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Is the Black Harrier *Circus maurus* a specialist predator? Assessing the diet of a threatened raptor species endemic to Southern Africa

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26 **Abstract**

27 Studying the diet of wild animals is central for understanding their flexibility in food requirements.
28 The Black Harrier *Circus maurus* is an endangered raptor in South Africa and Namibia. To date,
29 information about the diet of the species is insufficient for a comprehensive understanding of their
30 ecology. We studied the diet composition of breeding Black Harriers using ca. 1000 pellets (> 1700
31 identified prey) collected at nest sites in two geographical regions (coastal vs. interior-mountain)
32 over 10 breeding seasons (2006-2015). We quantified the importance of small mammals in Black
33 Harrier diet (64.4 % and 78.2 % of prey and consumed biomass, respectively), with the Four Striped
34 Mouse *Rhabdomys pumilio* being a main trophic resource. We also reveal the importance of birds
35 and reptiles as alternative prey, particularly in inland regions, and show inter-annual variations in
36 diet in both regions. Our study confirms that this species can be considered a small mammal
37 specialist. Specialist predators are more vulnerable than generalist ones and diet specialisation has
38 been linked with a poorer conservation status in other species. Our results thus have implications for
39 the conservation of this species in southern Africa. These are highlighted for the long-term
40 sustainability of this threatened endemic species.

41 INTRODUCTION

42 Understanding the feeding habits of animals and assessing food resources use is at the core of
43 ecological research (Martinez del Rio et al. 2009). Food supply is often the main factor affecting
44 population densities of many bird species, including raptors (Newton 1979). The study of diet
45 provides basic background information to understand food requirements, which is a crucial step in
46 understanding any species' ecology (Arroyo 1997).

47 Specialist species use a narrow range of resources and preferentially feed on a given food
48 type regardless of its abundance (see Pyke et al. 1977; Stephens et al. 2007), while generalists feed
49 on a broader range of food types, varying opportunistically in response to changes in availability
50 (Terraube and Arroyo 2011; Nadjafzadeh et al. 2016). However, there is often a continuum from
51 specialization to generalization within and between species (Partridge and Green 1985; Woo et al.
52 2008). Typically, specialists are more efficient than generalists when foraging for their favoured prey,
53 which is possibly associated with better adaptations or search images (MacArthur and Pianka 1966;
54 Dukas and Kamil 2001; Terraube et al. 2010, 2014). However, the foraging success of specialists may
55 be much lower than that of generalists when they target alternative prey (Terraube et al. 2010). In
56 this context, a broader diet in specialist species may indicate a general decrease in the abundance or
57 availability of the primary prey (Steenhof and Kochert 1988) that forces individuals to feed on
58 alternatives and may be associated with a lower reproductive success (Korpimäki 1992; Bolnick et al.
59 2003; Arroyo & Garcia 2006; but see Whitfield et al. 2009 and Murgatroyd et al. 2016 for
60 contradictory results).

61 The Black Harrier *Circus maurus* is an endemic ground-nesting raptor of southern Africa. The
62 population of this medium-sized bird has been estimated at less than 1000 breeding individuals, and
63 the species is listed as endangered in both South Africa and Namibia (Simmons et al. 2015; Taylor et
64 al. 2015), which holds the totality of its breeding range. Black Harriers breed in natural vegetation in
65 both coastal and interior-mountain regions of south western South Africa (Curtis et al. 2004; Curtis
66 2005, Garcia-Heras et al. 2016). The species has been tentatively described as a small mammal
67 specialist (Van der Merwe 1981; Steyn 1982), although quantitative information on its diet is scarce
68 and inconclusive. A previous study based on a relatively small sample size over three years (2000-
69 2002) suggested that the diet may vary with geographical location: individuals breeding along the
70 coast appeared to feed primarily on small mammals, while those breeding in interior or
71 mountainous areas had a more diverse diet, including more birds (Curtis et al. 2004). Nonetheless,
72 detailed information about the diet of this endangered species, and annual or regional variations, is
73 overall lacking.

74 The aim of this paper is to describe the diet composition of this scarce and endangered
75 species, to evaluate the numerical and biomass importance of the different categories of prey, and
76 to examine potential regional or inter-annual variations in the diet. For this, we used a large data set
77 of pellets (ca. 1000; 1760 identified prey) collected at active Black Harrier nests in South Africa
78 during 2006-2015 across the breeding range.

