

Trophic responses of desert predators to clumped marine subsidies

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Abstract

Allochthonous subsidies can have far-reaching effects on recipient ecosystems. By altering local resource availability, the spatial distribution of such subsidies can structure consumer diets, shape communities, and influence ecosystem dynamics. We used stable isotope analyses to determine how patchily distributed colonies of Cape fur seals (*Arctocephalus pusillus pusillus*) along the coastal Namib Desert influenced the diet and dietary niches of brown hyenas (*Parahyaena brunnea*). We further compared brown hyena reliance on these marine subsidies with that of black-backed jackals (*Lupulella mesomelas*) residing within travel distance of a seal colony. Brown hyena dietary niches expanded with distance from the coast, while seal

consumption was highest at colonies (64% [50–75]), slightly lower at coastal sites (50% [33–65]) despite their proximity to colonies, and lowest inland (11% [2–26]). These fine-scale spatial differences in seal reliance suggest that hyenas did not relax territoriality in response to abundant resource clumps, departing from the resource dispersion hypothesis. In contrast, black-backed jackals exhibited a narrow dietary niche, showing extreme reliance on Cape fur seals (75% [69 - 81]), exceeding that of coastal brown hyenas and consistent with a territoriality breakdown in response to abundant, patchy food. Consistent with optimal foraging theory, the marine ecosystem subsidized both terrestrial species, precluding exploitation competition but potentially increasing interspecific encounter rates, and thus opportunities for aggression. Our study highlights how marine subsidies can shape terrestrial food webs and contribute to variation in carnivoran realized niches.

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

Introduction

Transboundary movements of allochthonous resources (i.e., organisms or other organic material entering a recipient ecosystem from a donor ecosystem) may create a strong linkage between ecosystems, which can profoundly affect the food webs of recipient ecosystems (Polis et al., 1997). Allochthonous subsidies may impact populations either directly (Leighton et al., 2024; Polis & Hurd, 1996; Rose & Polis, 1998) or indirectly, such as through a predator's numerical response to allochthonous prey or carrion (e.g., Johnson-Bice et al., 2025; Spiller et al., 2010). The magnitude of the effects of allochthonous resources can depend on consumer

characteristics (including trophic level, degree of specialization, behavior, or capacity for resource exploitation) or specific ecological context, (i.e., quality, timing, duration, frequency, or predictability of these subsidies; Subalusky & Post, 2019). The effects of allochthonous resources are usually strongest when the recipient ecosystem has low levels of similar resources, or when the elongated or fragmented boundaries of the recipient ecosystem magnify exposure to external inputs (Atkinson et al., 2017; Marczak et al., 2007; Subalusky & Post, 2019). Coastal ecosystems are thus particularly likely to receive allochthonous subsidies, which can represent an important dietary component for terrestrial predators (Carlton & Hodder, 2003; Darimont et al., 2009; Leighton et al., 2024).

In resource-poor ecosystems, subsidization by high-quality allochthonous resources may promote intra- and interspecific competition between consumers (Darimont et al. 2009, Subalusky & Post, 2019), which in turn, can promote dietary-niche variability within a population. For example, in British Columbia, wolves (*Canis lupus*) on islands adjacent to the mainland have wider isotopic niche breadths than wolves from the mainland or remote islands. This niche differentiation likely reflects a combination of relaxed interspecific competition, increased intraspecific competition for ungulates, and access to both terrestrial and marine resources (Darimont et al., 2009). While allochthonous resources are recognized as key drivers structuring animal communities, their influence on trophic ecology is rarely examined alongside local- and individual-scale ecological drivers. Yet diet and intrapopulation dietary-niche variation likely result from interacting ecological drivers across scales, including landscape characteristics, inter- and intraspecific interactions, and consumer traits (Marczak et al., 2007). Here, we assess how spatially clustered marine resources shape the trophic ecology and interactions of two

sympatric desert carnivorans with contrasting territorialities and foraging strategies, the brown hyena (*Parahyaena brunnea*) and the black-backed jackal (*Lupulella mesomelas*).

The Namib Desert coastline represents an ecotone between the highly productive southern Atlantic Ocean (Huntley, 2023; Ward et al., 1983) and a hyper-arid, unproductive desert, with the former subsidizing the latter. About 1.7 million cape fur seals (*Arctocephalus pusillus pusillus*) aggregate year-round into colonies along the coastline of southwestern Africa (Curtis et al., 2021). In Namibia colonies occupy the mainland or nearby offshore islands and, together with seabird colonies (e.g., cormorants, *Phalacrocorax sp.*), provide abundant food resources for terrestrial carnivorans (Skinner et al., 1995; Stander, 2019; Wiesel, 2010). These marine resources promote landscape heterogeneity, which likely influences predator space use, diet and/or territoriality (Macdonald & Johnson, 2015). The near-complete absence of fresh water in the coastal Namib limits habitat suitability to species capable of surviving without drinking water (Eckardt et al., 2013; Mitchell et al., 2020). Consequently, large-bodied terrestrial prey species are sparse and include springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), lagomorphs (*Lepus capensis*, *Pronolagus sp.*), and rodents (Skinner et al., 1995). Large carnivorans, like lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*) and leopards (*Panthera pardus*), remain dependent on rainfall (for vegetation cover and prey availability) and drinking water, which excludes them from the coastal central and southern Namib (Edwards et al., 2016; Heydinger et al., 2016; Portas et al., 2022; Skinner & Van Aarde, 1981). Because they can forgo drinking water (Loveridge & Nel, 2004; Skinner & Van Aarde, 1981), the brown hyena, with a body mass of around 40 kg, is the apex predator in this system, while the black-backed jackal, with a body mass of about 6-8 kg, is the only mesopredator.

Brown hyenas usually live in clans of up to 10 individuals (Mills, 1989; Wiesel, 2006) that cooperate to raise young and defend their territories (Goss, 1986). Clan members deposit lipid-rich pastes or use latrines to scent mark territories, especially near borders or resource hotspots, to effectively deter intruders (Gorman & Mills, 1984). Some adults (mostly males, which can become nomadic) and dispersing subadults of both sexes can live solitarily (either permanently or until immigrating into a non-natal clan). All brown hyenas forage alone, predominantly scavenging vertebrate carrion or opportunistically hunting small-bodied animals, sometimes across vast areas (Edwards et al., 2020; Mills, 1982, 1989). Hyenas more often display social dominance within clans when food is concentrated due to higher encounter rates between individuals (Goss, 1986; Owens & Owens, 1978). In the Namib, dominance is usually ritualized and the outcome is driven by age and size (Goss, 1986). Near the Namib desert's coast, brown hyenas rely heavily on seal pups (Kuhn et al., 2008; Skinner et al., 1995), which they hunt year-round, even as the pups grow older and the hunt becomes increasingly difficult (Wiesel, 2010). Reliance on these qualitative marine subsidies may vary among individuals, based on distance to the nearest seal colony or whether a clan territory includes a seal colony. While some clans can defend these valuable resources, and thus may rely on seals more exclusively, clans lacking regular access to a seal colony, nomadic males, and other solitary individuals may need to consume a broader range of prey. Consuming larger quantities of high-quality prey may have important consequences, such as improving body condition. Conversely, for a solitary forager, individuals in better body condition may be more capable of acquiring and defending access to high-quality prey, suggesting a potentially reciprocal relationship between prey use and body condition.

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

Here, we use stable isotope analyses to examine how clumped marine resources impact the diet and dietary niches of brown hyenas and black-backed jackals, two carnivorans exhibiting contrasting territoriality. A brown hyena clan that defends a seal colony ensures its members regular access, whereas frequency of access for other individuals likely depends on their distance to the nearest colony. Territorial defense and opportunistic incursions by neighboring individuals may further modify access locally. We hypothesize that territory-mediated access to marine resources structures hyena diet, leading to dietary niche differences that reflect the patchy distribution of seal colonies (H1), and further examined possible effects of qualitative marine resource on body condition. Given that jackals can relax territoriality when food is clumped and abundant, jackals residing within distance of a seal colony should maximize exploitation of abundant marine resources, leading to greater reliance on seal consumption than is seen in hyenas, including those residing on the coast (H2). Finally, abundant marine

subsidies should prevent dietary exclusion and promote shared prey use among these coexisting predators (H3).

In accordance with H1, we predict 1) reduced seal consumption in hyenas that lack territorial access or have greater travel distance to seal colonies (reflecting broader-scale patterns), and expect 2) reduced body condition in individuals that have limited seal access, due to scarcity of alternative, terrestrial resources. In accordance with H2, we predict 3) a greater proportion of marine subsidies in jackals residing within travel distance from seal colonies (which included all those captured in this study) compared to hyenas. Using isotopic niche as a proxy for dietary niche, we further predict that isotopic niche breadth 4) increases in hyenas from coast to inland (H1) and 5) is narrower in jackals than coastal hyenas (H2). In accordance with H3, 6) seals should account for a large proportion of the diet of both species, and 7) jackals' dietary niche should largely overlap with that of coastal hyenas.

