Sex-specific dietary specialization in a terrestrial apex predator, the leopard, revealed by stable isotope analysis

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**Sex-specific dietary specialization in a terrestrial apex predator, the leopard,
revealed by stable isotope analysis**

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Short title: Dietary specialization of leopards

Abstract

Apex predators in terrestrial ecosystems, such as leopards in the African savanna, feed on a wide variety of prey species, yet it is unknown whether individuals specialize on certain prey, and whether specialization changes with body traits. Here, we asked whether individual specialization of adult leopards varies with sex, body mass, body length and age classes. We used the variation of stable carbon and nitrogen isotope ratios in 643 segments of whiskers as a temporal record of past diets and established isotopic dietary niches for 36 adult leopards (18 males, 18 females). Based on a variance analysis for stable carbon isotope ratios, we found that between-individual variation was larger than within-individual variation, indicating a high degree of overall specialization within the studied leopards. Female adult leopards exhibited larger isotopic dietary niche widths than male adult leopards. Isotopic niche width did not vary with body mass, length or age. Our data suggest a difference in the level of specialization between the sexes, which might be explained by more opportunistic feeding of small-sized female leopards, most likely connected with a higher use of small prey species of different isotopic composition. Inter-sexual resource partitioning likely facilitates territory sharing between the sexes.

Key words: Dietary specialization, Namibia, predation, foraging, carnivores

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Introduction

Apex predators are important regulators of populations of prey species (Terborgh *et al.*, 2001; Salo *et al.*, 2010) and link food webs via trophic interactions (marine and terrestrial food webs: Hildebrand *et al.*, 1999; Darimont & Reimchen, 2002; C4 and C3 food webs: Voigt *et al.*, 2014). They are also of particular conservation interest, since many of them are in conflict with humans (Inskip & Zimmermann, 2009; Henschel, Abernethy & White, 2011). Compared to other faunal groups, apex predators are under stronger pressure from hunting, retaliatory killing in response to livestock predation and anthropogenic changes of their habitats (Macdonald, Loveridge & Rabinovitz, 2010; Balme *et al.*, 2014; Darimont *et al.*, 2015; Krofel *et al.*, 2015; Swanepoel *et al.*, 2014, 2015). Thus, understanding their feeding ecology is particularly rewarding. Yet, we lack a thorough understanding of specialization at the individual level for most apex predators. Recent research suggests that data on niche width and prey selection which is based on entire carnivore populations can be misleading when individual specialization is not taken into account (Elbroch *et al.*, 2016). This might be particularly relevant in the context of human-carnivore conflicts if an assumed specialization is leading to the killing of threatened carnivores (Linnell *et al.*, 1999). Also, there is a growing body of evidence on the importance of individual behavioural differences (Bell, Hankison & Laskowski, 2009; Wolf & Weissing, 2012), including the individuality of foraging behaviour in top predators (Cavalcanti & Gese, 2010; Steyaert *et al.*, 2014; Elbroch *et al.*, 2016). Individual specialization in predatory behaviour can have important consequences for ecology and evolution, including effects on population stability, predator-prey interactions, adaptive evolution and anti-predator behaviour (Wolf & Weissing, 2012; Modlmeier *et al.*, 2014; Elbroch *et al.*, 2016). In addition, incorporating the individual preferences of predation has the potential to improve our understanding of predator-prey dynamics (Bolnick *et al.*, 2011).

Dietary studies of top predators are hampered by the difficulty in obtaining comprehensive data on the composition of consumed dietary items for given individuals, mainly because of the difficulties related to consistently observing and accessing top predators. Thus, most studies either remain anecdotal, semi-quantitative or biased, e.g. when based on faecal samples or kill sites alone, or these studies provide only a brief temporary snapshot of what predators have consumed recently (Mills, 1992; Henschel *et al.*, 2005; Hayward *et al.*, 2006; Klare, Kamler & Macdonald, 2011; Wachter *et al.*, 2012). Stable isotope ratios of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) have been successfully used as proxies for dietary specialization in predators. Past studies followed one of two approaches. They either looked at $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of tissues with different isotopic retention times, e.g. muscle, liver and blood (Matich, Heithaus & Layman, 2011; Kim *et al.*, 2013; Voigt *et al.*, 2014) or at values from biologically inert body products with constant growth rate, i.e. tail hair, guard hair, whiskers or vibrissae (Darimont & Reimchen, 2002; Urton & Hobson, 2005; Newsome *et al.*, 2009; Codron *et al.*, 2012; Lehmann *et al.*, 2015).

