

1 **Marine subsidies, spatial heterogeneity, and territoriality drive trophic ecology in**  
2 **desert predators**

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14

15 **Abstract**

16 1. Allochthonous (including marine) subsidies can have far-reaching effects on recipient  
17 ecosystems. By altering local resource availability, the combined effects of these  
18 subsidies and landscape heterogeneity can structure consumer diets, shape  
19 communities and influence ecosystem dynamics.

- 20 2. We examined how marine subsidies, landscape heterogeneity, and territoriality drive  
21 resource use in desert carnivorans. Specifically, we used stable isotope analysis to  
22 determine how patchily distributed colonies of Cape fur seals (*Arctocephalus pusillus*  
23 *pusillus*) along the coastal Namib Desert influence the diet and dietary niches of  
24 territorial and variably social brown hyenas (*Parahyaena brunnea*) and black-backed  
25 jackals (*Lupulella mesomelas*), which can forego territoriality around rich resource  
26 clumps.
- 27 3. Dietary niches of brown hyenas expanded with greater distance to the coast, while  
28 seal consumption was highest at colonies (64% [50–75]), slightly lower at coastal  
29 sites (50% [33–65]) despite their proximity to colonies, and lowest inland (11% [2–  
30 26]). Heterogeneity in marine resource distribution thus played a strong role in  
31 driving diet at fine spatial scale, suggesting a departure from the resource dispersion  
32 hypothesis. By contrast, all studied black-backed jackals resided within travel  
33 distance of a seal colony, and exhibited a particularly narrow dietary niche, showing  
34 extreme reliance on Cape fur seals (75% [69 - 81]), consistent with a territoriality  
35 breakdown in response to abundant, patchy food.
- 36 4. The diet and dietary niche variation of brown hyenas likely reflected the effects of  
37 landscape heterogeneity, territoriality, opportunistic foraging, and scarcity of  
38 terrestrial resources. Consistent with optimal foraging theory, the abundance of seals  
39 largely subsidized both terrestrial species, precluding exploitation competition, but  
40 offering context for aggression due to higher encounter rates at seal colonies.

41           5. By integrating landscape and trophic ecology, our study underscores the crucial role  
42           of marine subsidies in shaping terrestrial communities and provides new insight into  
43           understanding variation in the realized niche of carnivorans.

44

45 **Key-words:** black-backed jackal, brown hyena, landscape heterogeneity, niche ecology, stable  
46 isotope analysis

#### 47 **Introduction**

48           Transboundary movements of allochthonous resources (i.e., organisms or other organic  
49 material entering a recipient ecosystem from a donor ecosystem) may create a strong linkage  
50 between ecosystems, which can profoundly affect the food webs of recipient ecosystems (Polis  
51 et al., 1997). Allochthonous subsidies may impact populations either directly (Leighton et al.,  
52 2024; Polis & Hurd, 1996; Rose & Polis, 1998) or indirectly, such as through a predator’s  
53 numerical response to allochthonous prey or carrion (e.g., Johnson-Bice et al., 2025; Spiller et  
54 al., 2010). The magnitude of the effects of allochthonous resources can depend on consumer  
55 characteristics (including trophic level, degree of specialization, behavior, or capacity for  
56 resource exploitation) or specific ecological context, (i.e., quality, timing, duration, frequency, or  
57 predictability of these subsidies; Subalusky & Post, 2019). The effects of allochthonous  
58 resources are usually strongest when the recipient ecosystem has low levels of similar  
59 resources, or when the elongated or fragmented boundaries of the recipient ecosystem magnify  
60 exposure to external inputs (Atkinson et al., 2017; Marczak et al., 2007; Subalusky & Post,  
61 2019). Coastal ecosystems are thus particularly likely to receive allochthonous subsidies, which  
62 can represent an important dietary component for terrestrial predators (Carlton & Hodder,  
63 2003; Darimont et al., 2009; Leighton et al., 2024).

64           In resource-poor ecosystems, subsidization by high-quality allochthonous resources may  
65 promote intra- and interspecific competition between consumers (Darimont et al. 2009,  
66 Subaluský & Post, 2019), which in turn, can promote dietary-niche variability within a  
67 population. For example, in British Columbia, wolves (*Canis lupus*) on islands adjacent to the  
68 mainland have wider isotopic niche breadths than wolves from the mainland or remote islands.  
69 This niche differentiation likely reflects a combination of relaxed interspecific competition,  
70 increased intraspecific competition for ungulates, and access to both terrestrial and marine  
71 resources (Darimont et al., 2009). While allochthonous resources are recognized as key drivers  
72 structuring animal communities, their influence on trophic ecology is rarely examined alongside  
73 local- and individual-scale ecological drivers. Yet diet and intrapopulation dietary-niche variation  
74 likely result from interacting ecological drivers across scales, including landscape characteristics,  
75 inter- and intraspecific interactions, and consumer traits (Marczak et al., 2007). Here, we assess  
76 how spatially clustered marine resources shape the trophic ecology and interactions of two  
77 sympatric desert carnivorans with contrasting territorialities and foraging strategies, the brown  
78 hyena (*Parahyaena brunnea*) and the black-backed jackal (*Lupulella mesomelas*).

79           The Namib Desert coastline represents an ecotone between the highly productive  
80 southern Atlantic Ocean (Huntley, 2023; Ward et al., 1983) and a hyper-arid, unproductive  
81 desert, with the former subsidizing the latter. About 1.7 million cape fur seals (*Arctocephalus*  
82 *pusillus pusillus*) aggregate year-round into colonies along the coastline of southwestern Africa  
83 (Curtis et al., 2021). In Namibia colonies occupy the mainland or nearby offshore islands and,  
84 together with seabird colonies (e.g., cormorants, *Phalacrocorax sp.*), provide abundant food  
85 resources for terrestrial carnivorans (Skinner et al., 1995; Stander, 2019; Wiesel, 2010). These

86 marine resources promote landscape heterogeneity, which likely influences predator space use,  
87 diet and/or territoriality (Macdonald & Johnson, 2015). The near-complete absence of fresh  
88 water in the coastal Namib limits habitat suitability to species capable of surviving without  
89 drinking water (Eckardt et al., 2013; Mitchell et al., 2020). Consequently, large-bodied terrestrial  
90 prey species are sparse and include springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*),  
91 lagomorphs (*Lepus capensis*, *Pronolagus sp.*), and rodents (Skinner et al., 1995). Large  
92 carnivorans, like lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*) and leopards (*Panthera*  
93 *pardus*), remain dependent on rainfall (for vegetation cover and prey availability) and drinking  
94 water, which excludes them from the coastal central and southern Namib (Edwards et al., 2016;  
95 Heydinger et al., 2016; Portas et al., 2022; Skinner & Van Aarde, 1981). Because they can forgo  
96 drinking water (Loveridge & Nel, 2004; Skinner & Van Aarde, 1981), the brown hyena, with a  
97 body mass of around 40 kg, is the apex predator in this system, while the black-backed jackal,  
98 with a body mass of about 6-8 kg, is the only mesopredator.

99         Brown hyenas usually live in clans of up to 10 individuals (Mills, 1989; Wiesel, 2006) that  
100 cooperate to raise young and defend their territories (Goss, 1986). Clan members deposit lipid-  
101 rich pastes or use latrines to scent mark territories, especially near borders or resource  
102 hotspots, to effectively deter intruders (Gorman & Mills, 1984). Some adults (mostly males,  
103 which can become nomadic) and dispersing subadults of both sexes can live solitarily (either  
104 permanently or until immigrating into a non-natal clan). All brown hyenas forage alone,  
105 predominantly scavenging vertebrate carrion or opportunistically hunting small-bodied animals,  
106 sometimes across vast areas (Edwards et al., 2020; Mills, 1982, 1989). Hyenas more often  
107 display social dominance within clans when food is concentrated due to higher encounter rates

108 between individuals (Goss, 1986; Owens & Owens, 1978). In the Namib, dominance is usually  
109 ritualized and the outcome is driven by age and size (Goss, 1986). Near the Namib desert's  
110 coast, brown hyenas rely heavily on seal pups (Kuhn et al., 2008; Skinner et al., 1995), which  
111 they hunt year-round, even as the pups grow older and the hunt becomes increasingly difficult  
112 (Wiesel, 2010). Reliance on these qualitative marine subsidies may vary among individuals,  
113 based on distance to the nearest seal colony or whether a clan territory includes a seal colony.  
114 While some clans can defend these valuable resources, and thus may rely on seals more  
115 exclusively, clans lacking regular access to a seal colony, nomadic males, and other solitary  
116 individuals may need to consume a broader range of prey. Consuming larger quantities of high-  
117 quality prey may have important consequences, such as improving body condition. Conversely,  
118 for a solitary forager, individuals in better body condition may be more capable of acquiring and  
119 defending access to high-quality prey, suggesting a potentially reciprocal relationship between  
120 prey use and body condition.

121 Like brown hyenas, black-backed jackals are also social, but they typically live in  
122 monogamous pairs or small family groups in which yearlings may stay as helpers. They can  
123 forage in groups or alone, opportunistically hunting a variety of small animals, scavenging  
124 vertebrate remains, or even eating plant material (Goldenberg et al., 2010; Stuart, 1976). Black-  
125 backed jackals can also kill young seal pups or other large prey, albeit not often (Hiscocks &  
126 Perrin, 1987; Kamler et al., 2010; Kolar, 2005). Large seal colonies attract jackals from home  
127 ranges up to 20 km away (Jenner et al., 2011; Wiesel, 2006). This patchy, highly abundant  
128 resource can lead to large aggregations of jackals and a breakdown of their territoriality (Jenner  
129 et al., 2011; MacDonald, 1983; Nel et al., 2013).

130           Here, we use stable isotope analyses to examine how clumped marine resources impact  
131 the diet and dietary niches of brown hyenas and black-backed jackals, two carnivorans  
132 exhibiting contrasting territoriality. A brown hyena clan that defends a seal colony ensures its  
133 members regular access, whereas frequency of access for other individuals likely depends on  
134 their distance to the nearest colony. Territorial defense and opportunistic incursions by  
135 neighboring individuals may further modify access locally. We hypothesize that territory-  
136 mediated access to marine resources structures hyena diet, leading to dietary niche differences  
137 (and thus differences in body condition) that reflect the patchy distribution of seal colonies  
138 (H1). Given that jackals can relax territoriality when food is clumped and abundant (whereas  
139 hyenas cannot), they should maximize exploitation of marine resources, leading to greater  
140 reliance on seal consumption than is seen in hyenas (H2). Finally, abundant marine subsidies  
141 should prevent dietary exclusion and promote shared prey use among these coexisting  
142 predators (H3).