Methods

Study areas

This study was conducted in Namibia, in the Tsau //Khaeb (Sperrgebiet) National Park and along the coast between the park and the Cape Cross Seal Colony (Fig. 1), in the southwestern part of the Namib Desert. The Namib Desert extends as a long (> 2,000 km) and narrow (< 200 km wide) strip along the coast of southwestern Africa, from the Carunjamba River in Angola to the Olifants River in South Africa (Ward et al., 1983; Nel et al. 1997; Huntley, 2023). The cool (annual mean temperature ~15°C), hyper-arid, coastal desert receives < 100mm of precipitation per year (Ward et al., 1983; Huntley, 2023). The Namib climate is mostly

maintained by three interacting atmospheric and oceanic processes: the offshore South Atlantic Anticyclone, the Benguela Upwelling current, and the winds that these two processes generate (Ward et al., 1983; Huntley, 2023).

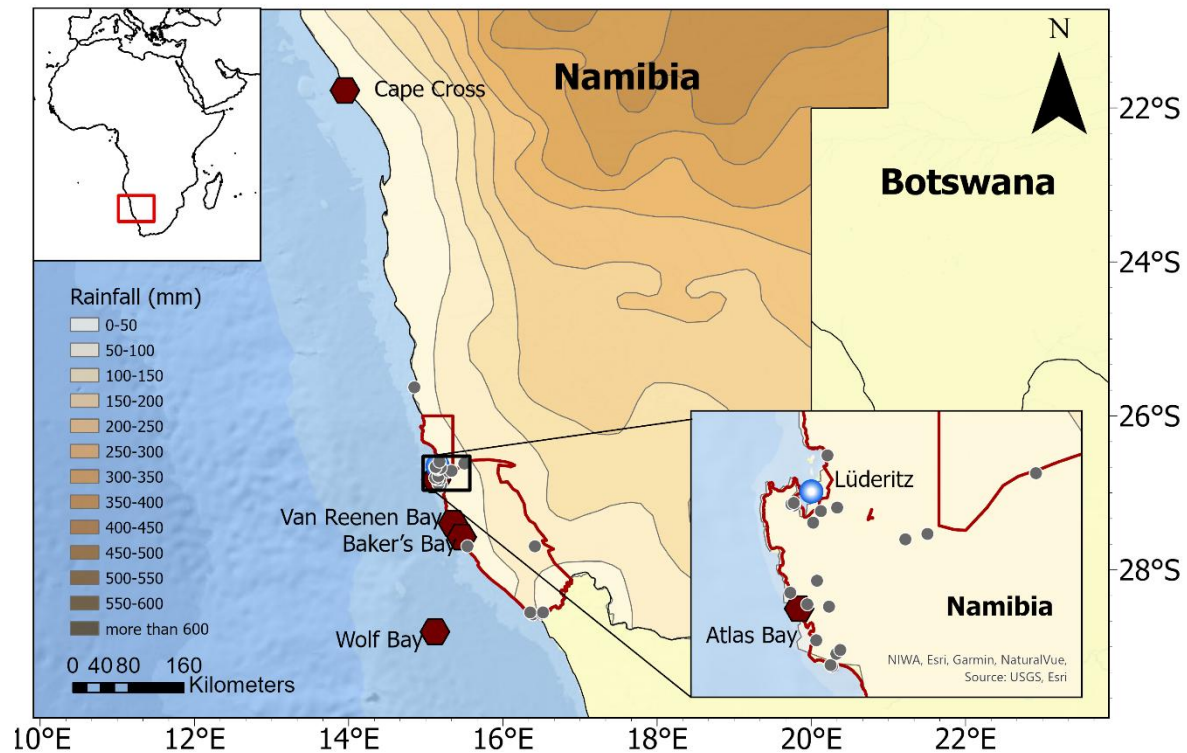


Fig. 1. Map of the study area. The borders of the Tsau//Khaeb (Sperrgebiet) National Park are depicted in red. Seal colonies are represented by red hexagons, and hyena samples are grey points. All jackal samples were collected at the Cape Cross seal colony or near Lüderitz (blue circle). The rainfall layer was obtained at https://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia/e1_download_climate_e.htm#annual_rainfall (Accessed 2026-03-27).

Sample and data collection

From 2000 to 2004, we collected hair samples from the back of live animals (18 brown hyenas and 54 jackals) captured using cage traps, modified foot snares (Frank et al., 2003),

padded softcatch foothold traps (No.4 Victor Softcatch, coil spring, Woodstream Corporation, Lititz, Pennsylvania, USA) or darted during concurrent studies (Gowtage-Sequeira, 2004; Wiesel, 2006), and from carcasses of 23 hyenas that were roadkill or died from natural causes. Live-captured animals were anesthetized using species-appropriate drugs and protocols (details on anesthesia in Gowtage-Sequeira (2004) and Wiesel et al. (2018)) and their health status was assessed. Jackals were trapped near Lüderitz or Cape Cross Seal Reserve (Fig. 1). Capture and handling of live animals was performed under the Namibian Ministry of Environment and Tourism permits 549/2001/2002-3, 33806, 421/2001, 548/2002, 693/2003 and 784/2004, and under Duke Institutional Animal Care and Use Committee protocol A190-02-06. Biological samples were imported into the U.S.A. under Federal Fish & Wildlife Management permit 037014-2.

Brown hyenas.— Most of the hyenas were individually known (from unique stripe patterns) and regularly followed, yearly, as part of a long-term survey established in 1997. For each sample obtained, we recorded latitude and longitude as a proxy for the animal's foraging range (Fig. 1). We anticipated that landscape heterogeneity interacting with territoriality could create non-linear patterns of seal accessibility: some coastal individuals without regular access to a seal colony could still access marine resources washed up on the shore. Life history data for most individuals (Wiesel, 2006; Spagnuolo et al., 2022) thus allowed us to classify accessibility to a seal colony (hereafter "access to seals"): "inland" (territory location did not enable access to seals), "coastal" (territory location enabled access to the coast but not to seals), "colony" (territory location enabled regular access to seals), "unknown" (the hyena was not a known individual). Whenever possible, we recorded body mass (kg), neck circumference (cm), age

estimate (class), and sex. Age class was estimated using dental eruption and tooth wear (Mills, 1982; Wiesel et al., 2018) or using cementum annuli counts by Matson's lab (Manhattan, Montana, USA). Tooth wear can reduce the ability of hyenas to chew bones and is associated with declines in body mass in older individuals, while age more generally may influence variation in body mass (Mills, 1982), providing a potential mechanism for age-related differences in diet. We subsequently classified the adults into two age classes: 4-6 years old ($n_{\text{Female}} = 5$, $n_{\text{Male}} = 11$, $n_{\text{Unk}} = 1$), > 7 years old ($n_{\text{Female}} = 13$, $n_{\text{Male}} = 7$, $n_{\text{Unk}} = 1$), referred to as "young" and "old" for simplicity. We determined body condition in hyenas *a posteriori* using the Scaled Mass Index (SMI) developed by Peig and Green (2009). Briefly, the SMI method estimates a scaling exponent between body mass and a linear morphometric measurement (here, we used neck circumference). Because we had to exclude individuals from specific analyses due to missing variables, we provide the sample size for each analysis separately.

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

Prey.— We collected potential prey samples to compare their isotopic ratios with those of the consumers in our diet reconstruction. We obtained muscle samples from seals ($n = 16$) legally harvested in 2001 and 2003 by the Namibian Ministry of Fisheries and Marine Resources

(Gowtage-Sequeira, 2004; Wiesel, 2006). In 2002-2004, we opportunistically collected muscle tissue from mussels ($n = 5$), hair from gemsbok ($n = 7$) and springbok ($n = 2$), and feathers from cormorants ($n = 2$) found dead throughout the study area, including at hyena dens. We further collected Tenebrionid sp. beetles ($n = 2$) and used their whole body.

Sample preparation and stable isotope value determination

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

Diet reconstruction

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

2024). The Bayesian approach allows for the incorporation of prior information, uncertainty in the parameter estimates, covariates, and variability within the consumer population (Stock et al., 2018; Stock & Semmens, 2016).