In a marine top predator, the Californian sea otter (*Enhydra lutris nereis*), animals exhibited highly variable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in vibrissae, suggesting that the study population made use of almost all suitable dietary species (Newsome *et al.*, 2009). However, variation in stable isotope ratios was best explained by inter-individual effects, indicating that individuals differed largely in the relative amount of consumed dietary species, i.e. individuals exhibited relatively constant choices of food items. Similar findings have been reported for cheetahs (*Acinonyx jubatus*) on commercial farmland in Namibia (Voigt *et al.*, 2014). In grey wolves (*Canis lupus*) of North America, inter-individual variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was high even in this socially foraging top predator (Urton & Hobson, 2005), indicating that individual specialization was also independent of social group composition. In summary, previous studies

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3 89 highlighted the applicability of the stable isotope approach for estimating isotopic dietary niches
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5 90 in top predators. Also, they underline that top predators make use of the full spectrum of prey
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8 91 species at the population level, yet individuals may specialize on different prey species. However,
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10 92 none of the previous studies investigated how specialization on isotopically different dietary
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12 93 items may change with body mass, body length, age and sex within a top predator species. Such
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14 94 information is not only of academic interest, but can also be important for example in the context
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17 95 of human-carnivore conflicts and to understand intra- and inter-specific competitions in
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19 96 carnivores.

21 97 Here, we studied the isotopic specialization of an apex predator in an African ecosystem,
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23 98 the leopard (*Panthera pardus*), by analyzing the variation in stable isotope ratios in incrementing
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26 99 segments of whiskers obtained from a total of 36 individuals. In leopards, whiskers grow at 0.65
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28 100 mm per day (Mutirwara, Radloff & Codron, 2017), i.e. a 10 cm whisker would be produced over
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31 101 about 154 days. Leopards are generally characterized by a highly variable diet (Hayward *et al.*,
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33 102 2006; Jooste *et al.*, 2013), which makes them a suitable model species to study interactions
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35 103 between individual traits and dietary niche. We estimated the isotopic dietary niche width of
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37 104 individuals based on the area encompassed by the 95% confidence intervals of Bayesian ellipses
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39 105 established for intra-individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Newsome *et al.*, 2007; del Rio *et al.*, 2009).
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41 106 If leopards feed on a variety of isotopically distinct prey species, such as grazers (high $\delta^{13}\text{C}$
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43 107 values) and browsers (low $\delta^{13}\text{C}$ values) or prey species with high or low $\delta^{15}\text{N}$ values (Voigt *et al.*,
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45 108 2015), the scatter plot of isotopic data from whiskers increments would be larger compared to
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47 109 specialist leopards that feed only on a subset of aforementioned species groups. Thus, the size of
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49 110 Bayesian ellipses based on individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values may inform about the level of
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52 111 specialization across individuals. However, it is important to keep in mind that feeding on many
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prey species may not necessarily lead to large isotopic variance in the consumer tissue, if prey species are isotopically similar (del Rio *et al.*, 2009).

On the population level, we expected leopards to derive food from all available food sources, indicated by a large range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across individuals. On the individual level, we expected small-sized leopards to depend more on smaller prey species (Sinclair *et al.*, 2003), which typically consist of more different species compared to large prey species. This includes juveniles of a certain species which leopards may not target as an adult prey animal. Therefore, the dietary niche of small-sized leopards should be broader than the one of larger leopard individuals, which are predicted to specialize on consuming larger prey species. Thus, given the sexual size dimorphism in leopards we expected females to have a larger isotopic dietary niche width than males. Also, based on the same argument, we expected the isotopic dietary niche width to decrease with increasing body mass or length in leopards. Lastly, we tested whether isotopic dietary niche width would correlate with the consumption of grazers (C4 diet) or browsers (C3 diet), as indicated by $\delta^{13}\text{C}$ values, or with trophic position, as indicated by $\delta^{15}\text{N}$ values.

