods for identifying wildlife corridors*

58   Accurate identification of functional corridors depends on knowledge of a species' dispersal

59   requirements (Vasudev *et al.* 2015). Currently, estimating landscape resistance to movement is

60   the most widely used technique to focus corridor planning on areas where dispersal is considered

61   most likely to occur (Sawyer, Epps & Brashares 2011). Landscape resistance models – or

62   'resistance surfaces' – assign a value in a landscape grid cell to each environmental variable of

63   interest (e.g. elevation, land cover) that represents the energetic or survival cost to the study

64   species of moving through that spatial position (Adriaensen *et al.* 2003), or the willingness of the

65   individual to cross the cell (Zeller, McGarigal & Whiteley 2012). Earlier efforts to estimate

66   landscape resistance based on expert opinion (e.g., LaRue & Nielsen 2008; Shen *et al.* 2008)

67   have been greatly advanced by technological and analytical tools that now allow researchers to

68   evaluate resistance directly from empirical data (Zeller, McGarigal & Whiteley 2012). Methods

4

69   for estimating resistance based on empirical data fall into the following two main approaches,

70   landscape genetics and resource selection functions.

71

72   Landscape genetics approaches measure the correlation of observed genetic distance between

73   individuals or subpopulations separated by hypothesized values of landscape resistance

74   (Cushman *et al.* 2006; Epps *et al.* 2007). Thus, landscape genetics infers the influence of

75   landscape variables on gene flow. These methods are a gold standard in connectivity modelling

76   when the process of interest is genetic connectivity. However, the few studies that have

77   attempted to validate genetic results with movement data indicate that while resistance models

78   derived from landscape genetics are useful in understanding large-scale effects on the process of

79   gene flow, they may not be as useful for predicting pathways of wildlife movement at finer,

80   management-relevant scales (Reding *et al.* 2013; Graves, Beier & Royle 2013). Additionally,

81   genetically-derived connectivity estimates can reflect past landscape permeability, due to the

82   time-lag to detect barriers (15-100 generations depending on methods and species traits;

83   Langduth *et al.* 2010), and thus may not capture current movement in rapidly evolving

84   landscapes, changing climates or for species dispersing short distances.

85

86   Given the uncertainties associated with applying landscape genetics to landscape planning at

87   finer spatial and temporal scales, we focused our review on the use of resource selection

88   functions (RSFs). In contrast to landscape genetic analyses, estimates of landscape resistance

89   derived from RSFs are thought to be effective at predicting areas for wildlife movement at more

90   immediate and fine scales; as a consequence, this approach is highly applicable to management

91   decisions (Chetkiewicz & Boyce 2009). Resource selection functions calculate the probability of

5

92   use of a given landscape variable (e.g., habitat type, elevation, slope) by statistically comparing

93   the characteristics of locations used by the study species with those in a control set of random

94   locations deemed available to, but presumably unused by, that species (Manly *et al.* 2002). These

95   analyses have recently been improved by the introduction of step selection (Fortin *et al.* 2005;

96   Thurfjell, Ciuti & Boyce 2014) and path selection (Cushman & Lewis 2010) functions, which

97   characterize movement as a series of linked steps or paths rather than a distribution of

98   independent points. Thus, while traditional RSFs, also known as point selection functions, are

99   well-suited for detection data, step and path selection analyses tend to be more useful for

100   relocation data because they account for changes in resource availability as an animal moves

101   through its landscape (Zeller, McGarigal & Whiteley 2012).

102

103   *The role of behaviour*

104   Use of RSFs in connectivity planning is largely based on the assumption that a habitat

105   occupied/selected by a species is predictive of the landscape conditions or features necessary for

106   successful dispersal (Vasudev *et al.* 2015). This critical assumption has been the subject of

107   debate, specifically regarding the degree to which resource selection models provide an accurate

108   proxy for movement preference as an animal navigates through a landscape (Beier, Majka &

109   Spencer 2008; Zeller, McGarigal & Whiteley 2012; Fatterbert *et al.* 2015). Resource selection

110   during dispersal may differ significantly from selection exhibited during daily residential

111   activities (Elliot *et al.* 2014; Vasudev *et al.* 2015; Gastón & Cabrera 2016). In particular, there is

112   increasing recognition that an animal's behavioural state (e.g. resource use vs. searching,

113   territory maintenance vs. dispersing) can strongly mediate patterns of resource selection (Wilson,

114   Gilbert-Norton & Gese 2012; Roever *et al.* 2013; Abrahms *et al.* 2015).

115

Behaviourally-mediated differences in resource selection can have important effects on estimates

of landscape resistance and resulting conservation actions. For example, a recent study by Zeller

and colleagues (2014) found opposite patterns of resistance to some landscape variables for

pumas (*Puma concolor*) in a 'resource use' behavioural state versus a directed 'movement' state.

Similarly, Elliot and colleagues (2014) found that landscape resistance differed between

dispersing and resident male lions (*Panthera leo*). Thus, failure to assess resource selection in

appropriate behavioural contexts may lead to misidentification of corridors for animal movement

and ineffective use of limited conservation funding (LaPoint *et al.* 2013; Elliot *et al.* 2014).