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

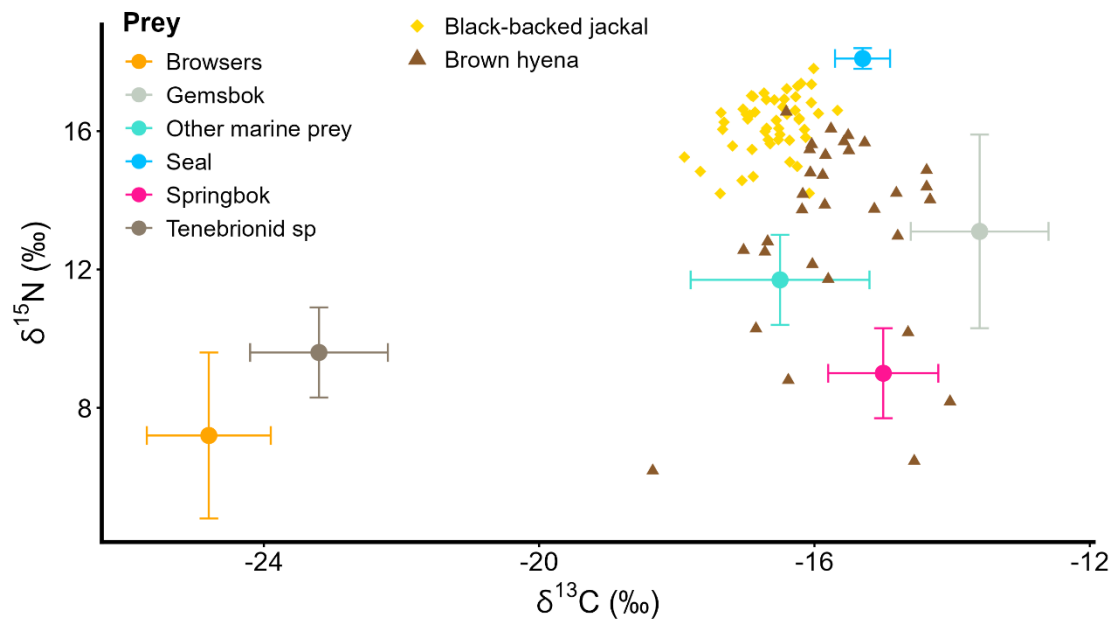


Fig. 2. Stable carbon and nitrogen isotope data from prey tissue, brown hyena hair and black-backed jackal hair, adjusted for diet–tissue discriminations. Hair and feather values of prey were adjusted for muscle equivalent. We used muscle for fur seals, and whole body for Tenebrionid sp. Data for browsers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

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

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

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

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

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

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

Hyena body condition

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

Dietary niche breadth

We used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niche size and location as a proxy to estimate the dietary niche breadth and overlap of hyenas and jackals. Visual assessments using the packages MASS v.7.3.60.2 (Venables & Ripley, 2002) and threejs v.0.3.3 (Lewis, 2020) confirmed that the data conformed to a multivariate normal distribution. We then built two data sets to obtain dietary niche parameters of hyenas and jackals. One dataset grouped hyenas by age class and sex and pooled all jackals (Fig. S1). The other dataset grouped hyenas by distance-to-coast normalized using a Box-Cox transformation. We binned distance measurements into four categories (< 1 km, 1-3 km, 3-13 km, ≥ 13 km), which corresponded to a change of unit in the Box-Cox transformed values and ensured relatively balanced groups. The threshold of the last bin also corresponded to the average nightly distance traveled by hyenas (Skinner et al., 1995).

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

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

To compare Bayesian standard ellipse areas between groups (species, demographics, or distance bins), we conducted pairwise comparisons based on 1,000 draws from the posterior distribution of the means and covariance matrices of the Bayesian ellipses and determined the proportion of cases in which draws were smaller in one group than the other. Specifically, we compared hyenas grouped by demographics or binned distance to the coast, and jackals with each hyena demographic group and with hyenas in the closest distance-to-coast bin. The models thus produced a distribution of measures of area overlap between each pair of ellipses, from which we obtained a mean. For each pair of ellipse-area draws and their overlap, we computed directional overlaps as follows:

$$\text{Proportion of hyena niche overlapped by jackal niche} = \text{area}_{\text{overlap}} / \text{area}_{\text{hyenas}}$$

$$\text{Proportion of jackal niche overlapped by hyena niche} = \text{area}_{\text{overlap}} / \text{area}_{\text{jackals}}$$

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

$$\text{Proportion of mutual overlap} = \text{area}_{\text{overlap}} / (\text{area}_{\text{hyenas}} + \text{area}_{\text{jackals}} - \text{area}_{\text{overlap}})$$

where $\text{area}_{\text{overlap}}$ is the area of overlap between the ellipses, $\text{area}_{\text{hyenas}}$ the ellipse area of a given hyena group, and $\text{area}_{\text{jackals}}$ the jackals' ellipse area. The mutual overlap index represents the total niche space that is shared, similar to the Jaccard index of similarity (Real and Vargas, 1996). Therefore, a proportion of 0 indicates complete separation, while a proportion of 1 indicates complete overlap. We summarized the proportion of dietary niche overlap by calculating the

mean $\pm$ SE (in text), standard deviation and 95% credible interval of the posterior estimates (Table 2).

Results

Diet reconstruction

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

Table 1. Relative dietary contribution (%) of seal, springbok, gemsbok, and browsers to the central Namib brown hyena population by age group (young < 7 years old and old ≥ 7 years old) given accessibility to a seal colony from their territory (Colony, Coastal, Inland). Population refers to the first model “seal access”. Old and Young values come from the “age + seal access” model.

Access to seal colonies	Age group	Relative dietary contribution (mean [95% CI])			
		Seal	Springbok	Gemsbok	Browsers
Colony	Population	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]
Coastal	Population	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]
Inland	Population	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]

When examining the effect of distance-to-nearest seal colony on hyena diet by age group, we found that dietary proportions of seal decreased as hyenas were found farther from the coast (Fig. 3; Fig. S2A). Consistent with the age + access to seals model reported above, we further found that old and young hyenas had slightly different diets. Old hyenas consumed more seals than springbok ($\text{mean}_{\text{seal}} = 55\%$, 95% CI: [37 - 71%]; $\text{mean}_{\text{springbok}} = 43\%$ [25 - 62%]), whereas young hyenas consumed more springbok than seals ($\text{mean}_{\text{seal}} = 34\%$ [15 - 51%]; $\text{mean}_{\text{springbok}} = 64\%$ [46 - 84%]). Consistent with our other models’ output, both young and old hyenas consumed similarly low proportions of browsers ($\text{mean}_{\text{young}} = 2\%$ [0 - 8%]; $\text{mean}_{\text{old}} = 2\%$ [0 - 8%]). Results of other models are provided in Table S1.

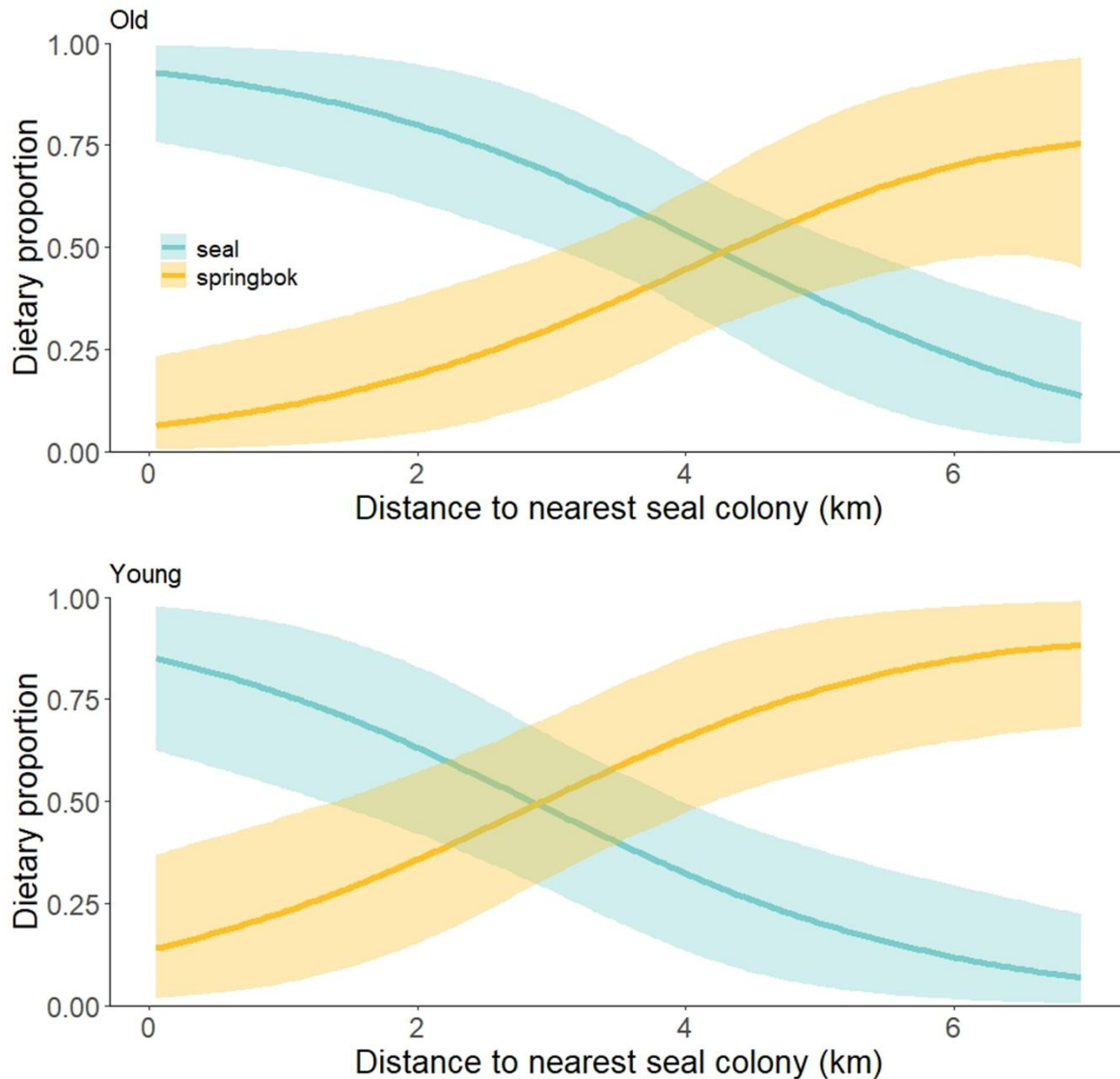


Fig. 3. Relation between the distance to the nearest seal colony on the consumption of Cape fur seals and springbok by old (≥ 7 years), and young (< 7 years) brown hyenas.