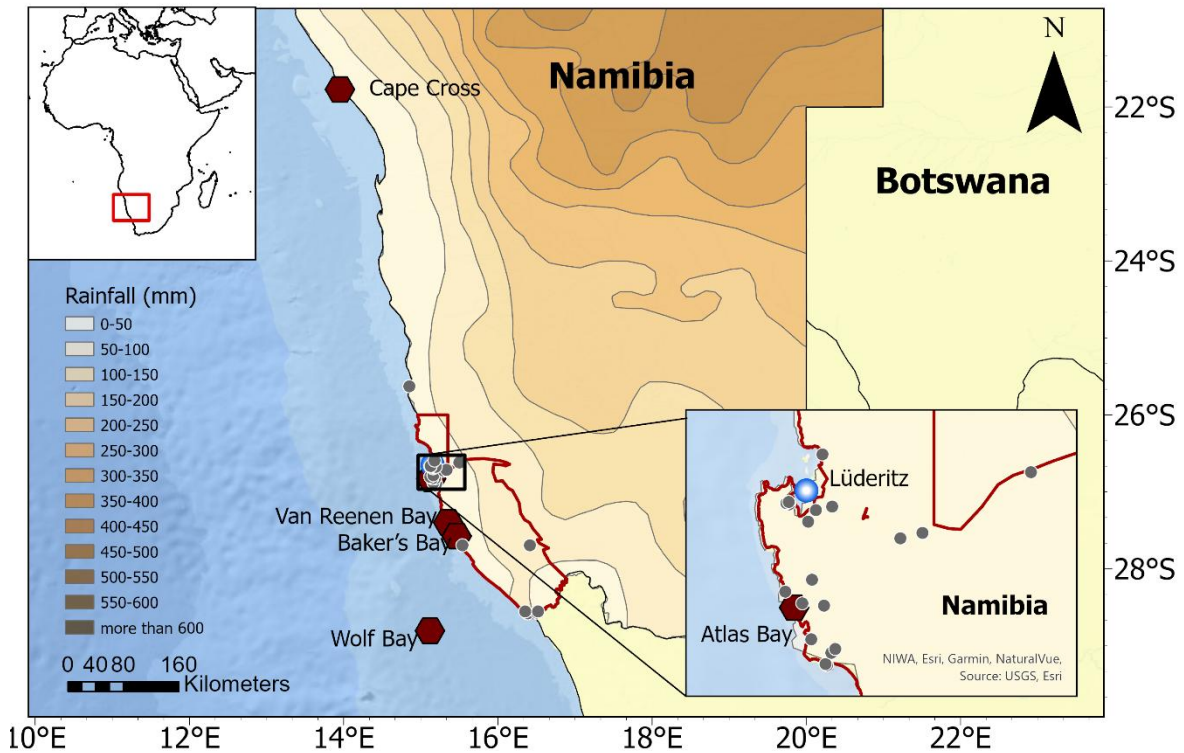
143           In accordance with H1, we predict 1) reduced seal consumption in hyenas that lack  
144 territorial access or have greater travel distance to seal colonies (reflecting broader-scale  
145 patterns), and 2) reduced body condition in individuals that have limited seal access, due to  
146 scarcity of alternative, terrestrial resources. In accordance with H2, we predict 3) a greater  
147 proportion of marine subsidies in jackals residing within travel distance from seal colonies  
148 (which included all those captured in this study) compared to that in hyenas. Using isotopic  
149 niche as a proxy for dietary niche, we further predict that isotopic niche breadth 4) increases in  
150 hyenas from coast to inland (H1) and 5) is narrower in jackals, largely overlapping with that of  
151 coastal hyenas (H2 and H3).

152

153 **Methods**

154 *Study areas*

155           This study was conducted in Namibia, in the Tsau //Khaeb (Sperrgebiet) National Park  
156 and along the coast between the park and the Cape Cross Seal Colony (Fig. 1), in the south-  
157 western part of the Namib Desert. The Namib Desert extends as a long (> 2,000 km) and narrow  
158 (< 200 km wide) strip along the coast of southwestern Africa, from the Carunjamba River in  
159 Angola to the Olifants River in South Africa (Ward et al., 1983; Nel et al. 1997; Huntley, 2023).  
160 The cool (annual mean temperature ~15°C), hyper-arid, coastal desert receives < 100mm of  
161 precipitation per year (Ward et al., 1983; Huntley, 2023). The Namib climate is mostly  
162 maintained by three interacting atmospheric and oceanic processes: the offshore South Atlantic  
163 Anticyclone, the Benguela Upwelling current, and the winds that these two processes generate  
164 (Ward et al., 1983; Huntley, 2023).



165  
 166 **Fig. 1.** Map of the study area. The borders of the Tsau//Khaeb (Sperrgebiet) National Park are  
 167 depicted in red. Seal colonies are represented by red hexagons, and hyena samples are grey  
 168 points. All jackal samples were collected at the Cape Cross seal colony or near Lüderitz (blue  
 169 circle). The rainfall layer was obtained at [https://www.uni-](https://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia/e1_download_climate_e.htm#annual_rainfall)  
 170 [koeln.de/sfb389/e/e1/download/atlas\\_namibia/e1\\_download\\_climate\\_e.htm#annual\\_rainfall](https://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia/e1_download_climate_e.htm#annual_rainfall)  
 171 (Accessed 2026-03-27).

172

173 *Sample and data collection*

174 From 2000 to 2004, we collected hair samples from the back of live animals (18 brown  
 175 hyenas and 54 jackals) captured using cage traps, modified foot snares (Frank et al., 2003),  
 176 padded softcatch foothold traps (No.4 Victor Softcatch, coil spring, Woodstream Corporation,  
 177 Lititz, Pennsylvania, USA) or darted during concurrent studies (Gowtage-Sequeira, 2004; Wiesel,  
 178 2006), and from carcasses of 23 hyenas that were roadkill or died from natural causes. Live-

179 captured animals were anesthetized using species-appropriate drugs and protocols (details on  
180 anesthesia in Gowtage-Sequeira (2004) and Wiesel et al. (2018)) and their health status was  
181 assessed. Jackals were trapped near Lüderitz or Cape Cross Seal Reserve (Fig. 1). Capture and  
182 handling of live animals was performed under the Namibian Ministry of Environment and  
183 Tourism permits 549/2001/2002-3, 33806, 421/2001, 548/2002, 693/2003 and 784/2004, and  
184 under Duke Institutional Animal Care and Use Committee protocol A190-02-06. Biological  
185 samples were imported into the U.S.A. under Federal Fish & Wildlife Management permit  
186 037014-2.

187 *Brown hyenas.*— Most of the hyenas were individually known (from unique stripe  
188 patterns) and regularly followed, yearly, as part of a long-term survey established in 1997. For  
189 each sample obtained, we recorded latitude and longitude as a proxy for the animal’s foraging  
190 range (Fig. 1). We anticipated that landscape heterogeneity interacting with territoriality could  
191 create non-linear patterns of seal accessibility: some coastal individuals without regular access  
192 to a seal colony could access marine resources washed up on the shore. Life history data for  
193 most individuals (Wiesel, 2006; Spagnuolo et al., 2022) thus allowed us to classify accessibility  
194 to a seal colony (hereafter “access to seals”): “inland” (territory location did not enable access  
195 to seals), “coastal” (territory location enabled access to the coast but not to seals), “colony”  
196 (territory location enabled regular access to seals), “unknown” (the hyena was not a known  
197 individual). Whenever possible, we recorded body mass (kg), neck circumference (cm), age  
198 estimate (class), and sex. Age class was estimated using dental eruption and tooth wear (Mills,  
199 1982; Wiesel et al., 2018) or using cementum annuli counts by Matson’s lab (Manhattan,  
200 Montana, USA). Tooth wear can reduce the ability of hyenas to chew bones and is associated

201 with declines in body mass in older individuals, while age more generally may influence  
202 variation in body mass (Mills, 1982), providing a potential mechanism for age-related  
203 differences in diet. We subsequently classified the adults into two age classes: 4-6 years old  
204 ( $n_{\text{Female}} = 5$ ,  $n_{\text{Male}} = 11$ ,  $n_{\text{Unk}} = 1$ ), > 7 years old ( $n_{\text{Female}} = 13$ ,  $n_{\text{Male}} = 7$ ,  $n_{\text{Unk}} = 1$ ), referred to as  
205 “young” and “old” for simplicity. We determined body condition in hyenas *a posteriori* using the  
206 Scaled Mass Index (SMI) developed by Peig and Green (2009). Briefly, the SMI method estimates  
207 a scaling exponent between body mass and a linear morphometric measurement (here, we  
208 used neck circumference). Because we had to exclude individuals from specific analyses due to  
209 missing variables, we provide the sample size for each analysis separately.

210 *Black-backed jackals.*— Jackals were captured as part of an epidemiology study on canid  
211 pathogens (Gowtage-Sequeira, 2004). Due to logistical constraints of that study, all jackals were  
212 captured inside seal colonies, indicating that all individuals had their home range within reach  
213 of a major seal colony (Gowtage-Sequeira, 2004). Jackals were sexed and assigned to one of the  
214 following age categories: juveniles ( $n_{\text{Female}} = 6$ ,  $n_{\text{Male}} = 1$ ), subadults ( $n_{\text{Female}} = 9$ ,  $n_{\text{Male}} = 10$ ), or  
215 adults ( $n_{\text{Female}} = 9$ ,  $n_{\text{Male}} = 15$ ) based on a combination of tooth wear and body mass (Gowtage-  
216 Sequeira, 2004).

217 *Prey.*— We collected potential prey samples to compare their isotopic ratios with those  
218 of the consumers in our diet reconstruction. We obtained muscle samples from seals ( $n = 16$ )  
219 legally harvested in 2001 and 2003 by the Namibian Ministry of Fisheries and Marine Resources  
220 (Gowtage-Sequeira, 2004; Wiesel, 2006). In 2002-2004, we opportunistically collected muscle  
221 tissue from mussels ( $n = 5$ ), hair from gemsbok ( $n = 7$ ) and springbok ( $n = 2$ ), and feathers from

222 cormorants (n = 2) found dead throughout the study area, including at hyena dens. We further  
223 collected Tenebrionid sp. beetles (n = 2) and used their whole body.

224

#### 225 *Sample preparation and stable isotope value determination*

226 We washed hair and feather samples three times with soap and water to remove surface  
227 contaminating material, then rinsed them thoroughly. Once dried, hair was homogenized using  
228 sterilized scissors (Elliott et al., 2017). Muscle and Tenebrionid samples were freeze-dried and  
229 lipid-extracted with petroleum ether using a Soxhlet apparatus (Elliott et al. 2017). We then  
230 weighed between 0.4 and 0.6 mg of the prepared samples and measured their stable isotope  
231 ratios on a continuous flow isotope ratio mass spectrometer (Thermo Finnigan Delta plus)  
232 coupled to a Costech 4010 Elemental Combustion system and a ConFlo III gas interface at the  
233 University of Central Florida. Measurement precision was within 0.1 ppt for carbon and 0.2 ppt  
234 for nitrogen. Five hyenas were sampled two to three times to ensure consistency in sample  
235 measurement: we only kept their first measurement to avoid pseudoreplication.