Because dispersal events are often difficult to detect in the field, resource selection measured

during directed movement states may provide an important proxy that can be used to infer

functional connectivity in addition to or in lieu of direct dispersal data. Yet, little work has

validated RSF-derived predictions of landscape connectivity with long-distance movement data

to assess this possibility.

We surveyed recent RSF-derived connectivity studies to 1) evaluate the extent to which these

efforts have incorporated movement behaviour and 2) identify best practices for considering

movement behaviour for future connectivity studies. While the range of definitions for animal

movement is vast (Nathan *et al.* 2008), we define 'movement behaviour' in the context of

connectivity science as directed movement toward a new location (i.e., taxis), typical of

movement between rest sites or resource patches (Schick *et al.* 2008). Using this definition, we

evaluated published studies with regard to how movement behaviour was considered in

estimating landscape resistance and predicting connectivity. Using data drawn from our studies

138 of African wild dogs, we demonstrate the sensitivity of corridor models to behavioural state and

139 test the validity of model predictions against empirical movement data. Specifically, we use

140 high-resolution GPS data from African wild dogs in northern Botswana to create least-cost path

141 predictions from two RSF-derived resistance models, one that ignores behavioural state and one

142 that isolates movement behaviour. We then test these predictions against observed long-distance

143 dispersal paths. We conclude by providing a framework and recommending strategies for

144 researchers and managers to develop more realistic connectivity models for future corridor

145 planning efforts.

146

147 **MATERIALS AND METHODS**

148 *Literature review*

149 To capture current trends in the literature, we searched ISI Web of Science for papers published

150 between January 2000 and February 2016 that contained the following key words: Topic =

151 (landscape resistance OR cost-distance OR effective distance) AND (corridor OR connectivity

152 OR linkage). We filtered the resulting 157 papers by restricting our search to the subject areas

153 Ecology, Environmental Sciences, Environmental Studies, Zoology, Biology, Biodiversity

154 Conservation, or Remote Sensing; this resulted in a subset of 137 papers. We further restricted

155 our review by excluding studies that did not use resource selection to estimate landscape

156 resistance and/or did not explicitly aim to model connectivity for the purpose of predicting

157 wildlife movement, resulting in a final set of 28 papers (Table 1). For each of the selected papers,

158 we evaluated: (1) the source of biological data (study species and data collection method), (2)

159 type of RSF employed (e.g., point selection, step selection), (3) whether movement behaviour

160   was explicitly considered in developing connectivity models, and (4) whether modelled corridors

161   were validated with independent movement data.

162

163   *African wild dog case study*

164   To determine whether isolation of directed movement behaviour improves predictions regarding

165   long-distance movement paths, we collected high-resolution GPS data from 15 free-ranging

166   African wild dogs in northern Botswana (Abrahms *et al.* 2015). African wild dogs are both the

167   widest ranging and most endangered of Africa's large carnivores; the International Union for

168   Conservation of Nature (IUCN) has linked the decline of wild dog populations to the species'

169   high sensitivity to habitat fragmentation (Woodroffe & Sillero-Zubiri 2013). Consequently, these

170   animals are a highly relevant focal species for assessing functional landscape connectivity.

171

172   Using collar-mounted accelerometers, we classified GPS locations into three discrete

173   behavioural states: traveling, chasing, and resting (Hubel *et al.* 2016). We used step selection

174   functions to quantify resource selection for a 'combined model' that included all available data,

175   ignoring behavioural state, and for a 'movement model' that included only the traveling dataset

176   (Thurfjell, Ciuti & Boyce 2014). Three of the 15 collared wild dogs exhibited long-distance

177   dispersal movements during the study period; these animals were excluded from the step

178   selection analysis to serve as test data against corridor model outputs. The data from the

179   remaining 12 individuals used to parameterize our models were collected from 12 different packs

180   to minimize risk of pseudoreplication. Habitat cover, land use type, proximity to road, and

181   proximity to human settlements were included as initial covariates after testing for collinearity

182   based on known influences on African wild dog space use (Woodroffe 2010; Whittington-Jones

183   *et al.* 2014; Abrahms *et al.* 2015). We used AIC forward model selection to determine which to

184   retain in our final models (Burnham & Anderson 2002). We used significant selection

185   coefficients from each model to create two corresponding resistance surfaces (Squires *et al.*

186   2013). For each resistance surface we used least-cost path (LCP) analysis to predict the dispersal

187   paths of the three dispersers, as this represents the most commonly used method for designing

188   wildlife corridors (Sawyer, Epps & Brashares 2011). Finally, to address the uncertainty inherent

189   in least-cost modelling we estimated least-cost corridors that overcome the single-pixel width

190   limitation of LCPs (Beier, Majka & Newell 2009). Following published recommendations

191   (Harrison 1992; Beier, Majka & Spencer 2008), we buffered our LCPs by a conservative

192   estimate of half the average home range width for African wild dogs (8km; Woodroffe 2010) to

193   determine biologically-informed corridor widths of 16 km.