When testing the effect of body condition on diet while controlling for access to seals, we found a trend for better body condition to be associated with higher seals consumption (Fig.4; Fig. S2B). Among colony hyenas, predicted dietary proportions shifted from an approximately equal contribution of seals and springbok at low SMI values to diets clearly dominated by seals at high SMI values. Among coastal hyenas, individuals in poorer body

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

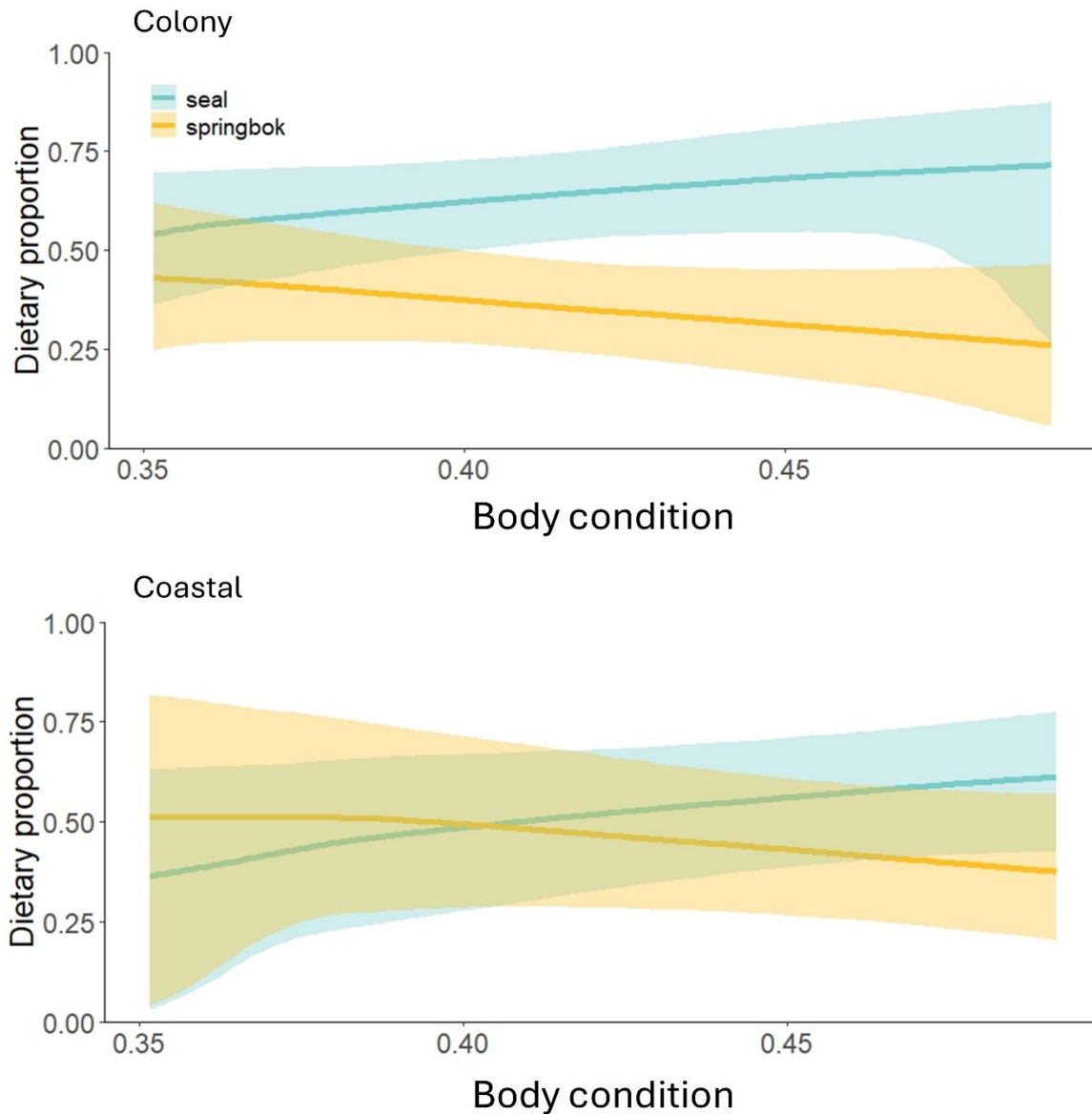


Fig. 4. Relation between body condition (scaled mass index — Peig and Green, 2008) on the consumption of Cape fur seals and springbok by brown hyenas whose territory location enabled regular access to a seal colony (“Colony”) and hyenas whose territory location enabled access to the coast but not to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

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

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

Spatial differentiation in hyena body condition

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

Isotopic niche size and overlap

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

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

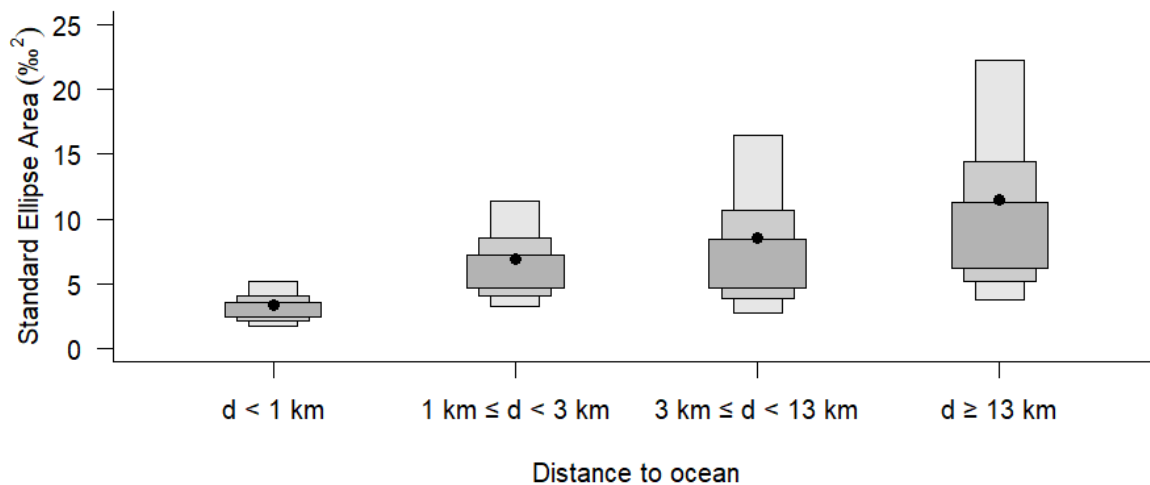


Fig. 5. Isotopic niche sizes of brown hyenas estimated from hair using Bayesian ellipses, grouped by Euclidean distance of sampling site to the coast.