79

80 **MATERIALS AND METHODS**

81 **Study sites**

82 This paper presents diet information collected over 10 years (2006-2015 breeding seasons) in two
83 Provinces of south western South Africa. Geographically this spans the coast of the Western Cape
84 Province (33°42'S - 18°27'; 33°08'S- 18°05'E), and inland in the Northern Cape Province in the
85 Nieuwoudtville area (31°19'S; 19°05'E). Nests were located in and around National Parks (South
86 African National Parks – SANParks properties), Provincial Protected Reserves (Cape Nature), or on
87 private lands, spanning two main biomes, the Succulent Karoo and Fynbos (see Mucina and
88 Rutherford 2006; Manning 2007; Garcia-Heras et al. 2016 for details on vegetation types).
89 Depending on its geographical location (i.e. a combination of altitude, distance to the coast and
90 biome), each nest was classified in two main regions, as either coastal or interior-mountain
91 (hereafter called “inland”). This classification was initiated by Curtis et al. (2004) to explore regional
92 differences in lay dates and productivity in Black Harriers, and it was also used and detailed by
93 Garcia-Heras et al. (2016). Environmental conditions between the two regions (e.g. climate
94 conditions, availability of prey) are also known to be different (see Mucina and Rutherford 2006;
95 Manning 2007, Curtis et al. 2004). Coastal nests were defined as those within 15 km from the coast
96 and with a maximal altitude of 100 mASL, and those nests located further than 15 km from the coast
97 and with an altitude higher than 100 mASL were considered as inland (see Garcia-Heras et al. 2016
98 for more details). Black Harrier nests in inland regions were mostly within the Karoo biome, whereas
99 those along the coast were within the Fynbos biome (see Garcia-Heras et al. 2016).

100

101 **Pellet collection and analyses**

102 The diet was assessed through analysis of regurgitated pellets containing prey remains such as
103 bones, scales, feathers or hairs. Pellet analysis is a widely accepted technique for diet studies in
104 raptors, including harrier (*Circus*) species (Errington 1930; Simmons et al. 1991; Arroyo et al. 1997;

105 Redpath et al. 2001). Some biases are inherent in analysing pellets, and sometimes other methods or
106 a combination of methods are preferred depending on diet composition (Simmons et al. 1991;
107 Redpath et al. 2001). However, since these biases are likely to be similar among areas and times of
108 year, they allow within-species comparisons.

109 Active breeding nests and perch sites (e.g. posts or dead bushes known to be used by a
110 specific breeding pair) were regularly checked for pellets. Pellet collection was extended over the
111 Black Harrier breeding season: August-December in the coastal regions and September-December in
112 the inland regions (Garcia-Heras et al. 2016). A total of 954 pellets were collected from 119 breeding
113 sites (660 pellets from 83 breeding sites in coastal regions, and 294 pellets from 36 in the inland
114 regions). Sample sizes varied between regions and years (Table 1).

115 After collection, pellets were air-dried and then transferred to individually labelled sealed
116 plastic bags until analysis. We identified prey to the lowest taxon level possible (i.e. to species level)
117 using the comparative osteology collections of the Iziko South African Museum, in Cape Town, South
118 Africa. We determined the minimum number of individuals per taxon in each pellet based on: 1) for
119 small mammals, the highest number of left or right mandibles, or left or right maxillaries, number of
120 incisors and skulls; 2) for birds, upper and lower bills, left or right tarsus or other items that indicates
121 presence; 3) for reptiles, left and right mandibles, maxillaries, or limbs that indicates presence.
122 Reptiles were divided into two size categories (large and medium-small) based on the size of the
123 largest skin scales within a pellet (i.e. <1mm for medium-small and >1mm for large). A relatively
124 small number of insect remains (n = 75) were present in some pellets, in the form of very small
125 pieces of body parts (e.g. mandibles, legs, elytra). However, we suspect that these came from the
126 stomach contents of the birds and/or reptiles also present in those pellets. Black Harriers have rarely
127 been described feeding on insects (Van der Merwe 1981; Steyn 1982; *authors personal*
128 *observations*). Therefore, as insects are probably rarely voluntarily ingested by Black Harriers, and
129 represented an insignificant amount of biomass, they were not considered in diet analyses.