194

195   To evaluate our models, we used two metrics as suggested by a recent study comparing the

196   utility of connectivity modelling validation methods (McClure, Hansen & Inman 2016) . Firstly,

197   we calculated the percentage of observed dispersal relocations overlapping with predicted least-

198   cost corridors, a metric relevant to conservation practitioners in assessing the proportion of

199   movement that would be protected by a potential corridor (Poor *et al.* 2012; McClure, Hansen &

200   Inman 2016). Secondly, we measured the path deviation of each model's LCP from the observed

201   dispersal paths, a straightforward statistic of how well the model agrees with the data (Pullinger

202   & Johnson 2010). All statistical analyses were performed using R 3.1.0 (R Core Team 2014). We

203   used ESRI ArcMap 10.2 to create resistance surfaces and Linkage Mapper software (McRae &

204   Kavanagh 2011) to generate least-cost paths. See Appendix S1 for full methods details.

205

206   **RESULTS**

207 *Literature review*

208 The majority of studies (82%) used animal relocation data from either GPS or VHF collars to

209 assess resource selection, while five (18%) relied on measures of indirect detection such as

210 animal sign or camera trap data. None of the detection-based studies made efforts to focus on

211 movement-related habitat use. In total, 11 of the 28 studies evaluated included efforts to

212 explicitly incorporate movement behaviour into their connectivity analyses. The remaining

213 studies conflated resource selection with connectivity requirements.

214

215 Only five studies (18%) validated connectivity predictions with movement data. LaPoint et al.

216 (2013) found poor agreement between corridor predictions for fishers (*Martes pennanti*) based

217 on GPS locations versus 'animal-defined' corridors delineated by quick, repeated, and linear

218 fisher movements. Deployment of camera traps demonstrated greater use by fishers of animal-

219 defined corridors than cost-based corridors. In contrast, Harju and colleagues (2013) found that

220 connectivity estimates based on resource selection during traveling and relocating movement

221 states for sage-grouse (*Centrocercus urophasianus*) were strong predictors of an independent test

222 set of locations for these movement states. Finally, Trainor *et al.* (2013) found a strong

223 correlation between connectivity predictions for red-cockaded woodpeckers (*Leuconotopicus*

224 *borealis*) based on resource selection during exploratory forays and an independent dataset of

225 short-distance dispersals.

226

227 *African wild dog case study*

228 The highest ranked movement model based on AIC model selection retained habitat cover, land

229 use type, and distance to roads as predictor variables; the highest ranked combined model

11

230   retained habitat cover and land use type (Table S2). Step selection results showed different, and

231   in some cases opposing, responses to landscape variables between the movement model and the

232   combined model (Fig.1, Table S3); these differences were reflected in the divergent patterns of

233   landscape resistance between the two models and resulting LCPs (Fig. 2). Least-cost corridors

234   from the movement model overlapped with the large majority of GPS locations from the three

235   dispersal paths (range 62 -100%, mean 87%; Table 3) while those from the combined model

236   included a lower percentage of GPS locations (range 0-100%, mean 33%). Path deviations

237   between the movement model LCPs and observed paths were significantly lower than those

238   between the combined model LCPs and observed paths.

239

240   **DISCUSSION**

241   *Literature review: inclusion of movement behaviour in corridor planning*

242   Collectively, the studies in our review that validated connectivity predictions with independent

243   movement data point to the importance of incorporating behavioural data in connectivity models

244   as a key step toward generating management strategies. As showcased by several such studies,

245   multiple data collection, technological and analytical approaches exist to aid conservation

246   scientists and practitioners in including movement behaviour in corridor planning. The ten

247   studies that considered animal movement behaviour in their connectivity predictions provide

248   informative examples for working with relocation data (Table 4). From these studies, we

249   identified two principal scales at which movement behaviour has been addressed: a behavioural

250   level and a demographic level. At the behavioural level, several studies identified the subset of

251   locations at which animals displayed behavioural states categorized broadly as movement

252   behaviour. These categorizations included a) 'traveling', 'relocating', or 'moving' based on step-

12

253   length distributions (Harju *et al.* 2013; Zeller *et al.* 2014); b) 'large-scale movements' delimited

254   by a threshold for movement rate (Pullinger & Johnson 2010); and c) 'active' versus 'resting'

255   behaviour based on both step-length and turn angle distributions (Squires *et al.* 2013). At the

256   demographic level, three studies employed a demographic approach by collaring and collecting

257   relocation data from juvenile dispersers (Richard & Armstrong 2010; Trainor *et al.* 2013; Elliot

258   *et al.* 2014). While behavioural and demographic approaches may be used in concert, we

259   distinguish a demographic approach from a behavioural one in that it may include all behavioural

260   states of a disperser. This approach may be ideal for determining how dispersers navigate their

261   landscape, but it is logistically challenging because it requires predicting which individuals in the

262   population will disperse. Perhaps not coincidentally, two of these three studies focused on birds,

263   where identification and tagging of juvenile dispersers is easier than it is for many other

264   vertebrates (Zeller, McGarigal & Whiteley 2012). To focus on dispersal movements, three other

265   studies collected location data during known dispersal seasons for their study species (Cushman

266   & Lewis 2010; Walpole *et al.* 2012; Roever, van Aarde & Leggett 2013).