Black-backed jackals had a much smaller isotopic niche than hyenas (jackals: $SEA_B = 1.15$ [0.87 – 1.53], $n = 50$), with a probability of 1 regardless of the hyena group considered (Fig. S3-S5). The mutual overlap (Table 2) between jackal and hyena isotopic niches was low, ranging from 0.03 ± 0.00 (hyena group closest to the coast) to 0.11 ± 0.00 (young female hyenas). Directional overlap revealed strong asymmetry: a large proportion of the jackal niche was

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

Table 2. Summary statistics (mean, standard deviation (SD), median and 95% Credible Interval (CI)) of mutual ($\leftrightarrow$) and directional ($\rightarrow$) overlaps between dietary niches, estimated from Bayesian ellipses, of brown hyenas (by hyena 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]
Coastal hyenas $\leftrightarrow$ Jackals	0.03	0.03	0.01	[0.00 - 0.12]
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]
Coastal hyenas $\rightarrow$ Jackals	0.10	0.14	0.05	[0.00 - 0.52]
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]
Jackals $\rightarrow$ Coastal hyenas	0.03	0.04	0.02	[0.00 - 0.14]

Discussion

Allochthonous resources and spatial heterogeneity can generate far-reaching effects on food webs (Polis et al., 1997). By examining how two terrestrial desert carnivorans exploited clumped marine subsidies, we found contrasting responses within and between species, likely driven by landscape heterogeneity and differences in territoriality. We found good support of our three hypotheses: both brown hyenas and black-backed jackals relied on abundant marine resources (Kuhn et al., 2008; Skinner et al., 1995; Wiesel, 2010), yet near the coast, hyenas

exhibited variation in trophic ecology, while the jackals' diet was more homogeneous. Note, however, that contrary to our second prediction, we found little effect of dietary seal proportion on body condition. In this two-predator system, the persistence of territoriality in the apex predator despite high resource abundance may create conditions whereby intraspecific competition becomes more ecologically relevant than interspecific competition. Hyenas consumed fewer seals farther from the coast, but for clan members residing on the coast, territory location relative to seal colonies was a major determinant of diet. Consequently, the patchy distribution of seal colonies was reflected in dietary differences among hyenas within travel distance to a seal colony, contrary to expectations under the resource distribution hypothesis (McDonald, 1983), and resulting in a non-linear relationship between diet and the distribution of the qualitative marine resource at finer spatial scale, with a general linear influence of the marine subsidies at broader spatial scale. Jackals, in contrast, increase territory size away from seal colonies, where food sources are not clumped (Jenner et al., 2011), and relax territoriality to exploit abundant marine resources, consistent with predictions from the resource dispersion hypothesis (MacDonald, 1983). Together, these findings suggest that marine subsidies exert strong but localized effects on the desert food web and illustrate how heterogeneous resource distribution may interact with consumer traits to shape realized niches (Subalusky & Post, 2019).

Possible implications of consuming marine subsidies

Marine subsidies in the Namib provide abundant, predictable prey requiring little search or handling effort (Kolar, 2005; Wiesel, 2010). In line with optimal foraging theory (Pyke, 1984)

both hyenas and jackals relied on seals rather than on scarcer, harder-to-kill terrestrial prey. In areas of high prey abundance, such as seal colonies with vulnerable pups, hyenas also engage in surplus killing — i.e., killing more prey than they consume (Wiesel, 2010). They preferentially feed on lipid-rich seal-pup brains (Wiesel, 2006) and milk — obtained from pumping the pups' stomach (Wiesel, pers. obs.) — and may leave the rest of the carcass, creating carrion that benefits smaller scavengers like jackals.

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

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

Intrapopulation trophic niche variation

Due to large isotopic separation between marine and terrestrial prey (e.g., Schoeninger & DeNiro, 1984), coastal ecotones — which usually have high prey diversity — are expected to broaden individual niches. However, unlike Arctic foxes (Dalerum et al., 2012; Tarroux et al., 2012), wolves from inner islands (Darimont et al., 2009), and caracals (Leighton et al., 2024), for which access both to terrestrial prey and marine subsidies expanded niches, hyena niches shrank closer to the coast. This apparent contradiction likely reflects the extreme scarcity of terrestrial prey in the Namib Desert, similar to the situation on remote islands of British Columbia, where wolves exhibited the narrowest niches of all subpopulations because terrestrial resources were scarce (Darimont et al., 2009).

A consequence of the resource dispersion hypothesis is that carnivores relax territoriality when resources are abundant and patchily distributed, because the costs of defending a territory large enough to encompass resource patches outweigh the benefits. Yet, brown hyenas in the Namib deviate from this expectation: individuals living on the coast but within travelling distance of a seal colony rely noticeably less on seals than neighboring hyenas with territory-mediated access to colonies. In the present resource context, intraspecific competition mediated by territoriality may therefore contribute to fine-spatial scale trophic heterogeneity (Goss, 1986; Wiesel, 2006). One study, based on a very small sample size, suggested that this pattern could reflect an evolutionary lag, whereby brown hyenas retain an obstinate strategy (i.e., territory size adapted to the lowest resource availability; von Schantz, 1984), shaped under past conditions when terrestrial resources fluctuated and seal populations were depleted (Goss, 1986).

Subtle dietary differences between age groups and the positive tendency of body condition to relate to seal consumption in hyenas with regular access to seals could suggest some level of intraspecific competition, including within clans. Although brown hyenas breed cooperatively, adults forage solitarily and may face some feeding competition with clanmates. Disputes over seal carcasses are occasionally observed, with larger, older hyenas in good body condition often prevailing (Goss, 1986; Wiesel, pers. obs.). During occasional intrusions into seal colonies in neighboring clan territories, individuals in better body condition may have a competitive advantage, which may increase foray success and explain the subtly higher proportion of seals in coastal hyenas in better condition. Additionally, higher seal consumption in older hyenas may reflect hunting experience and improved ability to kill larger seal pups that more mobile as they grow up (Wiesel, 2010).

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

Jackals exhibited a particularly narrow isotopic niche, with consistent diets across location, body mass, age, and sex. This uniformity likely reflects a breakdown in territoriality in response to concentrated food availability, consistent with the resource dispersion hypothesis (MacDonald, 1983). They may benefit individually from hyena surplus killing through scavenging, and their relatively high densities may also provide opportunities for kleptoparasitism (Fig. S6). Although their smaller body size relative to brown hyenas may limit the ability of a single jackal to kill and handle larger seal pups, cooperative hunting offsets this constraint by enabling the killing of larger seal pups (Merrifield, 2012; Murray et al., 2012). Their ability to exploit highly abundant marine resources may be constrained by mobility, when the energetic costs of travelling to seal colonies outweigh foraging benefits (Jenner et al., 2011). However, we could not assess the effect of distance to the coast, as all individuals sampled here had access to a seal colony.

Potential for interspecific competition

In areas where both species rely on terrestrial prey, several studies have reported a strong potential for competition and frequent agonistic encounters between brown hyenas and black-backed jackals, driven by dietary niche overlap (Destercke et al., 2025; Mills, 1978; Yarnell et al., 2013). Here, because food was not limiting, exclusion of jackals from high-quality marine resource through exploitation competition (i.e., resource depletion) was unlikely (Holdridge et al., 2016). However, the clumped distribution of seals likely increased encounter rates (Wiesel, 2006), possibly promoting interference competition at a fine spatial scale (Amarasekare, 2002;

López-Bao et al., 2016), which may explain frequent agonistic interspecific interactions and kleptoparasitism (Goss, 1986; Wiesel, 2006; Fig. S6).

At seal colonies, jackals far outnumber solitary-foraging hyenas. Group foraging can allow smaller competitors to dominate larger solitary foragers, like gray wolves dominating larger pumas (*Puma concolor*) (Elbroch & Kusler, 2018), white-backed vultures (*Gyps africanus*) outcompeting lappet-faced vultures (*Torgos tracheliotos*) (Kendall, 2013), and golden jackals (*Canis aureus*) negatively affecting striped hyenas (*Hyaena hyaena*) at carcasses (Panda et al., 2023). Although proximity to hyenas entails risks, including intraguild killing, opportunities for kleptoparasitism or scavenging likely outweigh the costs (Fig. S6; Prugh & Sivy, 2020).

Ecological implications

Although our study focused on a two-predator system, and results reflect the ecological conditions of the Namib desert, it has broader ecological implications. First, recipient-species traits may influence the impact of marine subsidies, leading to intraspecific niche variation, as shown in very different systems (e.g., Darimont et al., 2009). Second, the patchiness and spatial reach of allochthonous prey may interact with predator traits (e.g., mobility, territoriality) to influence the ecological relevance of localized indirect effects of predators — such as nutrient redistribution — especially in nutrient-poor systems (Johnson-Bice et al., 2023). While the role of subsidies in structuring communities is well established (Polis et al., 1997), the modulatory influence of community structure on recipient species remains underexplored. Finally, by integrating landscape and trophic ecology within frameworks, such as the resource dispersion

hypothesis, and optimal foraging theory, our findings offer new perspectives for exploring cross-ecosystem subsidy theory and predator niche dynamics.

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Author contribution:

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

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Appendix 2. Supplementary Tables and figures for:

Trophic responses of desert predators to clumped marine subsidies.

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).

In this appendix, we include tables and plot supporting the results presented in the main text. We further include results from preliminary analyses, which provide complementary information on the study system.