130 For pellets containing fur only, hair imprints were conducted to identify small mammal
131 species or group species, where possible. The microstructure of hairs (i.e. specific cuticular scale
132 patterns on the surface of the hair; Ryder 1973) is a useful tool for identifying mammals, and has
133 been widely used to assess carnivore diets (Bothma and Le Riche 1994; Breuer 2005) and the diets of
134 scavenger raptors such as vultures (Donazar et al. 2010). A thin coat of clear nail varnish was applied
135 to a clean microscope slide, and left to dry for about 5-10 seconds. Then, ten randomly selected hair
136 from the same pellet were placed on the nail polish and left to set over for 24 hours. The hairs were
137 then removed with tweezers, being careful to not damage the imprints. Each hair shape was then
138 analysed with a light microscope at 10x and 40x magnification, and compared to those illustrated in

139 Keogh (1975). This technique was applied to 105 pellets and resulted in the identification of 174
140 specimens to species or small mammal groups.

141 Overall, 1760 prey items we identified at the group or species level, 1685 without counting
142 the insects.

143

144 **Biomass estimation**

145 To assess the importance of prey categories in diets that includes very diverse prey in relation to
146 size, it is important to estimate their relative contribution in terms of biomass (Arroyo 1997). We
147 therefore present the dietary results as both the percentage of identified prey and their estimated
148 biomass. For prey identified to species level, we used the average weight described for the species in
149 Stuart & Stuart (1988) as an estimate of biomass. For broader prey categories, we used an estimated
150 average weight (Table 2). For the assignment of biomass for “unidentified birds”, we took into
151 account that the identified birds consumed in inland regions included a higher proportion of
152 Galliformes (particularly Common Quail *Coturnix coturnix*) than in coastal regions, where
153 Passeriformes were more frequently consumed (see results, Table 2). We calculated what would be
154 the average weight of an unidentified bird from the coast or from the inland regions taking into
155 account the relative proportion of identified Passeriformes and Galliformes in each region. Hence, an
156 “unidentified bird” found in the coastal region was attributed a weight of 45 g (since most identified
157 birds here were Passeriformes), while “unidentified birds” from the inland regions were attributed a
158 weight of 69 g (since most of the birds identified in inland pellets were Galliformes) (see Table 2).

159

160 **Statistical analyses**

161 We used R 3.2.3 (the R Foundation for statistical computing, 2015) for statistical analyses.
162 Differences in diet composition (relative proportions of small mammals, birds and reptiles) between
163 regions (coastal vs. inland) were investigated using Chi-square tests. Similarly, inter-annual variations
164 in diet composition in a given region were also tested using Chi-square tests. For this latter test, we
165 used only information from years for which we had a minimum of 25 identified prey. Thus, analyses
166 for the coastal region excluded the years 2006 (n = 18) and 2011 (n = 9). Similarly, analyses for the
167 inland regions were only conducted for the years 2009, 2011, 2013 and 2014, because sample size
168 was too small for 2006 (n = 14) and 2008 (n = 20), and because no pellets were collected in 2007,
169 2010, 2012 and 2015 (see Table 1). Coefficients of Variation were calculated as $100 \times \text{Standard deviation}/\text{mean}$, and diet diversity was calculated using the Shannon Diversity Index (H') as $H' = -$

171 $\sum P_i \log P_i$, where $P_i = X_i/X$, and X_i = number of prey items taken from class i ; X = total number of prey
172 items.

173

174

175 **RESULTS**

176 **Diet composition**

177 Black Harriers preyed upon three main prey types: small mammals (64.4 % of 1685 identified prey,
178 excluding insects), birds (19.2 %) and reptiles (16.3 %) (Table 2).