267

268   Advances in GPS collar technology over the last decade can contribute to connectivity science

269   by coupling discrete behavioural states with patterns of space use and movement preference. In

270   particular, activity sensors such as collar-mounted accelerometers, magnetometers, and

271   physiological loggers are becoming increasingly popular for classifying behavioural states

272   remotely (Brown, Kays & Wikelski 2013; Wilson *et al.* 2013; Nams 2014). However, the

273   literature also provides many methods for inferring behavioural state without the expense of

274   activity sensors, even for collars that operate at coarse spatiotemporal scales. For instance,

275   Pullinger & Johnson (2010) classified two behavioural states of resource use versus long-

276   distance movement for caribou (*Rangifer tarandus*) by examining movement rate between 3-

277   hour GPS fix intervals. Similarly, pairing movement rate with turn angle distributions revealed a

278   clear distinction between sedentary and exploratory behavioural states in elephants (Roever *et al.*

279   2013). Patterns of GPS clustering have been used to further partition relocation data, including

280   identifying kill sites, dens, and scent marking areas for pumas (Wilmers *et al.* 2013) and feeding

281   and bedding behaviours in grizzly bears (Cristescu, Stenhouse & Boyce 2015). The wide variety

282   of existing methods for inferring behavioural states necessitate the development of best practices

283   for their application and interpretation in the context of connectivity modelling.

284

285   As mentioned previously, advances have also been made in the analytical procedures associated

286   with resource selection analyses, such as the addition of step selection (Fortin *et al.* 2005;

287   Thurfjell, Ciuti & Boyce 2014) and path selection functions (Cushman & Lewis 2010). Both of

288   these analytical approaches can help to quantify selection specifically for movement paths,

289   though for the purposes of connectivity modelling care must still be taken to ensure resource

290   selection is measured for the appropriate behavioural state(s). In addition, the rapidly growing

291   field of movement ecology (Schick *et al.* 2008; Nathan *et al.* 2008) offers many analytical

292   approaches for remote identification of behavioural states such as hidden Markov (Patterson *et*

293   *al.* 2009) and state-space models (Jonsen, Flemming & Myers 2005; Patterson *et al.* 2008) that

294   have been developed for effectively analysing noisy or imperfect animal movement data.

295

296   Our result that none of the detection-based studies focused on movement-related habitat use

297   highlights a ripe opportunity for advancement. Indirect detection methods are often less costly

298   than obtaining direct relocation data and are sometimes the only feasible option for rare or

299 elusive species. For those using indirect detection based on sign to identify movement corridors

300 (e.g., Walpole *et al.* 2012; Mateo-Sànchez, Cushman & Saura 2014), locations with sign of

301 resource-use behaviour (e.g. gorilla nesting/feeding sign; McNeilage *et al.* 2006) grizzly bear

302 bedding sites, (Munro *et al.* 2006) can be excluded from resource selection analyses in favour of

303 travel-related sign (e.g., gorilla trampled vegetation, dung, footprints; Sawyer & Brashares 2013)

304 to limit inferences to more movement-focused habitat use. For studies relying on camera trap

305 data to identify corridors (e.g., Brodie *et al.* 2014; Wang *et al.* 2014), there are several

306 improvements that can be made beyond using standard abundance estimates to infer areas with

307 high connectivity. If individual identification from photos is possible, spatially-explicit

308 movement rates can be measured and related to landscape variables through spatial capture-

309 recapture methods (Royle *et al.* 2013a; b). If individual identification is not possible, camera trap

310 data can be used to associate habitat use with activity patterns of the study species (Rowcliffe *et*

311 *al.* 2014). Given that nearly 20% of the connectivity studies we evaluated relied on indirect

312 detection for their resource selection analyses, development and application of methods to better

313 assess movement behaviour in these data sets is greatly needed.

314

315 We propose a series of steps that can be taken through the data collection and analysis stages of

316 resource selection estimation to better emphasize movement behaviour in connectivity modelling

317 (Fig. 3). As is the case with all ecological fieldwork, the processes we suggest depend first on

318 what data can be feasibly collected for the target species. However, since location data are often

319 used for a variety of purposes and thus may not have been collected specifically for connectivity

320 analyses, we suggest that researchers working with such data sets apply the analytical approaches

321 outlined above to focus inferences on movement behaviour regardless of the methods employed

322 during the data collection stage.