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 Tsau//Khaeb
4 (Sperrgebiet) National Park. xi.C[y] and xi.N[y] are the median multiplicative error term
5 estimates for C and N. Seal Access refers to an individual access to a seal colony within its
6 territory and was determined based on detailed knowledge of the history of individuals that
7 are part of a long-term project (Inland = territory does not include coast; Coastal = territory
8 includes coast but no seal colony and is not located across islands where seal colonies
9 live), Colony (territory includes a seal colony, or is located across from an island with a seal
10 colony), Unknown (the hyena is not a known individual). Initials are: O = Old (> 6years old),
11 Y = Young (< 7 years old), F = 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]

12

13 **Table S3.** Relative model performance using the leave-one-out cross-validation (LOOic)
14 approach and model output (Mean dietary proportion for each source and 95% credible
15 interval) of the 6 models compared in reconstructing black-backed jackal diet of the
16 Tsau//Khaeb (Sperrgebiet) National Park. xi.C[y] and xi.N[y] are the median multiplicative
17 error term estimates for C and N. (initials are: CCSR = Cape Cross Seal Reserve, A = Adult, J
18 = Juvenile, S = Subadult, F = Female, M = Male, O = Old (> 6years old), Y = Young (< 7 years
19 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]		
F Luderitz	0.74 [0.59 - 0.84]		0.15 [0.06 - 0.23]		0.11 [0.00 - 0.32]		

M CCSR	0.76 [0.68 - 0.83]	0.16 [0.10 - 0.21]	0.08 [0.00 - 0.21]
M Luderitz	0.74 [0.59 - 0.84]	0.14 [0.06 - 0.22]	0.12 [0.00 - 0.34]
Sex + Age			
FA	0.77 [0.67 - 0.84]	0.14 [0.08 - 0.20]	0.09 [0.01 - 0.23]
FJ	0.72 [0.57 - 0.81]	0.18 [0.08 - 0.25]	0.10 [0.00 - 0.32]
FS	0.77 [0.70 - 0.83]	0.17 [0.11 - 0.23]	0.06 [0.00 - 0.18]
MA	0.76 [0.67 - 0.84]	0.15 [0.08 - 0.20]	0.09 [0.00 - 0.23]
MJ	0.72 [0.67 - 0.82]	0.18 [0.09 - 0.27]	0.09 [0.00 - 0.32]
MS	0.77 [0.68 - 0.83]	0.18 [0.11 - 0.23]	0.06 [0.00 - 0.19]

Table S4. Prior calculation for brown hyena Bayesian mixing models. We integrated four sources: stomach content from hyenas from this project (Appendix 1), feces content from Skinner et al. (1995), direct observations from Skinner & Van Aarde (1981), and remains at dens from Kuhn, Skinner & Wiesel, (2008). Following Stock et al. (2018) we multiplied the frequency of occurrence of major prey items by the number of sources in the model and divided by the total number of samples.

source	area	method	species	frequency	total_obs	model	prior	comment
Skinner & van Aard (1980)	central Namib	scats	seal	51	68	4 prey	3.00	
Skinner & van Aard (1981)	central Namib	scats	gemsbok	0	68	4 prey		method inappropriate
Skinner & van Aard (1981)	central Namib	scats	springbok	0	68	4 prey		method inappropriate
Skinner & van Aard (1981)	central Namib	scats	hare	1	68	4 prey	0.06	grouped in Browsers
Skinner & van Aard (1981)	central Namib	scats	hyrax	2	68	4 prey	0.12	grouped in Browsers
Skinner & van Aard (1981)	central Namib	scats	gerbil	13	68	4 prey	0.76	grouped in Browsers
Skinner et al. (1995)	central Namib	direct obs	seal	119	194	4 prey	2.45	
Skinner et al. (1995)	central Namib	direct obs	springbok	1	194	4 prey	0.02	
Skinner et al. (1995)	central Namib	direct obs	rodent	1	194	4 prey	0.02	Browsers
Kuhn et al. (2008)	Sperrgebiet	remains at den	Seal	4206	5807	4 prey	2.90	
Kuhn et al. (2008)	Sperrgebiet	remains at den	springbok	85	5807	4 prey	0.06	
Kuhn et al. (2008)	Sperrgebiet	remains at den	gemsbok	122	5807	4 prey	0.08	
Kuhn et al. (2008)	Sperrgebiet	remains at den	small mammals	24	5808	4 prey	0.02	Browsers
Appendix 1	current study area	stomach content	seal	38	46	4 prey	3.30	
Appendix 1	current study area	stomach content	porcupine	7	46	4 prey	0.61	grouped in Browsers
Appendix 1	current study area	stomach content	Cape hare	7	46	4 prey	0.61	grouped in Browsers
Prey list								
browsers			Priors					
gemsbok			seals	3				
seal			gemsbok	0.1				
springbok			springbok	0.1				
			browser	0.5				

Kuhn, B.F., Skinner, J.D. & Wiesel, I. (2008) Diet of brown hyaenas (*Parahyaena brunnea*) on the Namibian coast. *Trans. R. Soc. South Africa* 63, 150–159.

Skinner, J.D. & Aarde, R.J. Van. (1981) The distribution and ecology of the brown hyaena *Hyaena brunnea* and spotted hyaena *Crocuta crocuta* in the central Namib Desert. *MADOQUA* 12, 231–239.

Skinner, J.D., Aarde, R.J. van & Goss, R.A. (1995) Space and resource use by brown hyenas *Hyaena brunnea* in the Namib Desert. *J. Zool.* 237, 123–131.

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

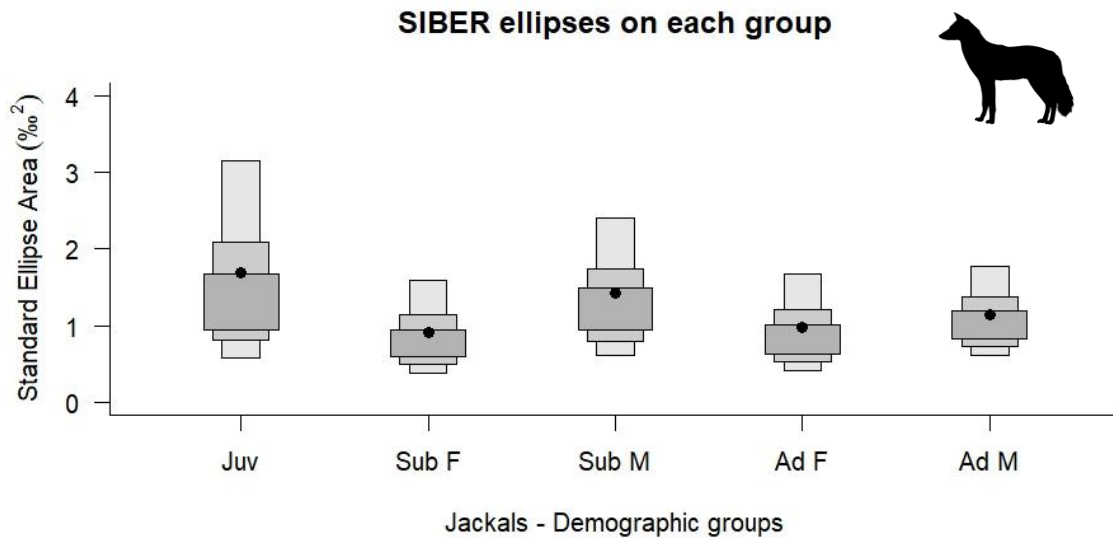


Figure S1. Isotopic niche sizes estimated from hair of black-backed jackals (n = 50) grouped by age class (Juvenile, Subadult, Adult) and sex (M, F) using Bayesian ellipses. This model was part of preliminary analyses.