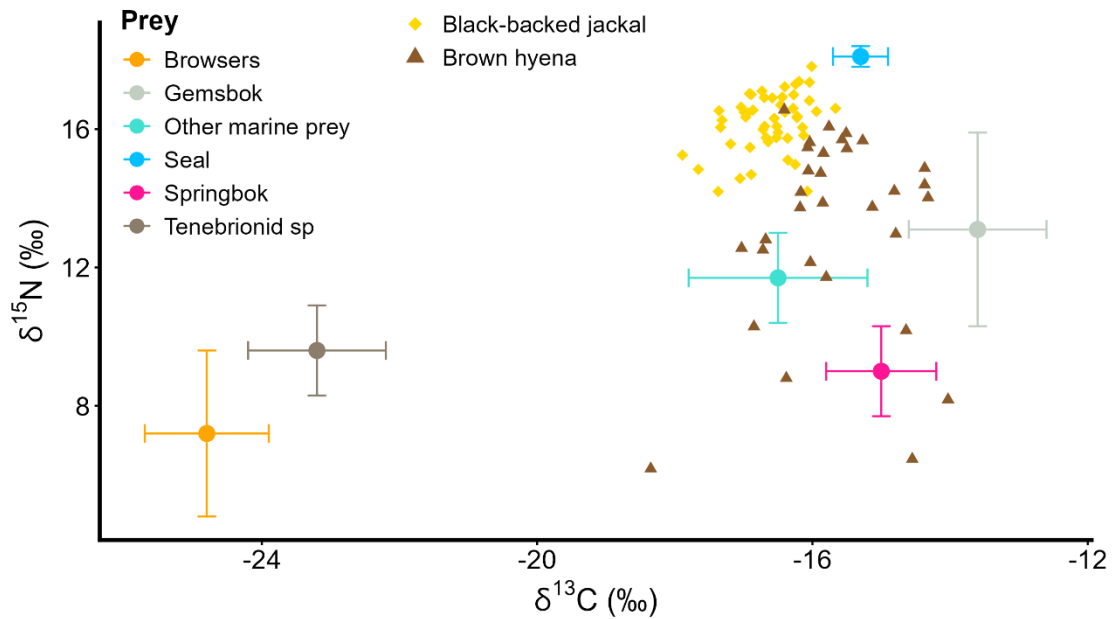
236

#### 237 *Diet reconstruction*

238 We used stable isotope analysis to reconstruct the diet of brown hyenas and black-  
239 backed jackals. We assessed the effect of covariates on diet composition by fitting species-  
240 specific Bayesian Mixing models using JAGS v.4.3.1 (Plummer, 2003) through MixSIAR v.3.1.12  
241 (Stock et al., 2018) in R v. 4.4.1 (R Core Team, 2024) within RStudio v. 2024.9.0.375 (Posit Team,  
242 2024). The Bayesian approach allows for the incorporation of prior information, uncertainty in

243 the parameter estimates, covariates, and variability within the consumer population (Stock et  
244 al., 2018; Stock & Semmens, 2016).

245 We used carbon (C) and nitrogen (N) stable isotope ratios ( $\delta^{13}\text{C} \sim ^{13}\text{C}/^{12}\text{C}$  and  $\delta^{15}\text{N} \sim$   
246  $^{15}\text{N}/^{14}\text{N}$ ) from hyena and jackal hair as our mixture and defined their isotopic space using  $\delta^{13}\text{C}$   
247 and  $\delta^{15}\text{N}$  from prey tissues (Fig. 2). Due to unknown molt patterns in both species, we could not  
248 determine the exact timeframe each hair sample represented. We, however, ensured adequate  
249 seasonal representation (hyenas:  $n_{\text{December-June}} = 19$ ,  $n_{\text{July-November}} = 23$ ; jackals:  $n_{\text{October-November}} =$   
250  $42$ ,  $n_{\text{July-August}} = 12$ ) and no bias regarding the factors used in our analyses. Collectively, the  
251 samples reflected the yearly diet for both species. We used the hair-to-diet trophic  
252 discrimination factor for carnivorans with a mixed (terrestrial and marine) diet from Stephens et  
253 al. (2022). We offset prey hair  $\delta^{13}\text{C}$  by  $-1.6\text{‰}$  (Codron et al., 2007), and cormorant feather  $\delta^{15}\text{N}$   
254 by  $-2\text{‰}$  (Vanderklift & Ponsard, 2003) to approximate prey muscle values. We assessed model  
255 fit and convergence using Gelman–Rubin and Geweke diagnostics, visual inspection of trace,  
256 autocorrelation, and running-mean plots to confirm stability and independence of posterior  
257 draws, effective sample sizes  $> 500$  for all variables, and verification that multiplicative error  
258 terms  $< 1$  or that their credible intervals included 1 (Stock et al., 2018; Stock & Semmens,  
259 2016).



260

261 **Fig. 2.** Stable carbon and nitrogen isotope data from prey tissue, brown hyena hair and black-  
 262 backed jackal hair, adjusted for diet–tissue discriminations. Hair and feather values of prey were  
 263 adjusted for muscle equivalent. We used muscle for fur seals, and whole body for Tenebrionid  
 264 sp. Data for browsers (bushbuck, steenbok and grey duiker) are from Codron et al. (2007), which  
 265 provided muscle-adjusted values.

266

267 We first tested if hyena diet depended on access to seals, grouping individuals by age  
 268 and sex to control for potential demographic effects ( $n_{F\text{-young}} = 5$ ,  $n_{M\text{-young}} = 11$ ,  $n_{F\text{-old}} = 10$ ,  $n_{M\text{-old}} =$   
 269 5). We selected prey to delimit the isospace based on dietary studies from our area (Kuhn et al.,  
 270 2008; Skinner et al., 1995) and stomach content of hyenas from this project (Appendix 1). We  
 271 thus included springbok, gemsbok, and seal from this study, as well as a “browser” category  
 272 from the literature (i.e., bushbuck, steenbok and grey duiker feeding predominantly on woody-  
 273 plant material; Codron et al. (2007). This browser isotopic values were close to those of our only  
 274 Cape hare sample, but provided a standard deviation to help inform uncertainty.

275 For hyenas, we ran 8 Bayesian mixing models across three sets of analyses. We first  
276 compared 6 models using the leave-one-out cross-validation approach ("LOOic"; Stock et al.,  
277 2018; Vehtari et al., 2017): no covariate (null model), age group (young vs. old), sex, age group +  
278 sex, access to seals (Colony, Coastal, Inland, and we coded "unknown" as a factor level to allow  
279 the model to run on the same data set, which is necessary to perform the leave-one-out cross-  
280 validation), age group + access to seals. Each of these models used three Markov Chain Monte  
281 Carlo (MCMC) chains of 6,000,000 iterations, with 5,000,000 burn-in, and thinning = 500.

282 We further designed two models using only three prey species (seal, springbok,  
283 browsers) to simplify the models and aid convergence. One model included distance-to-nearest  
284 seal colony (Box-Cox transformed Euclidean distance between sample location and nearest seal  
285 colony;  $n_{\text{hyenas}} = 34$ ) as a continuous covariate and age group as a fixed factor (three MCMC  
286 chains: iterations = 10,000,000, burn-in = 8,000,000 and thinning = 800). The other model  
287 included body condition index as a continuous covariate and access to seals as a random factor  
288 ( $n_{\text{hyenas}} = 24$ ; three MCMC chains: iterations = 6,000,000, burn-in = 5,000,000 and thinning =  
289 500). Although access to seals only had three levels, we modelled it as a random effect  
290 (Semmens et al., 2009) to account for variation in diet associated with seal access when  
291 estimating the relationship between body condition and diet.

292 To incorporate prior ecological knowledge of hyena diet into the mixing models, we  
293 informed Dirichlet vague priors by integrating four sources: stomach content from hyenas from  
294 this project (Appendix 1), feces content from Skinner et al. (1995), direct observations from  
295 Skinner & Van Aarde (1981), and remains at dens from Kuhn, Skinner & Wiesel, (2008). We used

296 the frequency of occurrence of major prey items reported in these four sources, which we  
297 multiplied by the number of prey and divided by the total number of samples (Appendix 2).

298         Based on dietary studies of jackals in our area (Goldenberg et al., 2010; Hiscocks &  
299 Perrin, 1987; Stuart, 1976) and preliminary model testing, we defined the prey isospace using  
300 seals, tenebrionid beetles, and an “other marine” category (i.e., mussels and cormorants). To  
301 identify drivers of jackal diet, we compared 6 models ( $n_{\text{jackals}} = 49$ ) using leave-one-out cross-  
302 validation: no covariate (null model), location (Lüderitz, Cape Cross Seal Reserve), sex + location,  
303 age (juvenile, subadult, adult) + location, age + sex, and body mass. We used vaguely  
304 informative Dirichlet priors based on the frequency of occurrence of major prey items in jackal  
305 feces (which we treated as explained for hyenas) at Cape Cross Seal Reserve (Hiscocks & Perrin,  
306 1987). We ran each jackal model with 3 MCMC chains: iterations = 900,000, burnin = 500,000,  
307 thinning = 400.

308

### 309 *Hyena body condition*

310         We tested if hyena body condition decreased with greater distance-to-coast by running  
311 two linear mixed models (link identity). Model 1 used distance-to-coast (shortest Euclidean  
312 distance from sample location to coast) as a predictor; model 2 used access to seals. Both  
313 models included the full dataset and controlled for repeated measures by including hyena ID as  
314 a random effect. Data exploration followed recommendations by Zuur et al. (2010). The models  
315 were run in R v.4.4.1 (R Core Team, 2024) within RStudio v.2024.9.0.375 (Posit Team, 2024)  
316 using glmmTMB v.1.1.9 (Brooks et al., 2017) with diagnostics via DHARMA v.0.4.7 (Hartig, 2024).

317

318 *Dietary niche breadth*

319 We used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic niche size and location as a proxy to estimate the dietary  
320 niche breadth and overlap of hyenas and jackals. Visual assessments using the packages MASS  
321 v.7.3.60.2 (Venables & Ripley, 2002) and threejs v.0.3.3 (Lewis, 2020) confirmed that the data  
322 conformed to a multivariate normal distribution. We then built two data sets to obtain dietary  
323 niche parameters of hyenas and jackals. One dataset grouped hyenas by age class and sex and  
324 pooled all jackals. The other dataset grouped hyenas by distance-to-coast normalized using a  
325 Box-Cox transformation. We binned distance measurements into four categories (< 1 km, 1-3  
326 km, 3-13 km,  $\geq 13$  km), which corresponded to a change of unit in the Box-Cox transformed  
327 values and ensured relatively balanced groups. The threshold of the last bin also corresponded  
328 to the average nightly distance traveled by hyenas (Skinner et al., 1995).