323

324 *African wild dog case study*

325 Results from our African wild dog case study mirror a small set of recent publications (e.g.,

326 Harju *et al.* 2013; Trainor *et al.* 2013) indicating that including only movement behaviour in

327 resistance surfaces analyses reveals markedly different patterns of connectivity than models

328 measuring resource selection without consideration of behavioural state. For the goal of

329 predicting and protecting dispersal, the movement model (i.e., only GPS positions when the dogs

330 were in a 'traveling' behavioural state) outperformed the combined model (i.e., all available GPS

331 positions independent of behavioural state) according to both validation metrics used in our

332 analysis (Table 3). The movement model least-cost corridor (LCC) fully incorporated two of the

333 three observed dispersal paths, overlapping with a total of 87% of movement locations compared

334 with only 33% for the combined model LCC. In addition, the path deviation statistic indicated

335 greater agreement between the least-cost paths derived from the movement model and the

336 observed wild dog dispersal paths than those from the combined model. These results suggest

337 that a general resource selection analysis may be insufficient in predicting and protecting

338 movement pathways for African wild dogs.

339

340 The divergent patterns of resource selection by African wild dogs revealed by our models have

341 significance for the conservation and management of this species. African wild dogs displayed

342 large differences in habitat preference when traveling compared to when behavioural state was

343 not considered. Our behaviourally informed model also revealed that African wild dogs showed

16

344   a higher tolerance for human-modified landscapes and features (pastoral areas, roads) when

345   dispersing, an outcome that has been reported for other dispersing carnivores including lions

346   (Elliot *et al.* 2014) and Iberian lynx (Gastón & Cabrera 2016). While the ability of dispersing

347   carnivores to navigate potentially hostile landscapes may allow populations to maintain greater

348   levels of connectivity than previously thought (Mateo-Sánchez *et al.* 2015), this also places them

349   at higher risk of human-wildlife conflict. Because of increased tolerance for human disturbance

350   and proclivity to range beyond protected areas, African wild dogs in a dispersing or exploratory

351   state are more prone to human-caused mortality (Woodroffe *et al.* 2007; Davies-Mostert *et al.*

352   2012) and thus it is essential that creation of corridors for large carnivore movement be paired

353   with efforts to mitigate human-carnivore conflict (Elliot et al. 2014).

354

355   *Caveats*

356   A number of caveats and assumptions to this work are important to note. First, this work is

357   focused on corridor design for terrestrial vertebrates, and not for entire community assemblages.

358   The latter would rely less upon single-species dispersal requirements than broader estimates of

359   structural connectivity, such as landscape 'naturalness' (Theobald *et al.* 2012). We also focus on

360   connectivity as viewed through movement corridors, rather than the more spatially-expansive

361   lens of habitat contiguity. The first emphasizes the maintenance of pathways for effective

362   dispersal between populations while the second seeks to preserve viable habitat to ensure

363   occupancy of a focal species across fragmented landscapes. This distinction is important in the

364   context of our review because resource selection functions or other general assessments of

365   habitat use may be effective on their own where the conservation goal is simply to preserve a

366   connected system of occupied habitats.

367

We chose to employ least-cost path (LCP) analysis for our case study because it is the most

popular method for managers to delineate corridors (Sawyer, Epps & Brashares 2011), however

it requires a number of assumptions that may not be upheld in all cases. First, it assumes a

defined start and end point, which is appropriate when determining a connection between two

protected areas, or in our case a natal and dispersal range, but this assumption is often violated

when clear habitat patches cannot be demarcated. Similarly, LCP analysis cannot evaluate

multiple potential pathways between more than two patches. In addition, by weighting the

cumulative cost of a pathway by its total Euclidean distance, LCP analysis implicitly assumes

that animals have total knowledge of their landscape, which is especially likely to be violated

when animals are dispersing into new territory. Ultimately, when evaluating whether to use a

least-cost or alternative approach such as circuit-theory modelling, the movement ecology of the

focal species and the landscape context are key determinants that should be considered

(McClure, Hansen & Inman 2016).

381

A final and important limitation to our case study is the small number of known dispersal paths

for our study animals, despite data collection over a four-year period, highlighting the challenge

of collecting long-distance movement data for evaluating functional landscape connectivity.

Efforts such as ours to directly compare behaviour-informed predictions of connectivity with

known long-distance dispersal movements are accordingly rare. Nevertheless, the strong effect

sizes of our model validation metrics lend confidence to our inference that consideration of

behavioural state is critical, and that by focusing connectivity analyses on movement behaviour,

researchers can eliminate much of the noise that comes from analysing all data points.

390

391   *Conclusions and future directions*

392   While the protection of corridors for animal movement involves sociopolitical, economic and

393   other considerations that were not addressed in this assessment, our review and case study

394   suggest that the success of corridor efforts relies on an accurate understanding of how animals

395   move through their environment. Resource selection within an animal's home range may be a

396   suitable proxy for movement preference during dispersal for some species (Fatterbert *et al.*

397   2015), though researchers and conservation practitioners should be aware this is not always the

398   case and failure to recognize this distinction may have important consequences for preserving

399   landscape connectivity. Our findings underscore the need for examining animal movement in

400   appropriate behavioural contexts to ensure effective application of resource selection analyses

401   for corridor planning. Advances in monitoring technology are fostering new opportunities to

402   study wildlife movements that promise to enhance corridor conservation. At the same time,

403   current analytical tools that rely on indirect location data can be improved to more accurately

404   inform connectivity models. Given limited conservation resources and rapidly changing

405   environments, efficient and accurate corridor identification, establishment and management is a

406   critical need in conservation planning. Unifying the fields of movement ecology and connectivity

407   science promises to advance our knowledge of – and thus our ability to preserve – the

408   fundamental process of wildlife movement.