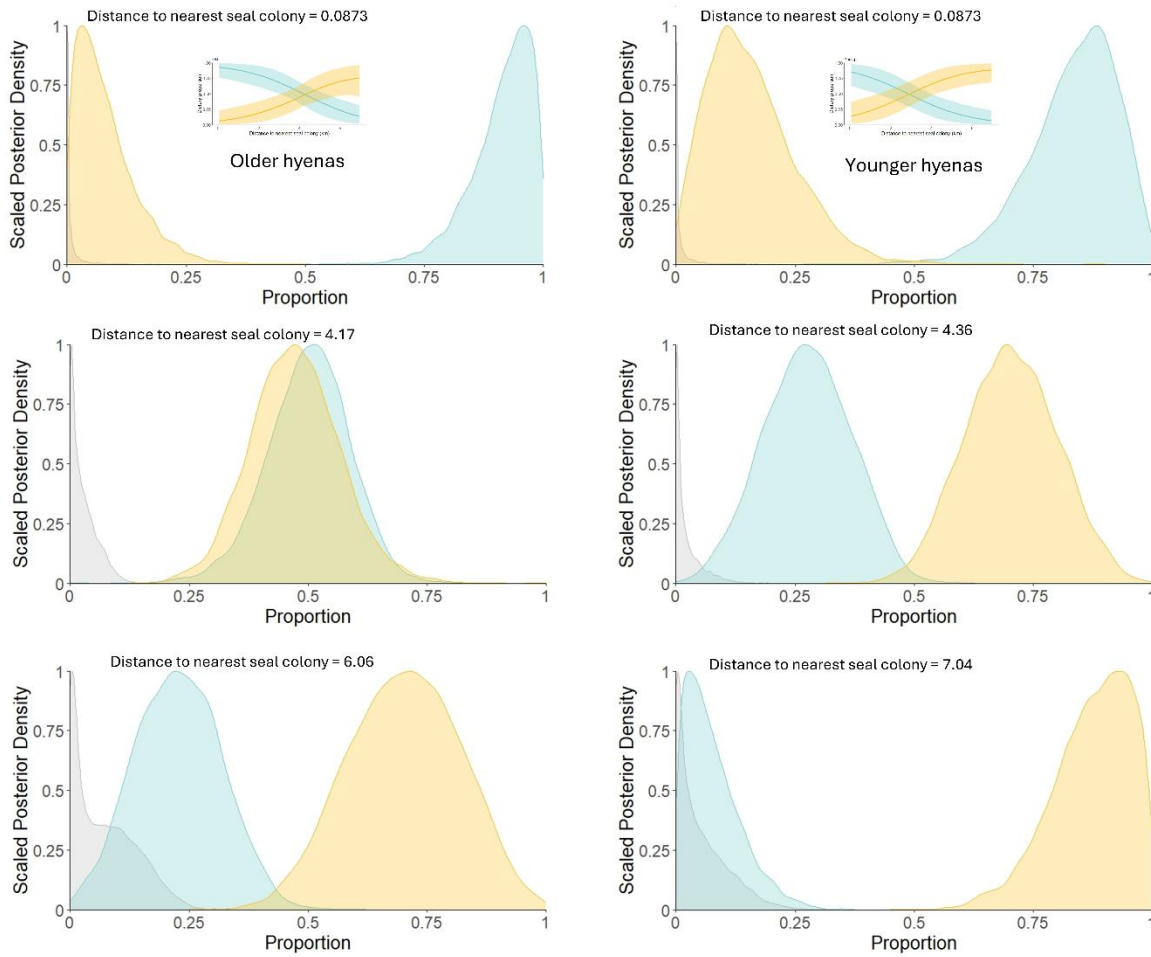


Figure S2A. Posterior estimates of dietary proportions of seals (Blue), springbok (Yellow) and browsers (grey) for Older (left) and younger (right) hyenas at minimum, median and maximum distance from the nearest seal colony. MixSIAR models continuous effects as linear relationships with the isometric log-ratio (ILR)-transformed dietary composition. For each continuous covariate, MixSIAR estimates $K - 1$ ILR coefficients for K dietary sources. The posterior median slopes were 1.15 (95% CrI: -1.02 to 3.28) for ILR1 and -0.33 (95% CrI: -1.97 to 0.81) for ILR2. The joint effect of the two ILR coefficients produced a pronounced change in predicted dietary composition across the observed distance gradient.

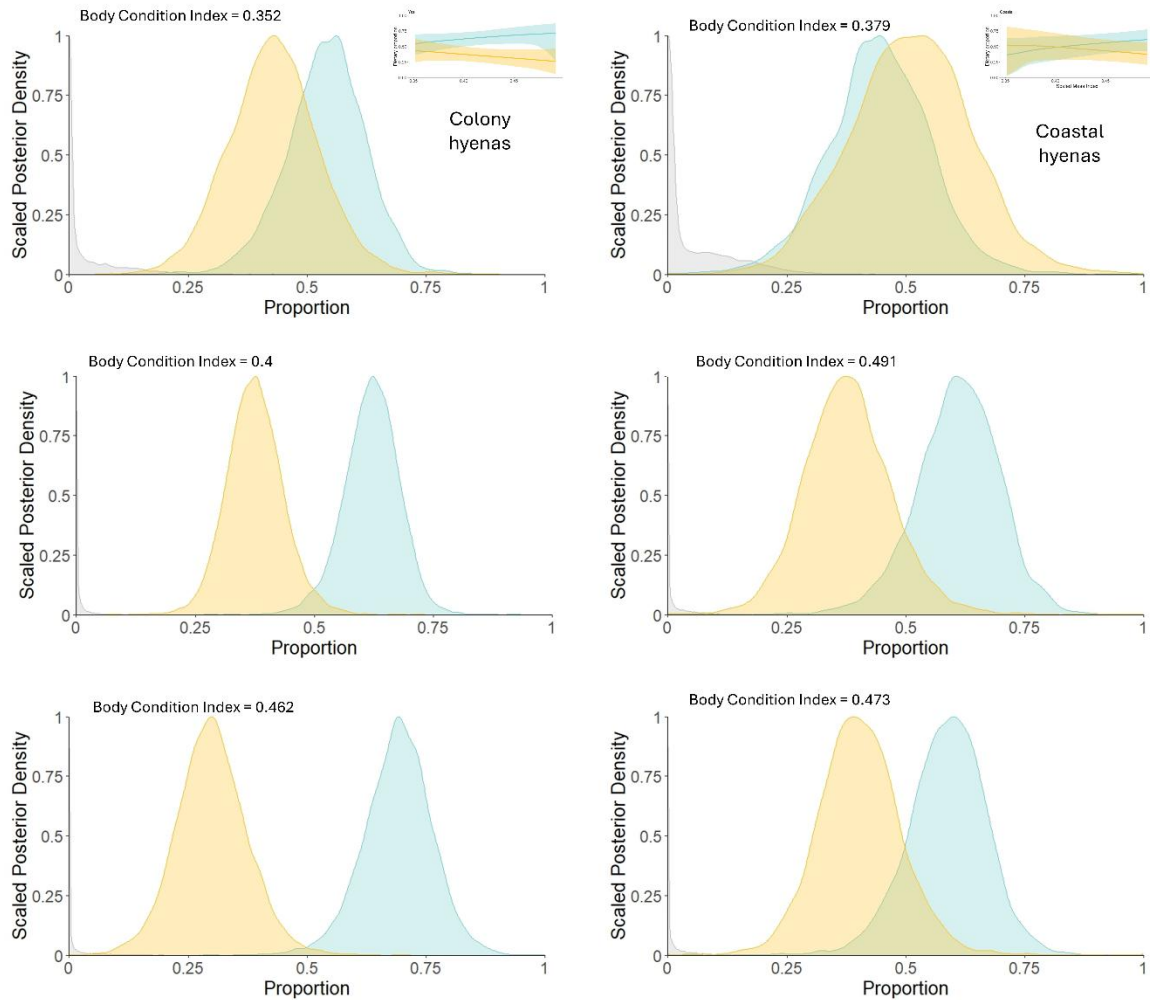


Figure S2B. Posterior estimate of dietary proportions of seals (Blue), springbok (Yellow) and browsers (grey) for hyenas with territory-mediated access to a seal colony (left) and coastal hyenas without territory-mediated access to a seal colony (right) at minimum, median and maximum body condition index estimated using the Scaled Mass Index (SMI) developed by Peig and Green (2009). The posterior median slopes were -0.63 (95% CrI: -6.22 to 4.76) for ILR1 and -0.21 (95% CrI: -3.41 to 2.94) for ILR2. The joint effect of the two ILR coefficients produced a change in predicted dietary composition across the observed SMI gradient that was relatively pronounced for hyenas with access to a seal colony, but less so for coastal hyenas. Note that the large credible intervals around the slopes indicate substantial uncertainty in the strength and direction of these relationships, possibly due to unmodelled variation with other factors.

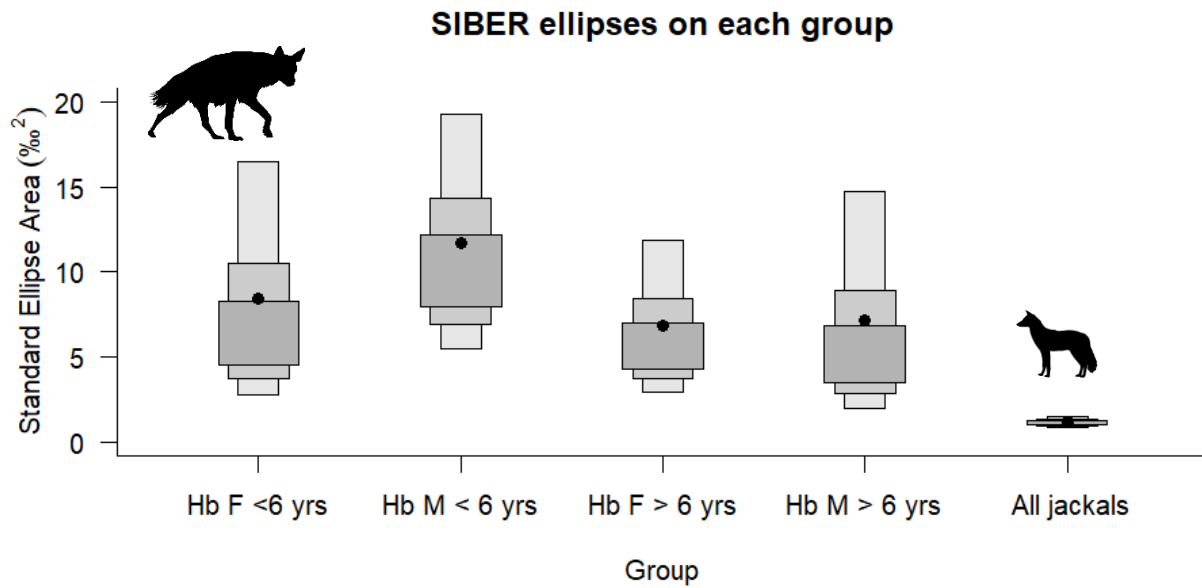


Figure S3. Isotopic niche sizes estimated from hair samples using Bayesian ellipses for brown hyenas (Hb) grouped by sex (Female, Male) and age class (4–6 years old and ≥7 years old), and black-backed jackals grouped together. Sample sizes for hyenas were: young females ($n = 5$), young males ($n = 11$), old females ($n = 10$), old males ($n = 5$), and jackals ($n = 50$).