179 Among the identified small mammals, Black Harriers fed primarily on the Four Striped
180 Mouse *Rhabdomys pumilio* (hereafter *R. pumilio*) (72.5 % of 487 identified small mammals), whereas
181 the second main group was formed by Otomyinae (*Myotomys unisulcatus* and/or *Myotomys*
182 *irroratus*), and *Micaeamys namaquensis* (25.3 % of the identified small mammals; Table 2). Black
183 Harriers also fed to a lesser degree (< 3.0 %) on Musk Shrews (*Crocidura cyanea*), Forest Shrews
184 (*Myosorex varius*), and Elephant Shrews (*Elephantulus* sp.), Grant's Golden Moles (*Eremitalpa granti*)
185 and Cape Dune Mole Rats (*Bathyergus suillus*) (Table 2). However, more than half (55.2 %) of small
186 mammal prey remained unidentified, because neither teeth nor jaws were found in the pellets, or
187 because the shape of some hair imprints did not allow identification (Table 2). Overall, small
188 mammals represented the main prey (78.2 % of consumed biomass).

189 Among birds, Passeriformes were the most common prey (73.5 % of 147 identified birds),
190 followed by Galliforms (25.2 %; mainly Common Quails *Coturnix coturnix*). The remainder 1.3 % were
191 identified as Columbiformes (Table 2). In some cases, bones and feathers were too damaged to
192 allow identification to species level, and 176 (54.5%) birds remained as "unidentified". Information
193 from identified prey showed that, in the inland regions, Black Harriers fed on Galliformes and
194 Passeriformes in equal proportions, whereas in the coastal regions, they fed predominantly on
195 Passeriformes (Table 2). Overall, birds represented the second main prey in terms of contributed
196 biomass (16.6 %) (Table 2).

197 Among reptiles, pellet analyses showed that Black Harriers mostly consumed prey of small-
198 medium size (58.8 %), but larger prey were also common (41.1%). We believe all of the reptiles to be
199 lizards (i.e. Cape Skinks, authors', unpublished information).

200

201 **Diet variation**

202 Diet composition of Black Harriers differed significantly between regions (Chi square tests, $X^2 =$
203 28.52, $df = 2$, $p < 0.0001$). Small mammals were more prevalent in the diet in coastal than in inland

204 regions, both numerically (67.8 % vs. 57.2 %, respectively) and in percentage of biomass (Table 2),
205 whereas contribution of birds was higher in inland regions, where contribution in biomass was
206 almost three times higher than in coastal areas (28.9 % vs 10.8 %. Respectively, Table 2). The
207 consumption of reptiles was equivalent in both regions, both numerically (16.5 % vs. 16.3 % for
208 coastal and inland respectively) and in terms of biomass (Table 2).

209 We also found significant inter-annual variation in diet composition within both coastal ($X^2 =$
210 28.11 , $df= 14$, $p = 0.014$) and inland regions ($X^2 = 34.82$, $df= 6$, $p< 0.0001$) (Figure 1). Considering the
211 Coefficients of Variation, the proportion of small mammals and reptiles was more variable among
212 years in inland (CV = 24.6 and 68.4%, respectively) than in coastal regions (CV% = 14.4 and 50.8%,
213 respectively), while an opposite pattern was found for the proportion of birds, with higher variability
214 among years in the coastal region (CV = 40.4%) than in inland regions (CV = 25.6%). Shannon
215 Diversity Index in coastal regions varied among years between 0.24 and 0.44, while in inland regions
216 it ranged between 0.35 and 0.47, being on average higher in the latter than in the former (0.41 vs.
217 0.33 respectively).

218

219 **DISCUSSION**

220 Our study highlights the importance of small mammals in the diet of breeding Black Harriers, which
221 represented about 65% of the total identified prey and 78% of consumed biomass. This confirms
222 that this endemic and endangered raptor specialises in small mammals, as suggested in a previous
223 study (Curtis et al. 2004). As with other South African raptor species (e.g. African Marsh Harrier
224 *Circus ranivorus*, Simmons et al. 1991), our study also highlights the particular importance of the
225 Four Striped Mouse *R. pumilio* in the Black Harrier's diet. This species is a common and locally
226 abundant omnivorous rodent, described as resilient to fluctuations in environmental conditions
227 and/or food availability, which probably explains its widespread distribution and capacity to inhabit
228 very different biomes within South Africa (De Graaff 1981). Its diurnal habits and high seasonal
229 productivity (Perrin 1980) may also explain its importance in Black Harrier diet, through a temporal
230 overlap in activity patterns of both prey and predator (see activity diurnal patterns in Simmons
231 2000).