409

420

421   **DATA ACCESSIBILITY**

422   Movement data will be archived in MoveBank's online database, www.movebank.org.

423

424   **SUPPORTING INFORMATION**

425   Additional supporting information may be found in the online version of this article.

426   **Appendix S1.** Detailed methods for African wild dog case study.

427   **Table S1.** Pack identities and data collected per collared individual.

428   **Table S2.** AIC model selection results for step selection functions.

429   **Table S3.** Step selection parameter estimates.

430   **Table S4.** Results of sensitivity analysis for 1-hour fix intervals.

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659

660 **Table 1.** Summary of studies evaluated that used resource selection analyses to model connectivity for wildlife movement.

Study	Species	Data Collected	RSF Type[1]	Consideration of Movement Behavior	Validation of Connectivity Predictions with Independent Movement Data
Braaker *et al.* 2014	*E. europaeus*	Relocation – GPS	PSF	None	None
Brodie *et al.* 2014	*H. derbyanus; H. malayanus; N. diardi; R. unicolor; M. nemestrina*	Detection – Camera trap	PSF	None	None
Carvalho *et al.* 2015	*G. genetta*	Relocation – VHF	PathSF	None	None
Chetkiewicz & Boyce 2009	*U. arctos; P.concolor*	Relocation – GPS	PSF	None	None
Clark *et al.* 2015	*U. americanus luteolus*	Relocation – GPS	SSF	Removed relocations <100 m apart	None
Cushman & Lewis 2010	*U. americanus*	Relocation – GPS	PathSF	None	None
Elliot *et al.* 2014	*P. leo*	Relocation – GPS	PathSF	Resource selection of dispersing individuals	None
Harju *et al.* 2013	*C. urophasianus*	Relocation – GPS	SSF	Resource selection during traveling and relocating states	Validated with independent GPS data in traveling and relocating states
Kautz *et al.* 2006	*P. concolor coryi*	Relocation – VHF	PSF	None	None
Kindall & Manen 2007	*U. americanus*	Relocation – VHF	PSF	None	None
LaPoint *et al.* 2013	*M. pennanti*	Relocation – GPS	PSF	None	Validated with 'animal-defined' corridors based on rate of fast, linear movement
Mateo-Sánchez, Cushman & Saura 2014	*U. arctos*	Detection - Sign	PSF	None	None
McClure, Hansen & Inman 2016	*C. elephas; G. gulo*	Relocation – GPS, VHF	PSF	Resource selection for migratory or dispersal-related movements	Validated with independent GPS data for long-distance movements
O'Brien *et al.*	*R. tarandus caribou*	Relocation – GPS	PSF	None	None

Proctor *et al.* 2015	*U. arctos*	Relocation – GPS	PSF	None	None
Pullinger & Johnson 2010	*R. tarandus caribou*	Relocation – GPS	SSF	Resource selection during large-scale movements	Validated with independent GPS data identified as long-distance moveme...
Reding *et al.* 2013	*L. rufus*	Relocation – VHF	PathSF	None	None
Richard & Armstrong 2010	*P. longipes*	Relocation – VHF	SSF	Resource selection of dispersing individuals	None
Roever, van Aarde & Leggett 2013	*L. africana*	Relocation – GPS	PSF	None	None
Squires *et al.* 2013	*L. canadensis*	Relocation – GPS	SSF	Resource selection during movement state	None
Sutcliffe *et al.* 2003	*A. hyperantus; H. virgaureae*	Relocation – Mark-recapture	MSF	Resource selection for matrix with highest passage rates	None
Thatcher, van Manen & Clark 2009	*P. concolor coryi*	Relocation – VHF	HSF	None	None
Trainor *et al.* 2013	*P. borealis*	Relocation – VHF	PSF	Resource selection of dispersing individuals	Validated with frequency of dispersal events within predicted corridors
Verbeylen *et al.* 2003	*S. vulgaris*	Detection - Sign	MSF	None	None
Walpole *et al.* 2012	*L. canadensis*	Detection - Sign	PSF	None	None
Wang *et al.* 2014	*A. melanoleuca*	Detection – Camera Trap	PSF	None	None
Zeller *et al.* 2014	*P. concolor*	Relocation – GPS	PSF	Resource selection during movement state	None
Zeller *et al.* 2015	*P. concolor*	Relocation – GPS	SSF, PathSF	Removed relocations <200 m apart	None

661 [1]PSF = point selection function, SSF = step selection function, PathSF = path selection function, MSF = matrix selection function, HSF = home

662 range selection function (categories as defined by Zeller et al. 2012).

Table 2. Landscape variables used to quantify resource selection of African wild dogs.