329 For both data sets, we estimated standard ellipse area using a Bayesian approach  
330 implemented in JAGS v.4.3.1 (Plummer, 2003) via package SIBER v.2.1.9 (Jackson et al., 2011).  
331 This approach produces unbiased results relative to sample size and allows direct quantitative  
332 comparison of ellipses while quantifying the uncertainty of the sampling process (Jackson et al.,  
333 2011). Posterior values of mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and the covariance matrix defining the standard  
334 ellipse, were estimated from MCMC simulations with vague normal priors on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
335 means, an Inverse-Wishart prior on the covariance matrix, and a multivariate normal  
336 distribution on the likelihood (Jackson et al., 2011). For our first model, we ran 3 chains of  
337 500,000 iterations, with burn-in = 250,000 and thinning = 10, while for our second model, we  
338 ran 3 chains with 200,000 iterations with burn-in = 100,000 and thinning = 10. We confirmed  
339 convergence visually using trace and density plots and ensuring a Gelman-Rubin statistic <1.01

340 for each parameter of each standard ellipse (Jackson et al., 2011). Bayesian standard ellipse  
341 areas ( $SEA_B$ ) are reported as mode estimates with their 95% credible interval (CI).

342 To compare standard ellipse areas between groups (species, demographics, or distance  
343 bins), we conducted pairwise comparisons of the posterior draws and determined the  
344 proportion of cases in which draws were smaller in one group than the other. We finally  
345 calculated ellipse overlaps between hyena-demographic groups and jackals based on 1,000  
346 draws from the posterior distribution of the means and covariance matrices of the Bayesian  
347 ellipses. The model thus produced a distribution of measures of area overlap between each pair  
348 of ellipses, from which we obtained a mean. For each pair of ellipse-area draws and their  
349 overlap, we computed directional overlaps as follows:

350 Proportion of hyena niche overlapped by jackal niche =  $area_{overlap}/area_{hyenas}$

351 Proportion of jackal niche overlapped by hyena niche =  $area_{overlap}/area_{jackals}$

352 We also provide an estimate of the proportion of mutual overlap between the isotopic niches of  
353 hyena groups and jackals as follows:

354 Proportion of mutual overlap =  $area_{overlap} / (area_{hyenas} + area_{jackals} - area_{overlap})$

355 where  $area_{overlap}$  is the area of overlap between the ellipses,  $area_{hyenas}$  the ellipse area of a given  
356 hyena group, and  $area_{jackals}$  the jackals' ellipse area. The mutual overlap index represents the  
357 total niche space that is shared, similar to the Jaccard index of similarity (Real & Vargas, 1996).  
358 Therefore, a proportion of 0 indicates complete separation, while a proportion of 1 indicates  
359 complete overlap. We summarized the proportion of dietary niche overlap by calculating the  
360 mean  $\pm$  SE, standard deviation and interquartile range (25<sup>th</sup>–75<sup>th</sup> percentiles) of the posterior  
361 estimates.

362

363 **Results**

364 *Diet reconstruction*

365 Hair isotopic values in hyenas varied geographically. Hair  $\delta^{13}\text{C}$  was slightly higher in  
366 colony ( $-11.34 \pm 0.19\text{‰}$ ) than coastal ( $-11.87 \pm 0.24\text{‰}$ ) hyenas, and lower in inland hyenas ( $-$   
367  $12.52 \pm 0.52\text{‰}$ ). Hair  $\delta^{15}\text{N}$  was the highest and least variable in colony hyenas ( $17.67 \pm 0.27\text{‰}$ ),  
368 followed by coastal ( $16.41 \pm 0.69\text{‰}$ ), and inland ( $12.10 \pm 1.09\text{‰}$ ) hyenas. When testing for  
369 effects of differential access to seals and differences between hyena demographic groups, the  
370 seal access model had the strongest support (lowest LOOic), with a weight of 60%, while the age  
371 + seal access model came second with a weight of 40% and a dLOOic of 0.8, indicating that this  
372 second model could not be ruled out (Table S1). Under the seal access model, seals and  
373 springbok comprised the bulk of the hyena diet, regardless of location (Table 1), with slight but  
374 non-negligible differences between colony and coastal hyenas, and a clear reliance on terrestrial  
375 prey for inland hyenas (Table 1). Under the age + seal access model, seal and springbok  
376 comprised the bulk (range: 91% - 96%) of the diet for both younger and older hyenas, regardless  
377 of location. Most of the difference in the relative-dietary contribution of seal and springbok was  
378 explained by access to seals but for hyenas with similar access to seals, older individuals relied  
379 on seal more than did younger individuals (Table 1). Younger and older hyenas consumed  
380 similarly low proportions of browsers.

381

382 **Table 1.** Relative dietary contribution (%) of seal, springbok, gemsbok, and browsers to the  
383 central Namib brown hyena population by age group (young < 7 years old and old  $\geq$  7 years old)  
384 given accessibility to a seal colony from their territory (Colony, Coastal, Inland). Population

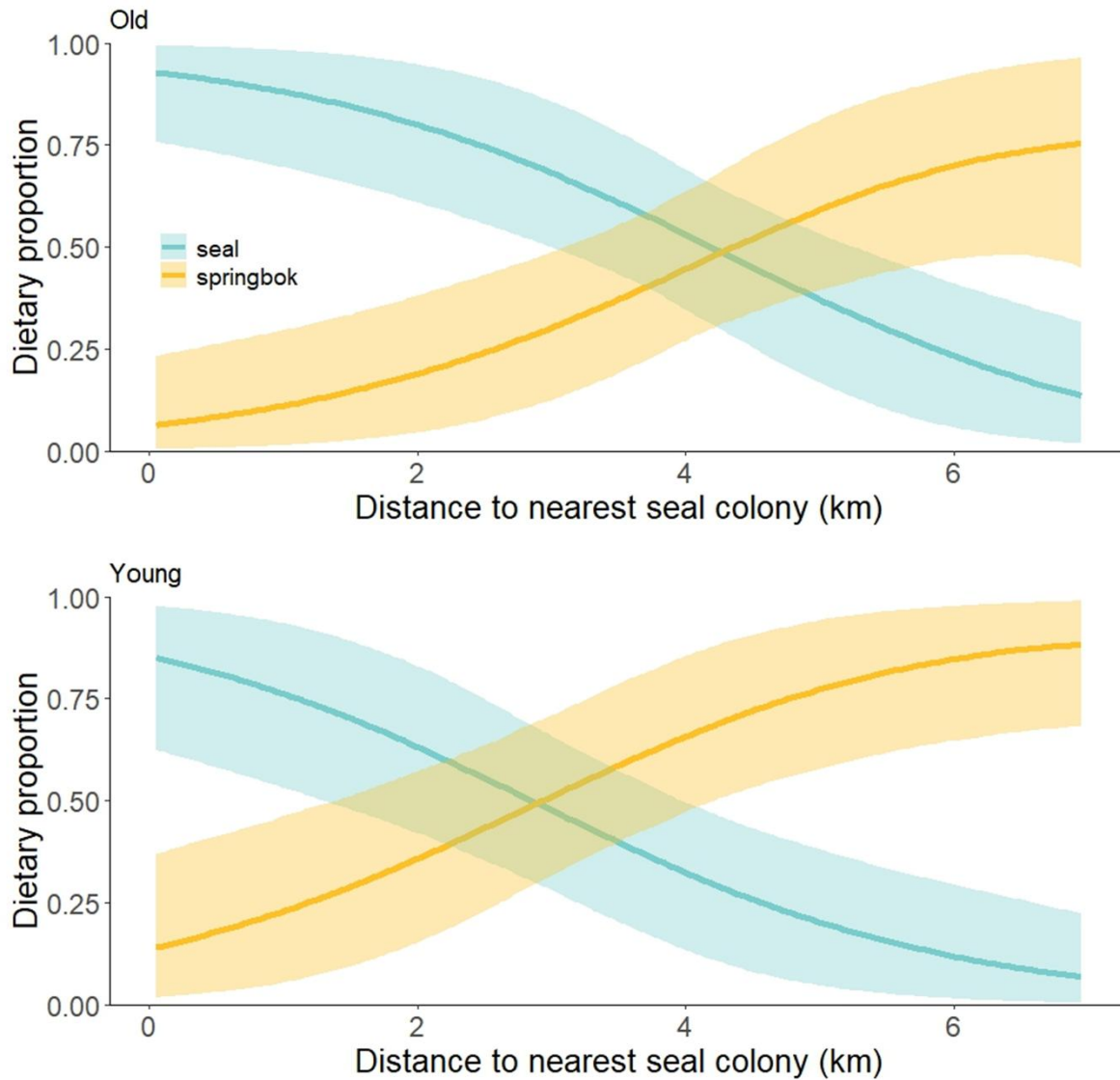
385 refers to the first model “seal access”. Old and Young values come from the “age + seal access”  
 386 model.

Access to seal colonies	Age group	Relative dietary contribution (mean [95% CI])			
		Seal	Springbok	Gemsbok	Browsers
<b>Colony</b>	<b>Population</b>	64 [50 - 75]	31 [14 - 44]	3 [0 - 26]	2 [0 - 7]
	Old	69 [50 - 85]	25 [6 - 41]	4 [0 - 33]	2 [0 - 7]
	Young	61 [43 - 74]	35 [17 - 51]	3 [0 - 25]	2 [0 - 7]
<b>Coastal</b>	<b>Population</b>	50 [33 - 65]	43 [23 - 62]	3 [0 - 25]	4 [0 - 13]
	Old	55 [35 - 74]	38 [13 - 59]	3 [0 - 30]	4 [0 - 12]
	Young	45 [25 - 63]	50 [28 - 71]	2 [0 - 18]	3 [0 - 13]
<b>Inland</b>	<b>Population</b>	11 [2 - 26]	80 [55 - 97]	2 [0 - 16]	6 [0-21]
	Old	15 [3 - 34]	76 [44 - 96]	3 [0 - 23]	6 [0 - 22]
	Young	10 [2 - 24]	84 [63 - 97]	1 [0 - 10]	4 [0 - 10]

387

388

389 When examining the effect of distance-to-nearest seal colony on hyena diet by age  
 390 group, we found that dietary proportions of seal decreased as hyenas were found farther from  
 391 the coast (Fig. 3). Consistent with the age + access to seals model reported above, we further  
 392 found that old and young hyenas had slightly different diets. Old hyenas consumed more seals  
 393 than springbok ( $\text{mean}_{\text{seal}} = 55\%$ , 95% CI: [37 - 71%];  $\text{mean}_{\text{springbok}} = 43\%$  [25 - 62%]), whereas  
 394 young hyenas consumed more springbok than seals ( $\text{mean}_{\text{seal}} = 34\%$  [15 - 51%];  $\text{mean}_{\text{springbok}} =$   
 395 64% [46 - 84%]. Consistent with our other models’ output, both young and old hyenas  
 396 consumed similarly low proportions of browsers ( $\text{mean}_{\text{young}} = 2\%$  [0 - 8%];  $\text{mean}_{\text{old}} = 2\%$  [0 -  
 397 8%]). Results of other models are provided in Table S1.