232 Species with a specialist narrow diet are frequently associated with a worse conservation
233 status (Ferrer and Negro 2004; Huang 2013). In these species, changes in the abundance of the
234 primary prey lead to strong declines in reproductive success (Newton 1998; Resano-Mayor et al.
235 2014). Some studies have also highlighted that the degree of dietary specialisation is often related

236 with the species' distributional range, and that specialists show smaller distribution ranges than
237 generalists (Boyes and Perrin 2009). Specialists are also likely to be less adaptable and more
238 vulnerable to rapidly changing environmental conditions compared to generalists (Devictor et al.
239 2008). Thus, the dietary dependence of Black Harriers on small mammals, and more particularly on
240 *R. pumilio*, may contribute to its scarcity and vulnerable status, which may further exacerbate in a
241 context of global change.

242 The western region of South Africa has been intensively modified over the last century, with
243 the anthropogenic conversion of the Fynbos and particularly Renosterveld vegetation losing over
244 90% of its former area to agriculture or urbanization (Curtis et al. 2004). This has reduced and
245 fragmented the breeding habitats of several species, including Black Harriers by > 90% in the most
246 productive regions of the Overberg. Furthermore, there has been a shift in rainfall and temperature
247 patterns in South Africa over the past 50 years, and most notably in the Cape Floral Kingdom and
248 Succulent Karoo (Midgley et al. 2002; Simmons et al. 2004). Here temperatures are predicted to
249 become warmer and winter-rainfall more scarce, with longer and more frequent droughts (Midgley
250 et al. 2002; Hockey et al. 2011; Cunningham et al. 2015). Given that several studies have described
251 the importance of rainfall for the reproduction of several small mammals, including the Four Striped
252 Mouse (Taylor and Green 1976; Jackson and Bernard 2006), these two phenomena combined could
253 consequently lead to a reduction in the abundance and/or availability of the primary prey of
254 specialist predators species like the Black Harrier, forcing them to switch to alternative prey. This in
255 turn may lead to decreased foraging success and breeding outputs, as evident in other predatory
256 species (e.g. Korpimäki 1992; Arroyo and Garcia 2006; Terraube et al. 2012).

257 However, some specialist species may show behavioural flexibility. For example, Verreaux's
258 Eagles *Aquila verreauxii* are considered to be highly specialised on hyrax species (Davies 1994, Davies
259 and Allan 1997), but a recent study showed that individuals breeding in agricultural landscapes had
260 the capacity to adapt positively to their changing environment (via the incorporation of energetically
261 profitable and highly available prey to a broader diet) without negative effects in breeding
262 performance (Murgatroyd et al. 2016). Within and between harrier species, there is a very wide
263 range of diet patterns. Some species (essentially from the European continent) are generalist with
264 broad diets, but may show specialist diets in certain contexts, like the Montagu's Harrier *Circus*
265 *pygargus* (Schipper 1973; Terraube & Arroyo 2011; Limiñana et al., 2012), the Hen Harrier *Circus*
266 *cyaenus* (Schipper 1973; Redpath et al. 2002; Millon et al. 2002; Garcia and Arroyo 2005), and the
267 European Marsh Harrier *Circus aeruginosus* (Schipper 1973; Gonzalez-Lopez 1991). On the other
268 hand, some species appear to be specialised on small mammals, for example the Pallid Harrier *Circus*

269 *macrourus* (Terraube et al. 2010), the Northern Harrier *Circus cyaeus hudsonius* (Hamerstrom 1986;
270 Barnard et al. 1987), or the Black Harrier (as shown in the present study), but the degree of diet
271 flexibility in the absence of small mammals varies among species.

272 It seems therefore essential to carefully assess the factors that define dietary strategies and
273 affect diet variation (e.g. prey abundance, availability and profitability) in this species, as well as their
274 ecological consequences, particularly in the context of rapid and long-term environmental change.
275 Further studies will also have to assess the long-term broader implications that diet specialisation
276 coupled with climate change and habitat fragmentation may play on the population dynamic of this
277 threatened endemic specialist predator.

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279

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438

439 Table 1: Sample sizes (number of pellets analysed, their corresponding number of contributed prey
 440 items (in brackets), and the corresponding number of nests [in square brackets]), for the Black
 441 Harrier diet analysis according to year and region (coastal and inland). Fresh pellets were collected at
 442 or near Black Harrier active nests during each breeding season (July-December).