Category	Variable Name	Description	Source
Habitat Cover	Swamp	Moist and seasonally flooded floodplains	Broekhuis *et al.* 2013
	Grassland	Former floodplains characterized by shrubbed grassland	
	Woodland	Mixed woodland dominated by *Acacia* spp.	
	Mopane	Woodland composed primarily of *Colophosphermum mopane* shrubs and trees	
Land Use Type	Game Reserve	IUCN Category IV Protected Area	Botswana Department of Lands
	National Park	IUCN Category II Protected Area	
	Wildlife Management Area (WMA)	Community-managed land gazetted for photographic and hunting tourism	
	Pastoral	Non-wildlife area dominated by pastoralism	
Anthropogenic Features	Road	Distance to nearest road	Okavango Delta Information System
	Settlement	Distance to nearest human settlement	

Table 3. Percentage overlap between least-cost corridors (LCC) and GPS points along observed dispersal paths, and path deviation between modelled and observed paths with p-values indicating significant differences between model performance.

	LCC Overlap	Path Deviation		
Model	*%*	*Mean (km)*	*SD*	*p*
Path 1- Movement	62	7.16	2.28	<0.001
Path 1- Combined	0	25.5	3.18	
Path 2- Movement	100	2.65	1.92	<0.001
Path 2- Combined	0	29.8	6.08	
Path 3- Movement	100	.34	.75	0.07
Path 3- Combined	100	1.93	1.55	

Table 4. Approaches for using movement behaviour to inform connectivity conservation.

| Approach	Description	# Studies	Example studies
Behavioral	Use localities when the individual is in a traveling/exploratory state versus a resource use state	7	Pullinger & Johnson 2010; Squires et al. 2013; Zeller et al. 2014
Demographic	Use localities from dispersing vs. resident individuals in the population	3	Elliot et al. 2014; Richard & Armstrong 2010; Trainor et al. 2013
Seasonal	Collect location data during the known dispersal season	3	Cushman and Lewis 2010; Roever et al. 2013; Walpole et al. 2012
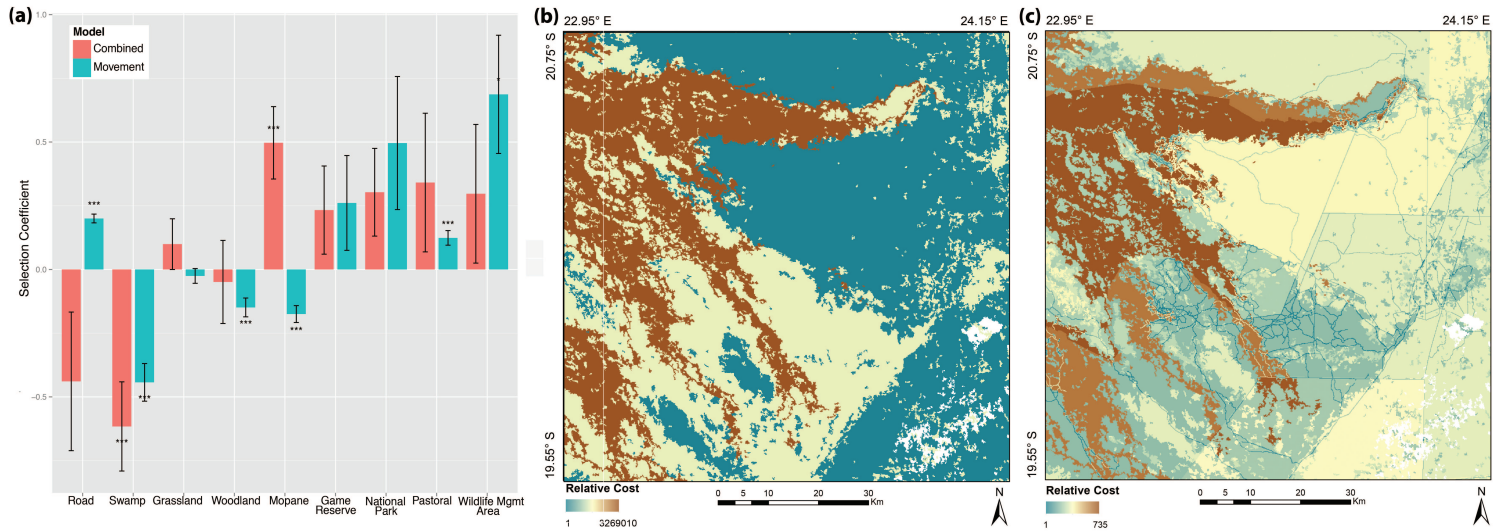
Figure 1. (a) Comparison of step selection parameter estimates and standard errors for the combined
model, measuring resource selection for all location data independent of behavioural state, and the
movement model, measuring resource selection only when wild dogs were in a 'traveling' behavioural
state (see Table S3 for listed values). Negative selection coefficients indicate avoidance of corresponding
landscape variables; positive values indicate selection for corresponding variables. P-values were
calculated from Wald tests. (b) Resistance surface derived from significant selection coefficients (p<0.05)
in the combined model. Resistance values were calculated as the inverse of scaled 'probability of use'
values $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + ...)$ where β_i is the selection coefficient for landscape variable x_i. Blue
cells and orange cells indicate low and high resistance to movement, respectively. (c) Resistance surface
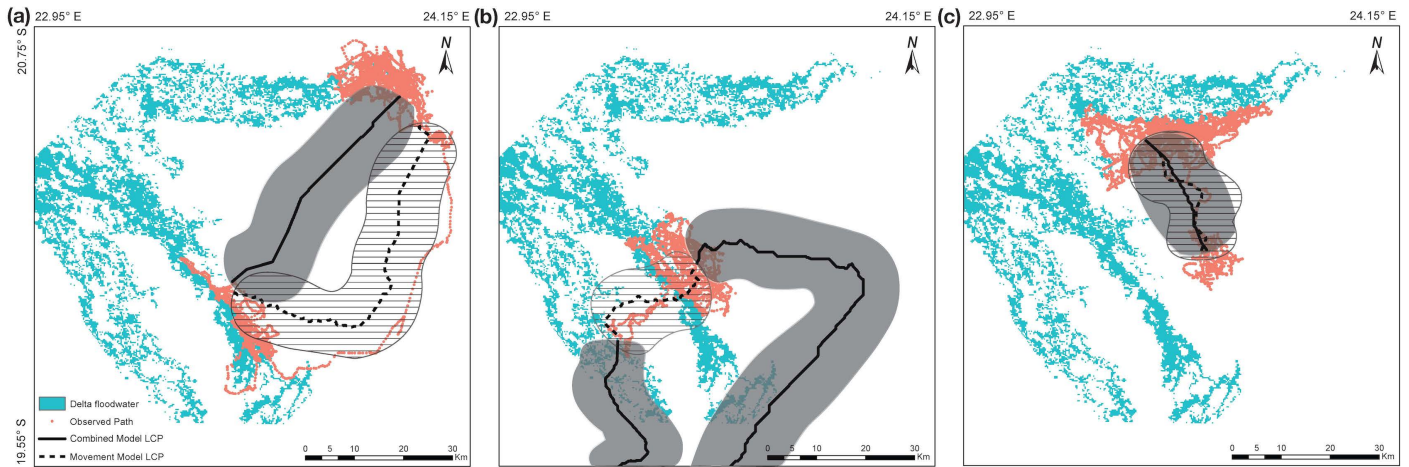derived from significant selection coefficients in the movement model.