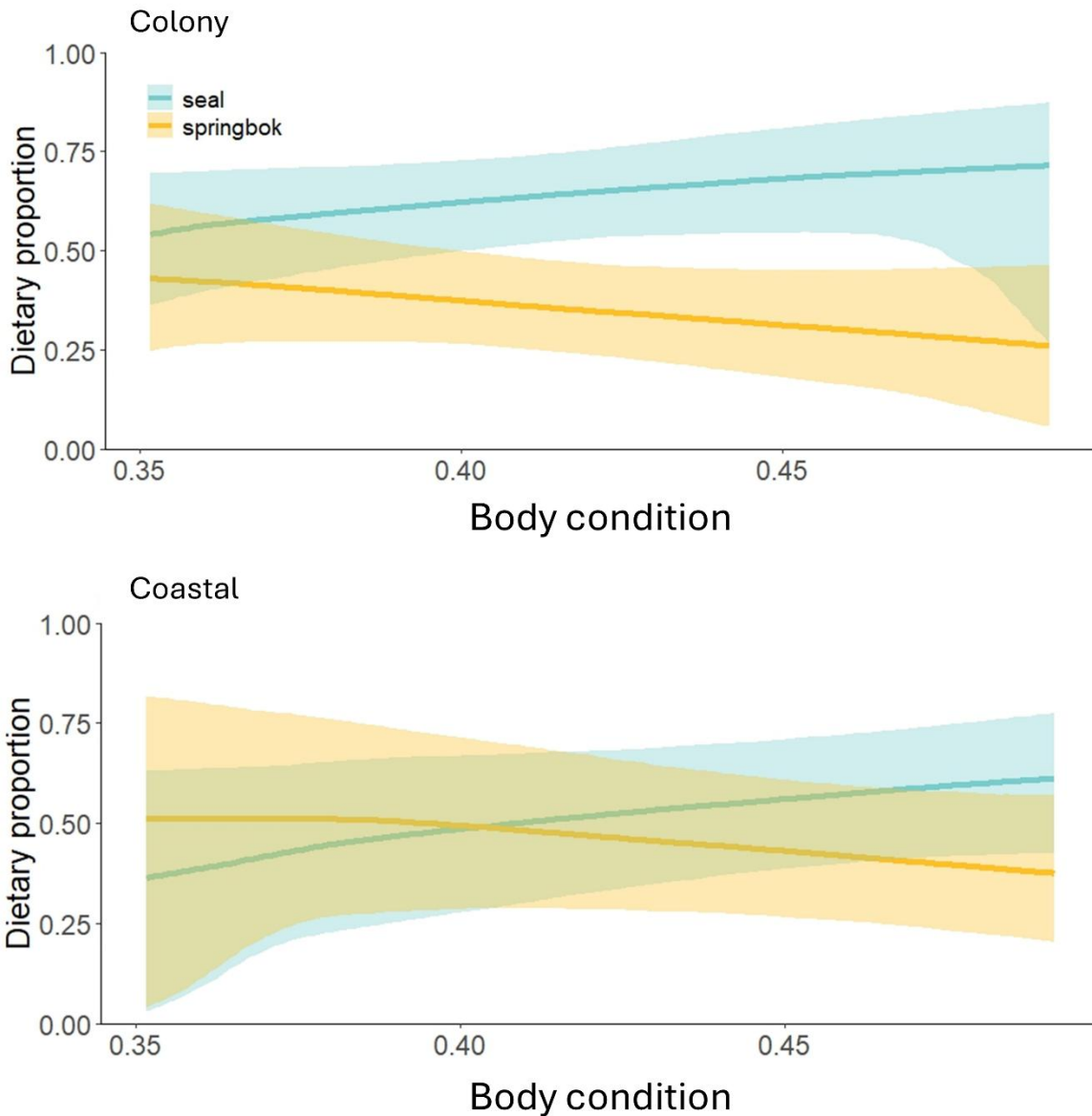
398

399 **Fig. 3.** Relation between the distance to the nearest seal colony on the consumption of Cape fur  
 400 seals and springbok by old ( $\geq 7$  years), and young ( $< 7$  years) brown hyenas.

401

402           When testing the effect of body condition on diet while controlling for access to seals,  
 403 we found that hyenas in better body condition consumed more seals (Fig.4). Among colony  
 404 hyenas, predicted dietary proportions shifted from an approximately equal contribution of seals  
 405 and springbok at low SMI values to diets clearly dominated by seals at high SMI values. Among  
 406 coastal hyenas, individuals in poorer body condition consumed proportionally more springbok

407 and less seal, whereas individuals in better body condition consumed more seals. However,  
408 predicted dietary proportions of seals and springbok remained relatively similar across the SMI  
409 gradient, and credible intervals broadly overlapped. (Fig. 4). The dietary proportion of seals for  
410 inland hyenas was too low to assess the link between SMI and seal consumption.. The mean  
411 global dietary values and dietary values according to access to seals were consistent with our  
412 other models (colony:  $\text{mean}_{\text{seal}} = 64\%$ , 95% CI: [53 - 75%];  $\text{mean}_{\text{springbok}} = 36\%$  [24 - 47%],  
413  $\text{mean}_{\text{browsers}} = 0\%$  [0 - 3%]; coastal:  $\text{mean}_{\text{seal}} = 51\%$  [32 - 58%];  $\text{mean}_{\text{springbok}} = 48\%$  [29 - 58%],  
414  $\text{mean}_{\text{browsers}} = 1\%$  [0 - 11%]; inland:  $\text{mean}_{\text{seal}} = 3\%$  [0 - 17%];  $\text{mean}_{\text{springbok}} = 96\%$  [81 - 100%],  
415  $\text{mean}_{\text{browsers}} = 1\%$  [0 - 8%]).



416

417 **Fig. 4.** Relation between body condition (scaled mass index — Peig and Green, 2008) on the  
 418 consumption of Cape fur seals and springbok by brown hyenas whose territory location enabled  
 419 regular access to a seal colony (“Colony”) and hyenas whose territory location enabled access to  
 420 the coast but not to a colony (“Coastal”).

421

422 For jackals, hair  $\delta^{13}\text{C}$  was generally lower ( $-12.65 \pm 0.07\text{‰}$ ) compared to hyenas, whereas  
 423  $\delta^{15}\text{N}$  was higher ( $18.96 \pm 0.12\text{‰}$ ). The null model had the lowest LOOic, which indicated that  
 424 variation in diet was not explained by sex, age, location, or body mass (Table S2). The location

425 and body mass models came second and third, with low weights of 18% and 11%, respectively.  
426 Under the null model, seal accounted for 75% of the jackals' diet (95% CI: [69 - 81%]), whereas  
427 beetles (i.e., *Tenebrionid sp.*) accounted for 15% (95% CI: [11 - 19%]), and other marine  
428 resources (i.e., cormorants and mussels) accounted for 10% (95% CI: [2 - 18%]). Results of other  
429 models are provided in Table S2.

430

#### 431 *Spatial differentiation in hyena body condition*

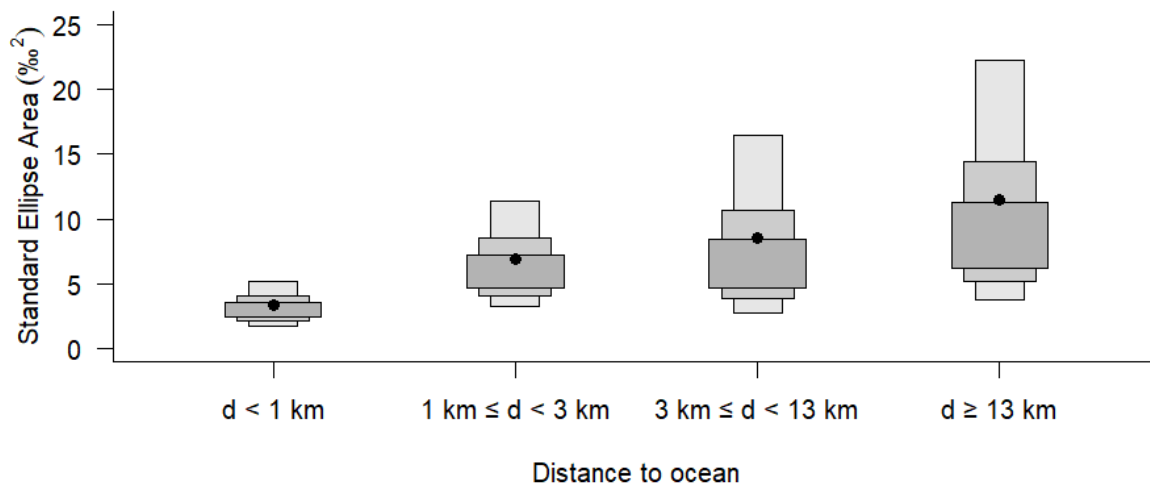
432 Hyena body condition was not explained by distance to coast ( $z = -1.51$ ,  $p = 0.13$ ;  $n_{\text{hyenas}}$   
433  $= 24$ ). We found that hyenas with regular access to seals were not in better body condition than  
434 coastal ( $z = 0.97$ ,  $p = 0.33$ ) or inland ( $z = -0.76$ ,  $p = 0.45$ ) hyenas. Our models' residuals showed  
435 no notable patterns.

436

#### 437 *Isotopic niche size and overlap*

438 Within hyenas, young males had a larger isotopic niche ( $SEA_B = 9.76$ , 95% CI: [5.49 –  
439 19.34],  $n = 11$ ) than did other demographic groups. The probability of their dietary niche  
440 breadth being larger than that of young females, older females, and older males was 0.76, 0.88,  
441 and 0.84, respectively. We did not find noticeable differences between the dietary niche  
442 breadth of the other hyena demographic groups (young females:  $SEA_B = 6.04$  [2.77 – 16.38],  $n =$   
443 6; older females:  $SEA_B = 5.52$  [2.89 – 11.80],  $n = 9$ ; older males:  $SEA_B = 4.86$  [2.03 – 14.71],  $n =$   
444 5). The probability of young females having a smaller niche than older females and older males  
445 was 0.37 and 0.38, respectively, and the probability of older females having a smaller niche than  
446 older males was 0.48.

447 The isotopic niche of hyenas increased with distance to coast (Fig. 5). Hyenas sampled <  
448 1 km from the coast had the smallest isotopic niche ( $SEA_B = 2.93 [1.75 - 5.23]$ ,  $n = 14$ ). Hyenas  
449 sampled 1-3 km away from the coast had a larger niche ( $SEA_B = 5.68 [3.22 - 11.40]$ ,  $n = 11$ ) than  
450 that of hyenas near the shore but comparable to individuals captured 3–13 km from the coast  
451 ( $SEA_B = 6.12 [2.78 - 16.49]$ ,  $n = 6$ ). Hyenas captured farther than 13 km from the coast had the  
452 largest isotopic niches ( $SEA_B = 8.48 [3.53 - 22.08]$ ,  $n = 6$ ).



453  
454 **Fig. 5.** Isotopic niche sizes of brown hyenas estimated from hair using Bayesian ellipses, grouped  
455 by Euclidean distance of sampling site to the coast.

456  
457 Black-backed jackals had a much smaller isotopic niche than hyenas (jackals:  $SEA_B = 1.15$   
458  $[0.87 - 1.53]$ ,  $n = 50$ ), with a probability of 1 regardless of the hyena demographic group  
459 considered. The mutual overlap (Table 2) between jackal and hyena isotopic niches was  $0.11 \pm$   
460  $0.001$  for young females,  $0.10 \pm 0.001$  for young males,  $0.09 \pm 0.001$  for old females, and  $0.07 \pm$   
461  $0.002$  for old males. Directional overlap revealed strong asymmetry: a large proportion of the

462 jackal niche was encompassed by hyena niches, whereas jackals encompassed only a small  
 463 fraction of each hyena-group niche (Table 2).