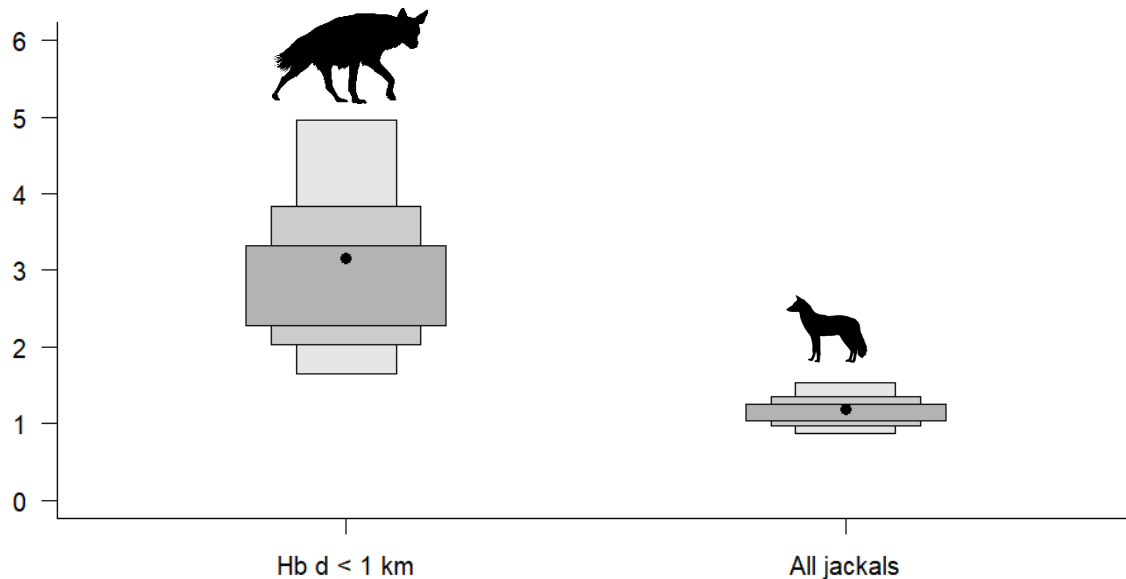


Figure S4. Isotopic niche sizes estimated from hair samples using Bayesian ellipses for brown hyenas (Hb) residing < 1 km from the coast and black-backed jackals grouped together. Sample sizes were: hyenas $d < 1$ km ($n = 14$) and jackals ($n = 50$).

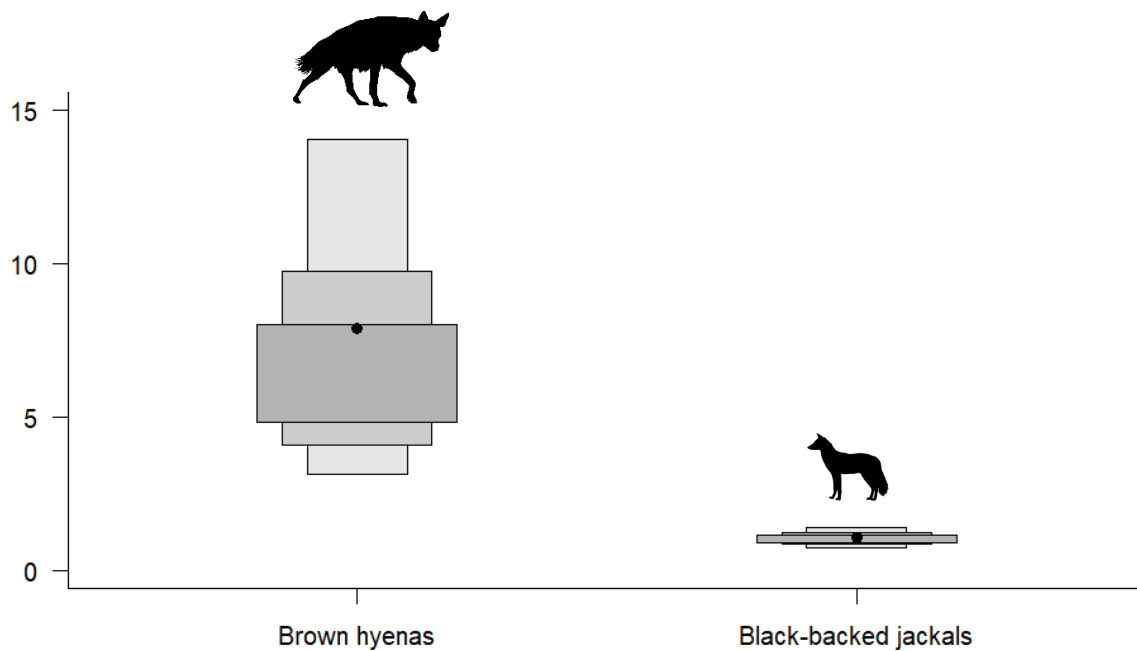


Figure S5. Isotopic niche sizes estimated from hair samples using Bayesian ellipses for brown hyenas (Hb) and black-backed jackals sampled in Lüderitz. Sample sizes were: Lüderitz hyenas ($n = 8$) and Lüderitz jackals ($n = 13$). This model was part of preliminary analyses.

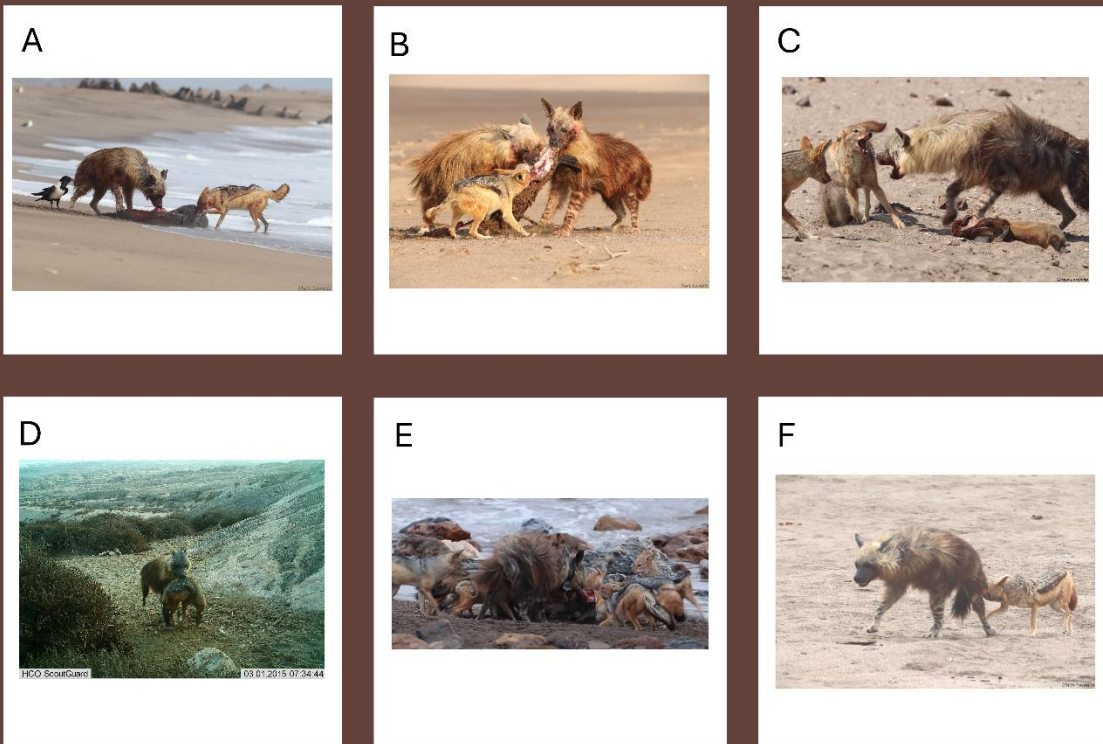


Figure S6. Examples of interactions between brown hyenas and black-backed jackals at or near seal colonies. (A) no aggressive behavior was observed, (B) successful attempt at kleptoparasitism by the jackal, while two hyenas were in dispute over a seal carcass, (C) the hyena defends its prey from jackals, (D) Intraguild predation by a hyena on a jackal, (E) the high density of jackals may provide an advantage in kleptoparasitism events, and occasionally hyenas have no choice but to abandon their prey to jackals, (F) a jackal aggresses a hyena, biting its leg, although no food was involved. (Photo credit: Marie Lemerle, Brown Hyena Research Project).