Materials and Methods

Field work was conducted on commercial cattle and game farmland in central Namibia (22°00' S to 23°00' S and 16°40' E to 18°20' E) between December 2011 and February 2016. Our study was approved by the Ministry of Environment and Tourism (MET) in Windhoek, Namibia (permit numbers 1514/2011, 1689/2012, 1813/2013, 1914/2014, 2067/2015). Leopards were captured in box traps and then chemically immobilized with 0.08 mg/kg medetomidine hydrochloride (Medetomidine 10 mg/ml, Kyron Laboratories, South Africa) and 3.9 mg/kg ketamine (Ketamine 1G, Kyron Laboratories, South Africa) and reversed with 0.11mg/kg atipamezole (Antisedan®,

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3 136 Pfizer, South Africa). After immobilization, leopards were weighed with a spring scale attached
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5 137 to a stretcher carrying the leopard (accuracy 0.1 kg) and body length was measured from the tip
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7 138 of the nose to the base of the tail (accuracy 0.5 cm). We did not obtain body length measurements
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10 139 of 2 females and 1 male and thus discarded these datasets from further statistical analysis. We
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12 140 also had access to three leopards legally shot as problem animals of which one hunter had
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14 141 measured the body mass of one leopard before it was skinned. We categorized the adult
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16 142 individuals into three age classes, young adults, medium aged adults and old adults, by the wear
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18 143 and tear of teeth and fur. Animals with no missing and broken teeth, shiny coat and/or no scars
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20 144 were categorized as young adults, animals with a few missing and broken teeth, and/or a few
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23 145 scars were categorized as medium aged adults and animals with several missing and broken teeth,
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26 146 dull coat and/or several scars were categorized as old adults. To determine the degree of
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28 147 specialization based on stable isotope ratios, we collected the longest available whisker from each
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30 148 individual. Samples were put separately into envelopes and shipped to the stable isotope
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32 149 laboratory of the Leibniz Institute for Zoo and Wildlife Research in Berlin, Germany under the
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35 150 corresponding export and import CITES permits.

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37 151 Whiskers were cleaned of external contaminants using a chloroform-methanol solution
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39 152 (2:1) and afterwards dried in an oven over 24 hours at 50°C. Then, whiskers were cut into small
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41 153 segments of 0.5 cm, each segment considered to integrate isotopically over a growth period of 8
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43 154 days. From each segment, we put a 0.5 mg sample in a tin capsules (IVA Analysetechnik e.K.
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45 155 Meerbusch, Germany). Capsules were folded and then placed in an autosampler. Samples were
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47 156 combusted and analyzed using an elemental analyzer (CE 1110 EA; Thermo Finnigan, Bremen,
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49 157 Germany) coupled to a Delta Plus isotope ratio mass spectrometer (Thermo Finnigan, Bremen,
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51 158 Germany) in continuous flow. Atmospheric nitrogen was used as the standard for stable nitrogen
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55 159 isotopes and Vienna-PDB as the standard for stable carbon isotopes. The methodological

approach in analyzing stable carbon and nitrogen isotope ratios has been described in detail in Popa-Lisseanu *et al.* (2012). All stable isotope ratios are expressed in the delta notation as parts per mille (‰) deviations of the sample isotope ratios from the ratios of respective international standards (air nitrogen for $\delta^{15}\text{N}$ and V-PDB for $\delta^{13}\text{C}$ values). Precision of measurements was always better than 0.4‰ (one standard deviation; SD). We calculated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each individual separately, before the values entered the analyses.

Body traits of animals were compared using Student t-tests when requirements for parametric testing were fulfilled. We used the element that covered the largest per mille range ($\delta^{13}\text{C}$ values) to obtain variance measures of the intra- and inter-specific variation of the isotopic composition using a one-way ANOVA. Further, isotopic dietary niche metrics were calculated and plotted based on stable isotope ratios of segments for each individual whisker using the SIBER package (Jackson *et al.* 2011) in R (version 3.3.1). Standard ellipse area (SEA) values were corrected for small sample size (SEA_c) using SIBER (Jackson *et al.*, 2011), version 4.2, in R. We defined the 95 % CI of these niches as the actual boundaries of individual isotopic niches during the study period (see Jackson *et al.*, 2012). We then tested whether males and females differed in mean SEA_c using Student t-test. Further, we tested whether SEA_c co-varied with individual body parameters, such as body mass, body length and age classes using a general linear model. Finally, we tested in both sexes whether SEA_c was related to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using Spearman correlation coefficients. Alpha values were set to 0.05. Statistics were calculated with either R (R Core Team 2014) or SYSTAT (Systat Software Inc., Richmond, U.S.A.). Data is presented as mean values $\pm$ one SD.