464

465 **Table 2.** Summary statistics (mean, standard deviation (SD), median and 95% Credible Interval  
 466 (CI)) of mutual ( $\leftrightarrow$ ) and directional ( $\rightarrow$ ) overlaps between dietary niches, estimated from  
 467 Bayesian ellipses, of brown hyenas (by hyena demographic group) and black-backed jackals.

Overlap direction	mean	SD	median	95% CI
Young females $\leftrightarrow$ Jackals	0.11	0.05	0.11	[0.03 - 0.20]
Young males $\leftrightarrow$ Jackals	0.10	0.03	0.10	[0.05 - 0.17]
Old females $\leftrightarrow$ Jackals	0.09	0.04	0.09	[0.02 - 0.19]
Old males $\leftrightarrow$ Jackals	0.07	0.05	0.06	[0.00 - 0.19]
Young females $\rightarrow$ Jackals	0.74	0.24	0.80	[0.03 - 0.20]
Young males $\rightarrow$ Jackals	0.91	0.14	1.00	[0.05 - 0.17]
Old females $\rightarrow$ Jackals	0.55	0.27	0.54	[0.02 - 0.19]
Old males $\rightarrow$ Jackals	0.46	0.33	0.42	[0.00 - 0.19]
Jackals $\rightarrow$ Young females	0.12	0.05	0.11	[0.03 - 0.20]
Jackals $\rightarrow$ Young males	0.10	0.03	0.10	[0.05 - 0.17]
Jackals $\rightarrow$ Old females	0.10	0.04	0.09	[0.02 - 0.19]
Jackals $\rightarrow$ Old males	0.08	0.05	0.07	[0.00 - 0.19]

468

469

## 470 Discussion

471 Allochthonous resources and spatial heterogeneity can generate far-reaching effects on  
 472 food webs (Polis et al., 1997). By examining how two terrestrial desert carnivorans exploited  
 473 clumped marine subsidies, we found contrasting responses within and between species, likely  
 474 driven by landscape heterogeneity and differences in territoriality. We found good support of  
 475 our three hypotheses: both brown hyenas and black-backed jackals relied on abundant marine  
 476 resources (Kuhn et al., 2008; Skinner et al., 1995; Wiesel, 2010), yet hyenas exhibited variation  
 477 in trophic ecology including at fine spatial scale, while the jackals' diet was more homogeneous.

478 In this two-predator system, the persistence of territoriality in the apex predator may create  
479 conditions whereby intraspecific competition becomes more ecologically relevant than  
480 interspecific competition, despite an abundant and predictable food source. Hyenas consumed  
481 fewer seals farther from the coast, and for clan members, territory location relative to seal  
482 colonies was a major determinant of diet. Consequently, the patchy distribution of seal colonies  
483 was reflected in dietary differences among hyenas resulting in a non-linear relationship  
484 between diet and the distribution of the qualitative marine resource. Hyena clans whose  
485 territory includes a seal colony do not tolerate intruders despite abundant resources, deviating  
486 from the resource dispersion hypothesis. Jackals, in contrast, increase territory size away from  
487 seal colonies, where food sources are not clumped (Jenner et al., 2011), and relax territoriality  
488 to exploit abundant marine resources, consistent with predictions from the resource dispersion  
489 hypothesis (MacDonald, 1983). These findings suggest that marine subsidies exert strong but  
490 localized effects on the desert food web and illustrate how heterogeneous resource distribution  
491 interacts with consumer traits to shape realized niches (Subalusky & Post, 2019).

492

#### 493 *Consumption of marine subsidies*

494 Marine subsidies in the Namib provide abundant, predictable prey requiring little search  
495 or handling effort (Kolar, 2005; Wiesel, 2010). In line with optimal foraging theory (Pyke, 1984)  
496 both hyenas and jackals relied on seals rather than on scarcer, harder-to-kill terrestrial prey. In  
497 areas of prey overabundance, such as seal colonies with vulnerable pups, hyenas also engage in  
498 surplus killing — i.e., killing more prey than they consume (Wiesel, 2010). They preferentially  
499 feed on lipid-rich seal-pup brains (Wiesel, 2006) and milk — obtained from pumping the pups'

500 stomach (Wiesel, pers. obs.) — and may leave the rest of the carcass, creating carrion that  
501 benefits smaller scavengers like jackals.

502         Mesocarnivores often rely on carrion produced by apex predators, with implications for  
503 their population dynamics and, subsequently, community structure (Wilson & Wolkovich, 2011).  
504 For example, polar bears (*Ursus maritimus*) provide an estimated  $7.0 \times 10^6$  kg/year of carrion  
505 that enhances Arctic fox survival and breeding success (Gamblin et al., 2026; Nater et al., 2021;  
506 Roth, 2003). Interactions among carnivores range from facilitation to suppression. Yet, despite  
507 its key role in structuring animal communities, facilitation remains underappreciated (Prugh &  
508 Sivy, 2020).

509         High seal abundance may promote cooperation among hyena clan members by reducing  
510 food value and the cost of sharing (Goss, 1986; Mills, 1981), potentially enhancing recruitment  
511 in the Namib-Desert hyena population through greater maternal care. Unlike nursing mothers in  
512 the southern Kalahari, that may leave their cubs for up to five-day stretches to forage (Mills,  
513 1981), nursing mothers in the coastal Namib are provisioned by clan members, allowing more  
514 time for maternal care, likely increasing cub survival (Engebretsen et al., 2024; Goss, 1986).

515

### 516 *Intrapopulation niche variation*

517         Due to large isotopic separation between marine and terrestrial prey (e.g., Schoeninger  
518 & DeNiro, 1984), coastal ecotones — which usually have high prey diversity — are expected to  
519 broaden individual niches. However, unlike Arctic foxes (Dalerum et al., 2012; Tarroux et al.,  
520 2012), wolves from inner islands (Darimont et al., 2009), and caracals (Leighton et al., 2024), for  
521 which access both to terrestrial prey and marine subsidies expanded niches, hyena niches

522 shrank closer to the coast. This apparent contradiction likely reflects the extreme scarcity of  
523 terrestrial prey in the Namib Desert, similar to the situation on remote islands of British  
524 Columbia, where wolves exhibited the narrowest niches of all subpopulations because  
525 terrestrial resources were scarce (Darimont et al., 2009).

526         A consequence of the resource dispersion hypothesis is that carnivores relax  
527 territoriality when resources are abundant and patchily distributed, because the costs of  
528 defending a territory large enough to encompass resource patches outweigh the benefits. Yet,  
529 brown hyenas in the Namib deviate from this expectation: individuals living on the coast but  
530 within travelling distance of a seal colony rely noticeably less on seals than neighboring hyenas  
531 with territory-mediated access to colonies. In the present resource context, intraspecific  
532 competition mediated by territoriality may therefore contribute to fine-spatial scale trophic  
533 heterogeneity (Goss, 1986; Wiesel, 2006). One study, based on a very small sample size,  
534 suggested that this pattern could reflect an evolutionary lag, whereby brown hyenas retain an  
535 obstinate strategy (i.e., territory size adapted to the lowest resource availability; von Schantz,  
536 1984), shaped under past conditions when terrestrial resources fluctuated and seal populations  
537 were depleted (Goss, 1986). Subtle dietary differences between age groups and the positive  
538 effect of body condition on seal consumption in hyenas with regular access to seals could  
539 suggest some level of intraspecific competition, including within clans. Although brown hyenas  
540 breed cooperatively, adults forage solitarily and may face some feeding competition with  
541 clanmates. Disputes over seal carcasses are occasionally observed, with larger, older hyenas in  
542 good body condition often prevailing (Goss, 1986; Wiesel, pers. obs.). During occasional  
543 intrusions into seal colonies in neighboring clan territories, individuals in better body condition

544 may have a competitive advantage, which may increase foray success and explain the slightly  
545 higher proportion of seals in coastal hyenas in better condition. Additionally, higher seal  
546 consumption in older individuals may reflect hunting experience and improved ability to kill  
547 larger pups (Wiesel, 2010).

548 Marine resources can be especially valuable to terrestrial species where land-based food  
549 is scarce (Rose & Polis, 1998; Stapp & Polis, 2003). Coastal areas rich in marine subsidies might  
550 therefore support better body condition in consumers (Page et al., 2021). Nonetheless, hyena  
551 body condition did not differ between coastal and inland areas. Together with the broader  
552 isotopic niche of inland hyenas, this result likely reflects their adaptation to the unsubsidized  
553 parts of this extreme environment. Brown hyenas are opportunistic foragers, as shown by the  
554 diverse prey remains at dens farther from the coast (Kuhn et al., 2008). Rather than affecting  
555 body condition, limited access to seals may influence inland hyena behavior, such as prolonged  
556 foraging time (Goss, 1986), and reduced reproductive success.

557 Jackals exhibited a particularly narrow isotopic niche, with consistent diets across  
558 location, body mass, age, and sex. This uniformity likely reflects a break down in territoriality in  
559 response to concentrated food availability, consistent with the resource dispersion hypothesis  
560 (MacDonald, 1983). They may benefit individually from hyena surplus killing through  
561 scavenging, and their relatively high densities may also provide opportunities for  
562 kleptoparasitism. Although their smaller body size relative to brown hyenas may limit the ability  
563 of a single jackal to kill and handle larger seal pups, cooperative hunting offsets this constraint  
564 by enabling the killing of larger seal pups (Merrifield, 2012; Murray et al., 2012). Their ability to  
565 exploit highly abundant marine resources may be constrained by mobility, when the energetic

566 costs of travelling to seal colonies outweigh foraging benefits. However, we could not assess the  
567 effect of distance to the coast , as all individuals sampled here had access to a seal colony  
568 (Jenner et al., 2011).

569

#### 570 *Potential for interspecific competition*

571 In areas where both species rely on terrestrial prey, several studies have reported a  
572 strong potential for competition and frequent agonistic encounters between brown hyenas and  
573 black-backed jackals, driven by dietary niche overlap (Destercke et al., 2025; Mills, 1978; Yarnell  
574 et al., 2013). Here, because food was not limiting, exclusion of jackals from high-quality marine  
575 resource through exploitation competition (i.e., resource depletion) was unlikely (Holdridge et  
576 al., 2016; Fig S3). However, the clumped distribution of seals likely increased encounter rates  
577 (Wiesel, 2006), promoting interference competition at a fine spatial scale (Amarasekare, 2002;  
578 López-Bao et al., 2016), which may explain frequent agonistic interspecific interactions and  
579 kleptoparasitism (Goss, 1986; Wiesel, 2006; Fig. S3).