Years	Coastal Pellets (prey item) - [number of nests]	Inland Pellets (prey item) - [number of nests]	Total Pellets (prey item)
2006	8 (18)-[2]	7 (16)-[6]	15 (34)
2007	24 (46)-[3]	-	24 (46)
2008	27 (41)-[6]	-	27 (41)
2009	29 (58)-[7]	24 (54)-[5]	53 (112)
2010	69 (116)-[15]	-	69 (116)
2011	5 (9)-[2]	16 (35)-[4]	21 (44)
2012	96 (163)-[15]	-	96 (163)
2013	98 (162)-[14]	100 (214)-[13]	198 (376)
2014	186 (347)-[15]	147 (244)-[10]	333 (591)
2015	118 (237)-[12]	-	118 (237)
Total	660 (1197)-[91]	294 (563)-[38]	954 (1760)

443

444

445 Table 2: Prey categories and species identified in Black Harrier pellets (n= 954) according to regions
 446 (coastal and interior-mountain), collected during the 2006-2015 breeding seasons. A weight (in g) is
 447 also given for each prey category as an estimate of biomass of a prey unit: this is the average weight
 448 described for the species, or when prey could only be identified at a genus or family level, an
 449 estimated weight (ψ) was used (see materiel and methods).

450

	Prey weight (g)	Coastal N prey (% Biomass*)	Inland N prey (% Biomass*)
Small mammals			
<i>Bathyergus suillus</i>	750	1 (1.08)	-
<i>Crocidura cyanea</i>	9	1 (0.01)	-
<i>Elephantulus sp.</i>	46	1 (0.07)	4 (0.56)
<i>Eremitalpa granti</i>	23	2 (0.07)	-
<i>Micaelamys namaquensis</i>	50	-	1 (0.15)
<i>Myosorex varius</i>	14	2 (0.04)	-
<i>Myotomys unisulcatus</i>	125	3 (0.54)	8 (3.04)
<i>Rhabdomys pumilio</i>	50	255 (18.40)	98 (14.92)
Otomyinae ψ	150	95 (20.56)	16 (7.31)
Unidentified ψ	72	416 (43.21)	182 (39.90)
Total small mammals		776 (83.98)	309 (65.88)
Birds			
<i>Alaudidae galerida</i>	45	1 (0.06)	-
<i>Coturnix coturnix</i>	95	4 (0.55)	33 (9.54)
<i>Crithagra flaviventris</i>	18	1 (0.03)	-
<i>Estrilda astrild</i>	9	1 (0.01)	-
<i>Ploceus capensis</i>	44	1 (0.06)	-
<i>Ploceus velatus</i>	34	2 (0.10)	3 (0.31)
<i>Pycnonotus capensis</i>	39	3 (0.17)	-
<i>Streptopelia senegalensis</i>	81	1 (0.12)	1 (0.25)
Alaudidae ψ	45	2 (0.13)	1 (0.14)
Coliidae ψ	51	2 (0.15)	-
Fringillidae ψ	20	4 (0.12)	-
Ploceidae ψ	40	1 (0.06)	2 (0.24)
Pycnonotidae ψ	40	3 (0.17)	-
Sylviidae ψ	20	1 (0.03)	-
Passeriforme (medium size) ψ	40	36 (2.08)	16 (1.95)
Passeriforme (small size) ψ	20	16 (0.46)	12 (0.73)
Unidentified	45 and 69 ϕ	101 (6.56)	75 (15.76)
Total birds		180 (10.85)	143 (28.92)

451

452 Table 2- continued

453

	Prey weight (g)	Coastal N prey (% Biomass*)	Inland N prey (% Biomass*)
Reptiles			
Large Lizard ^ψ	25	75 (2.71)	39 (2.97)
Medium/small Lizard ^ψ	15	114 (2.47)	49 (2.24)
Total reptiles		189 (5.17)	88 (5.21)
Insects			
Locust		22	14
Coleoptera		1	-
Mantidae		1	1
Orthoptera		2	-
Scarabidae		21	8
Unidentified		5	-
Total insects		52	23
Total prey		1197	563

454 *values calculated excluding insects.

455 ^φfor coastal and inland regions, respectively (see methods)

456

457