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183 **Results**

184 On average, we obtained 17.6 (± 3.8, range: 10 - 22) whiskers segments from male and 18.1 (±

185 4.1, range: 12 - 29) from female leopards and measured stable isotope ratios in a total of 643

186 segments. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individual whiskers ranged over 9.2 ‰ (range: -13.4 to -

187 19.1 ‰) and 5.5 ‰ (range: 8.1 to 13.6 ‰), respectively, in male and over 10.5 ‰ (range: -20.3 to

188 -9.8 ‰) and 4.1 ‰ (range: 8.2 to 12.3 ‰), respectively, in female leopards (Fig. 1 and 2).

189 Overall, $\delta^{13}\text{C}$ values of leopards averaged -13.4 ± 2.6 ‰ in male and -14.1 ± 3.1 ‰ in female

190 individuals, and $\delta^{15}\text{N}$ values averaged 11.2 ± 1.5 ‰ for male and 10.1 ± 1.4 ‰ for female

191 leopards. Following a one-way ANOVA, individuals differed significantly in the consumption of

192 isotopically different prey ($F_{607,35} = 32.9$, $P < 0.001$). Based on a variance component analysis,

193 we found that between-individual variation explained 65.5% and within-individual variation

194 34.5% of the variation in $\delta^{13}\text{C}$ values.

195 Adult male leopards were on average 22.6 kg heavier than adult female leopards (males:

196 57.9 ± 8.5 kg, females: 33.8 ± 5.3 kg; $t_{31} = 9.6$, $P < 0.001$). Also, male leopards were larger than

197 females (body length: males: 127 ± 14 cm; females: 114 ± 6 cm; $t_{26.7} = 9.8$, $p < 0.001$). Twelve

198 leopards were assigned to age class ‘young adult’ (4 males, 8 females), 21 to age class ‘medium

199 aged adult’ (12,9) and 3 to age class ‘old adult’ (2,1). Male and female leopards in our study were

200 of similar age ($X^2 = 1$, $P > 0.05$). According to a GLM, none of the individual traits (body mass:

201 $F_{27,1} = 0.38$; $P = 0.847$, length: $F_{27,1} = 0.09$, $P = 0.772$; age class: $F_{27,2} = 0.87$, $P = 0.206$), except sex

202 ($F_{27,1} = 4.71$, $P = 0.039$) correlated with the isotopic dietary niche size SEA_c (see Fig. 3 for sex-

203 specific differences in SEA_c) We then tested whether the isotopic dietary niche size varied with

204 $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, but detected no significant correlations for 3 out of 4 possible relationships

205 (male: $r_s = -0.31$ for $\delta^{13}\text{C}$ values, $P > 0.05$; $r_s = -0.134$ for $\delta^{15}\text{N}$, $P > 0.05$; female: $r_s = 0.07$ for

206 $\delta^{13}\text{C}$, $P > 0.05$). In females, SEA_c correlated negatively with $\delta^{15}\text{N}$ values ($r_s = -0.61$, $P < 0.05$).