580 At seal colonies, jackals far outnumber solitary-foraging hyenas. Group foraging can  
581 allow smaller competitors to dominate larger solitary foragers, like gray wolves dominating  
582 larger pumas (*Puma concolor*) (Elbroch & Kusler, 2018), white-backed vultures (*Gyps africanus*)  
583 outcompeting lappet-faced vultures (*Torgos tracheliotos*) (Kendall, 2013), and golden jackals  
584 (*Canis aureus*) negatively affecting striped hyenas (*Hyaena hyaena*) at carcasses (Panda et al.,  
585 2023). Although proximity to hyenas entails risks, including intraguild killing, opportunities for  
586 kleptoparasitism or scavenging likely outweigh the costs (Fig. S3; Prugh & Sivy, 2020).

587

588 *Ecological implications*

589           Although our study focused on a two-predator system, it has broad ecological  
590 implications. First, recipient-species traits may influence the impact of marine subsidies, leading  
591 to intraspecific niche variation. Second, the patchiness and spatial reach of allochthonous prey  
592 may interact with predator traits (e.g., mobility, territoriality) to influence the ecological  
593 relevance of localized indirect effects of predators — such as nutrient redistribution —  
594 especially in nutrient-poor systems (Johnson-Bice et al., 2023). While the role of subsidies in  
595 structuring communities is well established (Polis et al., 1997), the modulatory influence of  
596 community structure on recipient species remains underexplored. Finally, by integrating  
597 landscape and trophic ecology within frameworks, such as the resource dispersion hypothesis,  
598 and optimal foraging theory, our findings offer new perspectives for exploring cross-ecosystem  
599 subsidy theory and predator niche dynamics.

600

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612 **Author contribution:**

613 **Chloé Warret Rodrigues:** Conceptualization, Data Curation, Formal Analysis,  
614 Methodology, Validation, Visualization, Writing – Original Draft Preparation

615 **Ingrid Wiesel:** Conceptualization, Data Curation, Funding Acquisition, Investigation,  
616 Project Administration, Supervision, Writing – Review & Editing

617 **Christine M. Drea:** Conceptualization, Funding acquisition, Investigation, Project  
618 Administration, Writing – Review & Editing

619 **Jane M. Waterman:** Conceptualization, Funding Acquisition, Investigation, Resources,  
620 Writing – Review & Editing

621 **James D. Roth:** Conceptualization, Data Curation, Funding Acquisition, Investigation,  
622 Resources, Writing – Review & Editing

623 **Data availability:** Data will be published on Dryad upon acceptance

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**Appendix 2.** Supplementary information, mixing model output and Bayesian ellipse plots for:

**Marine subsidies, spatial heterogeneity, and territoriality drive trophic ecology in desert predators.**

We studied intrapopulation differences in diet and dietary niches in brown hyenas (*Parahyaena brunnea*) from the Namib desert (Tsau //Khaeb (Sperrgebiet) National Park and coastline between the park and the Cape Cross Seal Colony), and compared with part of the black-backed jackal population which could access a seal colony (either in Lüderitz or Cape Cross Seal Reserve).

To reconstruct the diet of these carnivores, we ran a total of 14 Bayesian mixing models across four sets of analyses, three of which concerned hyenas and one jackal. We then examined dietary niche differences between hyenas grouped by demographic class or distance to the nearest seal colony and compared with the dietary niche of jackals (pooled because no variable available explained dietary differences).

**Table S1.** Overview of model specifications, including analysis objective, species concerned, type of analysis (Bayesian mixing model or Bayesian ellipses), number of models per analysis set, covariates or grouping factors considered, total sample size, and sample size range, which provide the minimum and maximum sample size across groups and covariate levels.

analysis	species	Model	Num. models	Covariates or Grouping	Num. variables or groups	n total [min-max]
effect of access to seal and demographic on diet	Brown hyena	Mixing models	6	Age (young <7 / old ≥7), Sex (F/M), Seal access (Colony / Coastal / Inland / Unknown)	0-2	31 [4-31]
effect of distance to seal colony by age group on diet	Brown hyena	Mixing models	1	distance to seal colony (continuous), Age (young <7 / old ≥7)	2	31 [15 - 31]
effect of body condition controlling for access to seal on diet	Brown hyena	Mixing models	1	Body condition (continuous), Random effect: Seal access (Colony / Coastal / Inland)	1 + 1 random effect	25
effect of location, sex, age and body mass on diet	Black-backed jackal	Mixing models	6	Location (CCSR/Luderitz), Sex (F/M), Age (A/S/J), body mass (continuous)	0-2	49 [6 - 49]
effect of species and demographics on niche breadth	Black-backed jackal, brown hyenas	Bayesian ellipse	1	Jackals, hyenas F <7, hyena F ≥7, hyenas M <7, hyenas M ≥7	5	80 [5 - 49]
effect of distance to coast on niche breadth	Brown hyena	Bayesian ellipse	1	distance bins: <1km, 1≤d<3km, 3≤d<13km, d≥13km	4	37 [6 - 14]

1 **Table S2.** Relative model performance using the leave-one-out cross-validation (LOOic)  
2 approach and model output (Mean dietary proportion for each source and 95% credible  
3 interval) of the 6 models compared in reconstructing brown-hyena diet of the  
4 Tsau//Khaeb (Sperrgebiet) National Park. xi.C[y] and xi.N[y] are the median  
5 multiplicative error term estimates for C and N. Seal Access refers to an individual  
6 access to a seal colony within its territory and was determined based on detailed  
7 knowledge of the history of individuals that are part of a long-term project (Inland =  
8 territory does not include coast; Coastal = territory includes coast but no seal colony  
9 and is not located across islands where seal colonies live), Colony (territory includes a  
10 seal colony, or is located across from an island with a seal colony), Unknown (the hyena  
11 is not a known individual). Initials are: O = Old (> 6years old), Y = Young (< 7 years old), F  
12 = Female, M = Male.

Model	LOOic	se_LOOic	dLOOic	se_dLOOic	weight	xi.C[y]	xi.N[y]
Seal access	37.2	15.8	0	NA	0.599	0.4	1.9
Age + Seal access	38	15.2	0.8	3	0.401	0.4	2.2
Null	65.4	16.9	28.2	10.6	0	0.6	7
Age	66.7	15.4	29.5	10.9	0	0.6	6.3
Sex	69	16.9	31.8	11.2	0	0.6	6.9
Sex + Age	70.2	15.5	33	11.2	0	0.5	6.5
Model output							
Model	Mean prey proportion [95% Credible interval]						
	Seal	Springbok	gemsbok	Browsers			
Seal access							
Colony	0.64 [0.50 - 0.75]	0.31 [0.14 - 0.44]	0.03 [0.00 - 0.26]	0.02 [0.00 - 0.07]			
Coastal	0.50 [0.33 - 0.65]	0.43 [0.23 - 0.62]	0.03 [0.00 - 0.25]	0.04 [0.00 - 0.13]			
Inland	0.11 [0.02 - 0.26]	0.80 [0.55 - 0.97]	0.02 [0.00 - 0.16]	0.06 [0.00 - 0.21]			
Unk	0.29 [0.07 - 0.53]	0.64 [0.24 - 0.91]	0.04 [0.00 - 0.42]	0.03 [0.00 - 0.13]			
Age + Seal access							
O Colony	0.69 [0.50 - 0.85]	0.25 [0.06 - 0.41]	0.04 [0.00 - 0.33]	0.02 [0.00 - 0.07]			
Y Colony	0.61 [0.43 - 0.74]	0.35 [0.17 - 0.51]	0.03 [0.00 - 0.25]	0.02 [0.00 - 0.07]			
O Coastal	0.55 [0.35 - 0.74]	0.38 [0.13 - 0.59]	0.03 [0.00 - 0.29]	0.04 [0.00 - 0.12]			
Y Coastal	0.45 [0.25 - 0.63]	0.50 [0.28 - 0.71]	0.02 [0.00 - 0.18]	0.03 [0.00 - 0.13]			
O Inland	0.15 [0.03 - 0.34]	0.76 [0.44 - 0.96]	0.03 [0.00 - 0.23]	0.06 [0.00 - 0.22]			
Y Inland	0.10 [0.02 - 0.24]	0.84 [0.63 - 0.97]	0.01 [0.00 - 0.10]	0.04 [0.00 - 0.19]			
O Unk	0.40 [0.09 - 0.68]	0.54 [0.18 - 0.88]	0.04 [0.00 - 0.38]	0.03 [0.00 - 0.14]			
Y Unk	0.30 [0.07 - 0.52]	0.65 [0.37 - 0.90]	0.03 [0.00 - 0.26]	0.02 [0.00 - 0.11]			
Null	0.48 [0.30 - 0.62]	0.39 [0.00 - 0.59]	0.07 [0.00 - 0.50]	0.06 [0.00 - 0.15]			
Age							
O	0.54 [0.35 - 0.70]	0.36 [0.00 - 0.56]	0.05 [0.00 - 0.45]	0.05 [0.00 - 0.13]			
Y	0.38 [0.14 - 0.58]	0.50 [0.00 - 0.77]	0.07 [0.00 - 0.64]	0.05 [0.00 - 0.16]			
Sex							

F	0.51 [0.31 - 0.68]	0.37 [0.00 - 0.60]	0.06 [0.00 - 0.50]	0.05 [0.00 - 0.16]
M	0.43 [0.16 - 0.63]	0.45 [0.00 - 0.72]	0.07 [0.00 - 0.61]	0.05 [0.00 - 0.15]
Sex + Age				
FO	0.55 [0.36 - 0.73]	0.37 [0.08 - 0.58]	0.04 [0.00 - 0.34]	0.04 [0.00 - 0.12]
FY	0.40 [0.14 - 0.65]	0.52 [0.08 - 0.81]	0.04 [0.00 - 0.48]	0.04 [0.00 - 0.14]
MO	0.51 [0.24 - 0.76]	0.42 [0.07 - 0.70]	0.04 [0.00 - 0.38]	0.04 [0.00 - 0.13]
MY	0.36 [0.10 - 0.60]	0.57 [0.08 - 0.85]	0.04 [0.00 - 0.50]	0.03 [0.00 - 0.14]

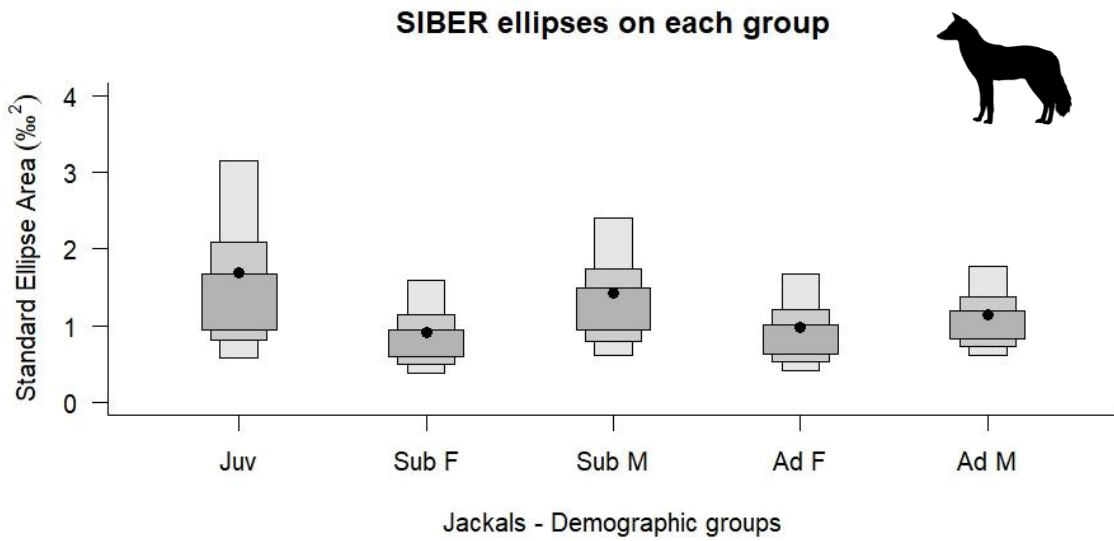
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14 **Table S3.** Relative model performance using the leave-one-out cross-validation (LOOic)  
15 approach and model output (Mean dietary proportion for each source and 95% credible  
16 interval) of the 6 models compared in reconstructing black-backed jackal diet of the  
17 Tsau//Khaeb (Sperrgebiet) National Park. xi.C[y] and xi.N[y] are the median  
18 multiplicative error term estimates for C and N. (initials are: CCSR = Cape Cross Seal  
19 Reserve, A = Adult, J = Juvenile, S = Subadult, F = Female, M = Male, O = Old (> 6years  
20 old), Y = Young (< 7 years old)).