Figure 2. Comparison between least-cost corridors derived from combined model (solid black lines), movement model (dashed black lines), and GPS-captured paths (orange dots) from three distinct dispersal events in (a) October 2014, (b) August 2013 and (c) January 2012 (Table S1). Okavango Delta floodwaters (light blue) are included for spatial reference.
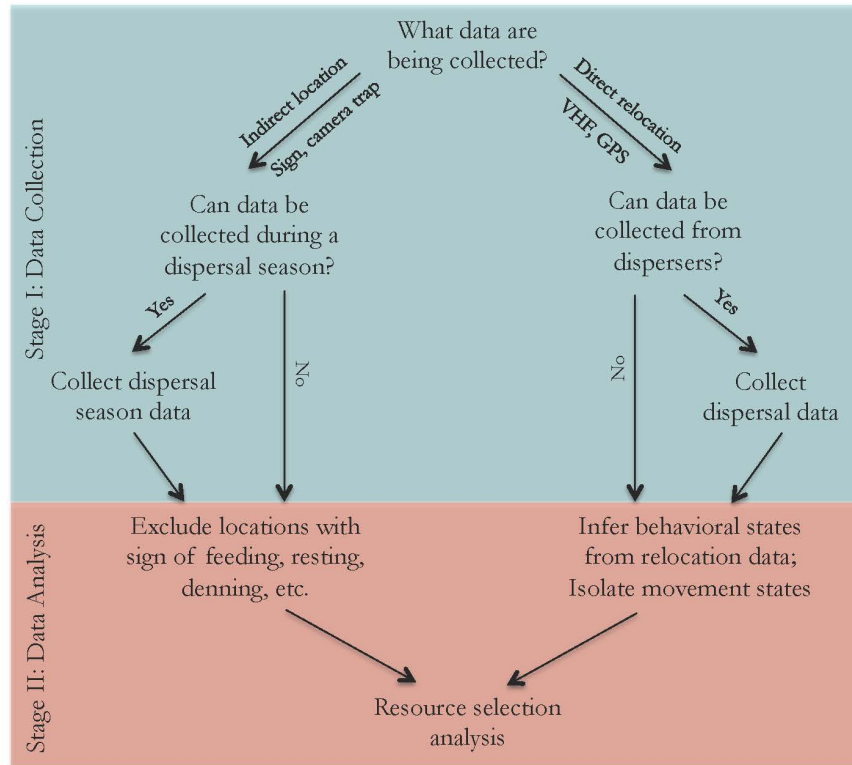
Figure 3. A decision tree for focusing resource selection analyses on animal movement for connectivity planning. At the data collection stage, decisions are made as to the type of data that can be collected and whether collection can be targeted toward dispersal seasonally or demographically. At the data analysis stage, the collected data can be analysed and cleaned to isolate locations for movement before inputting the dataset into a resource selection analysis.