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208 Discussion

209 We used the stable isotope record of whisker increments as a proxy for the dietary history and the
210 level of specialization in leopards on commercial farmland in Namibia. We used whiskers of
211 approximately 8-10 cm length, which integrates over a period of approximately 150 days when
212 assuming a growth rate of 0.65 mm per day reported for a single captive leopard (Mutirwara *et*
213 *al.*, 2017). Growth rates of free-ranging leopard may deviate from this measurement. Here, we
214 assume that growth rates do not vary systematically across individuals of our study populations.
215 A systematic difference in growth rates between groups of individuals may alter the estimate of
216 individual specialization, yet given the large number of segments included in this study
217 (approximately 18 segments per whisker), we do not anticipate this to affect our results. Mean
218 $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of leopard whiskers were broadly distributed across the isotopic space of the
219 potential prey species that are typically found in the study area. In a previous study, Voigt and
220 colleagues (2004) listed potential prey species of cheetahs on commercial farmland in Namibia.
221 Stable isotope data varied between -23.8 ‰ and -12.3 ‰ for carbon and between 7.6 ‰ and 10.7
222 ‰ for nitrogen (Voigt *et al.*, 2014), which is within the same range of leopard isotope data of this
223 study. The large variability in isotopic data between individuals suggests that, from a population
224 perspective, leopards made use of many prey species that differed markedly in their isotopic
225 composition. Variation of $\delta^{13}\text{C}$ values was large between individuals, indicating individual
226 specialization of leopards on the carbon scale. This confirms previous studies that populations of
227 apex predators consist of specialized individuals that focus on specific species within the
228 spectrum of available prey (Matich *et al.*, 2011; Newsome *et al.*, 2009; Voigt *et al.*, 2014;
229 Elbroch *et al.*, 2016; Broekhuis *et al.*, 2018). The broad use of prey species is also consistent with
230 previous reviews conducted at various locations throughout the distribution range of leopards

(Hayward *et al.*, 2006). For example, leopards from the Western Cape in South Africa consumed many small and medium-sized ungulate, rodent and bird species (Braczkowski *et al.*, 2011). In Gabon, almost 60% of the biomass consumed by leopards consisted of various ungulate species, followed by diurnal primate species and large rodent species (Henschel *et al.*, 2005). This high level of flexibility in foraging behaviour may be one of the keys to the success of leopards in anthropogenically modified landscapes.

At our study site, male leopards weighed almost twice as much as female leopards, yet sexes did not differ as strongly in body length. Female and male leopards in our study came from similar age classes, thus sex-specific difference in body traits in isotopic parameters could not be explained by age differences. We observed that adult female leopards exhibited a larger isotopic dietary niche (SEA_c) width than males, which highlights that female leopards are more generalist consumers than male leopards. We argue that small-sized leopards, such as most females, use smaller-sized and consequently more diverse prey species, which might correlate with an increase in isotopic dietary niche width. This diversity might also be linked to whether females are accompanied by cubs, which might require more flexibility in the choice of prey species, also depending on the age of the cubs. Furthermore, Pitman and colleagues suggested that female leopards may be limited in their foraging ability due to possible interactions with larger predator species, such as lions (*Panthera leo*) (Pitman *et al.* 2013).

We did not detect a correlation between biological variables and SEA_c in female and male leopards. We acknowledge that our descriptive and thus correlational approach does not allow differentiating between cause and effect. Nevertheless, our results are in line with previous studies that suggest larger leopards, i.e. males, hunt larger prey species more effectively (Bothma & le Riche, 1984; Bothma & Coertze, 2004; Stander, 1997) and are probably also more successful in defending their prey against kleptoparasites (Pitman *et al.*, 2013). Overall, large

individuals seem to be less dependent on hunting smaller prey. In addition to body size, males may exhibit morphological adaptations that are likely connected with hunting larger prey, such as the sagittal crest on top of the skull that serves as an attachment for jaw muscles (Sunquist & Sunquist, 2002). We found no correlation between SEA_c and any of the two stable isotope ratios, except for females for which SEA_c was negatively correlated with $\delta^{15}N$ values. For $\delta^{13}C$ values, this pattern indicates that a specialist or generalist diet is not related to a preference for browsing or grazing ungulates. If leopards would be specialist for grazers (C4 plant diet) or browsers (C3 plant diet), we would expect a correlation between SEA_c size and high or low $\delta^{13}C$ values, respectively. In contrast, our data suggests that leopards may specialize on any prey species, i.e. grazers or browsers alone, or a mix of both. The correlation between SEA_c and $\delta^{15}N$ values in female leopards might be related to more specialized female leopards foraging on prey species with higher $\delta^{15}N$ values, possibly on those at a higher trophic level.