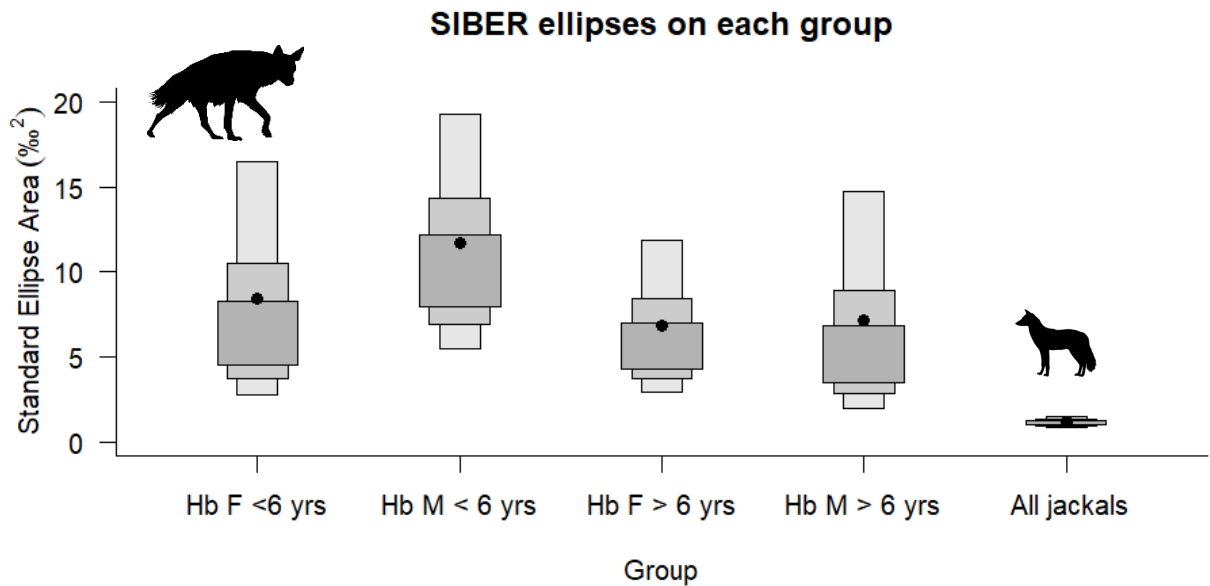
Model relative performance							
Model	LOOic	se_LOOic	dLOOic	se_dLOOic	weight	xi.C[y]	xi.N[y]
Null	22.9	15	0	NA	0.613	0.1	0.6
Location	25.4	14.7	2.5	1.5	0.176	0.1	0.6
Body mass	26.3	15.2	3.4	1.2	0.112	0.1	0.6
Age + Location	27.9	14.4	5	4.4	0.05	0.1	0.6
Sex + Location	29.1	15	6.2	1.5	0.028	0.1	0.6
Sex + Age	29.6	14.8	6.7	4.3	0.022	0.1	0.6
Model output							
Model	Mean prey proportion [95% Credible interval]						
	Seal		Beetles (Tenebrionid sp.)		other marine		
Null	0.75 [0.69 - 0.81]		0.15 [0.11 - 0.19]		0.10 [0.02 - 0.18]		
Location							
CCSR	0.76 [0.69 - 0.82]		0.16 [0.11 - 0.20]		0.09 [0.01 - 0.19]		
Luderitz	0.73 [0.60 - 0.83]		0.14 [0.06 - 0.21]		0.13 [0.01 - 0.32]		
Body mass							
Min	0.73 [0.48 - 0.86]		0.16 [0.10 - 0.28]		0.11 [0.00 - 0.50]		
Med	0.77 [0.62 - 0.85]		0.16 [0.03 - 0.25]		0.08 [0.00 - 0.34]		
Max	0.77 [0.55 - 0.88]		0.16 [0.03 - 0.27]		0.08 [0.00 - 0.36]		
Age + Location							
A CCSR	0.77 [0.69 - 0.83]		0.14 [0.08 - 0.19]		0.09 [0.01 - 0.22]		
A Luderitz	0.73 [0.60 - 0.83]		0.14 [0.06 - 0.21]		0.14 [0.01 - 0.32]		
J CCSR	0.72 [0.68 - 0.81]		0.18 [0.08 - 0.25]		0.10 [0.00 - 0.31]		
S CCSR	0.77 [0.70 - 0.83]		0.17 [0.11 - 0.22]		0.06 [0.00 - 0.17]		
S Luderitz	0.74 [0.61 - 0.83]		0.17 [0.08 - 0.26]		0.08 [0.00 - 0.28]		
Sex + Location							
F CCSR	0.76 [0.68 - 0.82]		0.16 [0.10 - 0.21]		0.08 [0.01 - 0.20]		



35 Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L. & Semmens, B.X. (2018) Analyzing mixing systems  
 36 using a new generation of Bayesian tracer mixing models. PeerJ 6, e5096.  
 37



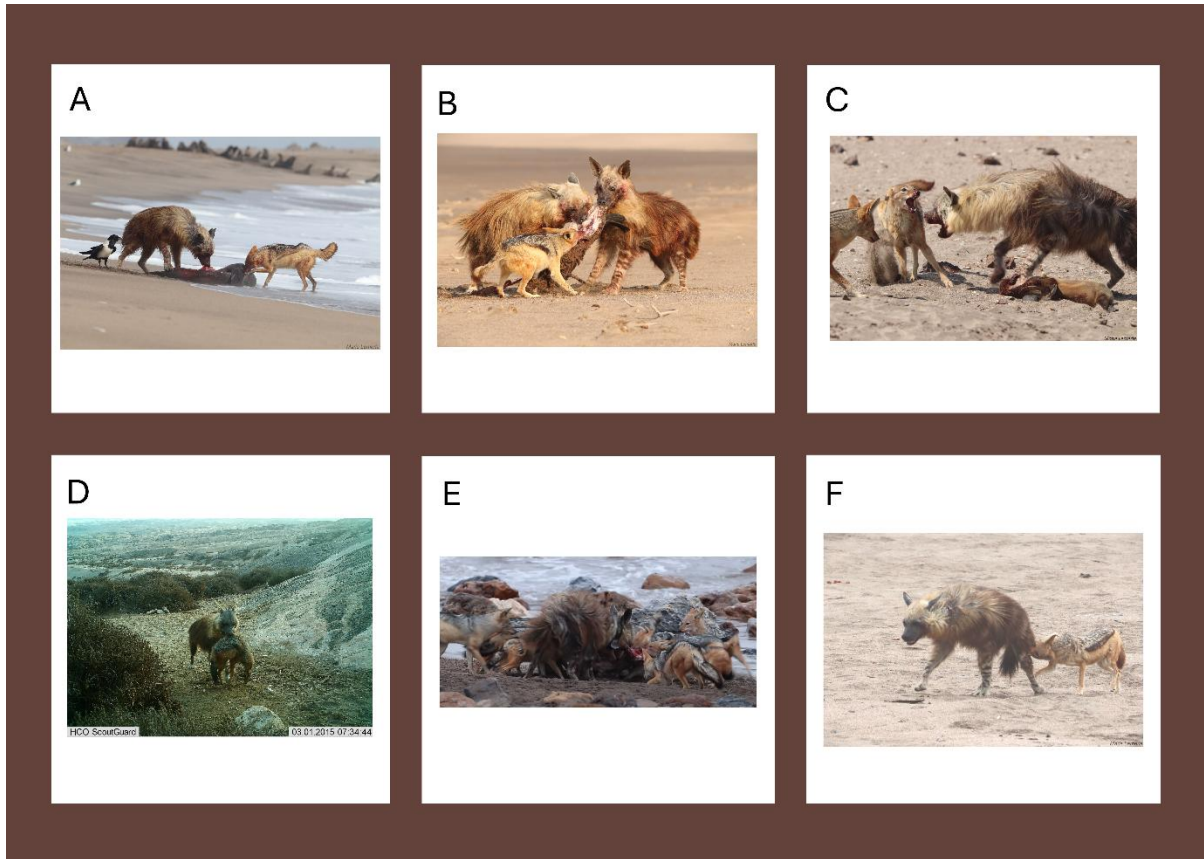
38  
 39 **Figure S1.** Isotopic niche sizes estimated from hair of black-backed jackals (n = 50)  
 40 grouped by age class (Jvenile, Subadult, Adult) and sex (M, F) using Bayesian ellipses.  
 41 This model was part of preliminary analyses.



42  
 43 **Figure S2.** Isotopic niche sizes estimated from hair samples using Bayesian ellipses for  
 44 brown hyenas (Hb) grouped by sex (Female, Male) and age class (4–6 years old and ≥7

45 years old), and black-backed jackals grouped together. Sample sizes for hyenas were:  
46 young females ( $n = 5$ ), young males ( $n = 11$ ), old females ( $n = 10$ ), old males ( $n = 5$ ), and  
47 jackals ( $n = 50$ ). This model was part of preliminary analyses.

48



49

50 **Figure S3.** Examples of interactions between brown hyenas and black-backed jackals  
51 at or near seal colonies. (A) no aggressive behavior was observed, (B) successful  
52 attempt at kleptoparasitism by the jackal, while two hyenas were in dispute over a seal  
53 carcass, (C) the hyena defends its prey from jackals, (D) Intraguild predation by a hyena  
54 on a jackal, (E) the high density of jackals may provide an advantage in kleptoparasitism  
55 events, and occasionally hyenas have no choice but to abandon their prey to jackals, (F)  
56 a jackal aggresses a hyena, biting its leg, although no food was involved. (Photo credit:  
57 Marie Lemerle, Brown Hyena Research Project).

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