Observed differences in feeding patterns between sexes could have several ecological and management implications. First, inter-sexual differences in diet may result in some level of intra-specific resource partitioning (Hayward *et al.*, 2006), which could reduce competition among leopards. Reduced inter-sexual food competition has been suggested to be one of the main drivers for the evolution of sexual size dimorphism in carnivores (Dayan & Simberloff, 1996). We suggest that the observed connection between diet, body mass and sex of leopards could be such a case. This is not unexpected given that leopards exhibit a land tenure-social system, in which mature individuals typically exclude conspecifics of the same sex from large parts of their territory, while territories usually overlap extensively between the sexes (Bailey, 1993; Stander *et al.*, 1997). A similar pattern could be expected for resource partitioning between adults and sub-adults, because in leopards offspring may remain within their natal home ranges several years

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3 278 after separating from their mothers (Fattebert *et al.*, 2015). Our study, however, did not include
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5 279 samples from sub-adults, thus further research is needed to investigate this idea.
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8 280 Since adult female leopards rely on more diverse prey species, their predation effects on
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10 281 prey populations are expected to be more diluted compared to that of adult male leopards.
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12 282 Therefore, the impact of females on a given prey species should be lower compared to the one of
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14 283 males. This is relevant from a game management perspective, as well as for livestock
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16 284 depredations. The relatively higher individual specialization of males on prey species suggests
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18 285 that males have a higher potential to specialize on hunting livestock or endangered wildlife
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20 286 species that may get repeatedly targeted by the same individual leopard (Bailey, 1993). This is
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22 287 confirmed by the higher proportion of males among leopards associated with livestock
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24 288 depredations (Linnell *et al.*, 1999; but see Kerth *et al.*, 2013).
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28 289 Overall, the high degree of specialization and high individual variation in the isotopic
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30 290 composition of the consumed diets in our data suggest that diet analyses need to be interpreted
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32 291 with caution. Datasets from a small number of individuals can lead to biased results which are not
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34 292 representative for the entire population. This may be particularly relevant for GPS telemetry
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36 293 studies on leopards, during which leopard location clusters are used to find prey remains and
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38 294 which are typically limited to small numbers of monitored individuals. Ensuring representative
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40 295 sample sizes should therefore be a prerequisite for such studies. Alternatively, we suggest
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42 296 combining results from several small-scale GPS studies in order to obtain reliable information
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44 297 based on sufficient sample sizes, ideally with evenly distributed sex and age classes, and thus
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46 298 improve leopard dietary research. Furthermore, studies in which telemetry data are used to locate
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48 299 prey remains are also potentially biased towards larger prey species and miss possibly important
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50 300 small prey species as part of the diet (Bailey, 1993; Mills, 1992, Pitman *et al.*, 2012). Only with a
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52 301 very labour intense sampling regime Pitman *et al.* (2013) were able to minimise the bias against
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smaller prey. Thus, such studies should be combined with scat analyses to detect also small prey species (e.g. Pitman et al., 2013; Martins *et al.*, 2011; Tambling et al., 2012). Isotope analyses overcome these difficulties, and samples obtained from individuals with respective information on their body mass, age and sex of the predator can provide further insights into the importance of these parameters in the foraging behaviour, as we demonstrated in the case of the leopard in Namibia.

In summary, we showed that male and female leopards use a broad isotopic dietary niche on commercial farmland in Namibia, and isotopic dietary niches were larger in females compared to males. We argue that the more variable isotopic niche width of female leopards might be associated with the consumption of smaller and isotopically more variable prey species compared with the prey spectrum of male leopards. Differences in isotopic niche width between males and females may allow both sexes to use the same area for foraging without necessarily engaging in exploitation competition.

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Figure legends

Figure 1: Stable carbon ($\delta^{13}\text{C}$) and nitrogen isotope ratios ($\delta^{15}\text{N}$) in subsequent segments of leopard whiskers of 18 males (blue color; A, B) and 18 females (red color; C, D). Individual leopards are indicated by different lines.

Figure 2: Bivariate plot of stable carbon and nitrogen isotope ratios in segments of whiskers collected from 18 male (A) and 18 female leopards (B). Individual leopards are indicated by differently colored symbols and lines.

Figure 3: Standard ellipsoid areas (SEA_c) as a measurement for isotopic dietary niche width, for 18 male and 18 female adult leopards.

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