

1 **FLEXIBILITY IN FORAGING STRATEGIES OF BROWN SKUAS IN RESPONSE TO**
2 **LOCAL AND SEASONAL DIETARY CONSTRAINTS**

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19 **Abstract** Brown Skuas *Stercorarius antarcticus lonnbergi* are an opportunistic species that
20 displays a high degree of flexibility in foraging tactics. In the present study, GPS and immersion
21 (activity) loggers were deployed on breeding Brown Skuas of known sex, body size and
22 condition at Admiralty Bay, King George Island, to examine the impacts of spatial and seasonal
23 fluctuations in prey availability on movements and foraging behavior. We also investigated
24 whether reversed sexual size dimorphism (females larger than males) in this species led to
25 differences between sexes in foraging behavior, and whether this or other factors contributed to
26 variation in breeding success. Analysis of the GPS data highlighted the high degree of plasticity
27 in foraging behavior among individuals. Although most skuas were flexible in their feeding
28 tactics, this was not enough to ensure a successful breeding season, as few pairs fledged chicks.
29 During early chick rearing, Brown Skuas spent most time on land, feeding almost exclusively on
30 penguin chicks. By late chick rearing, when the availability of penguins had diminished, Brown
31 Skuas supplemented the food obtained on land by travelling to the ocean. All foraging trips to
32 sea occurred during daylight, mostly during the early morning. Despite marked sexual size
33 dimorphism, we failed to find any difference in foraging tactics between males and females.
34 Furthermore, although laying date affected the number of chicks hatched (earlier pairs were more
35 successful), no relationship was found between breeding success and male or female body size,
36 condition, or the degree of dimorphism within pairs.

37 **Keywords** activity patterns; Antarctica; behavior; GPS tracking; prey availability; reversed size
38 dimorphism

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41 **Introduction**

42 Foraging strategies of individual seabirds can differ substantially according to sex, age, breeding
43 status and individual preferences, resulting in the exploitation of different niches (Phillips et al.
44 2011; Quillfeldt et al. 2011; Ceia et al. 2012). Sex differences may arise from the influence of
45 size dimorphism on inter-sexual competition, foraging and flight efficiency, or habitat
46 specialization, or reflect different parental roles during breeding (Phillips et al. 2004b; Quillfeldt
47 et al. 2011; Stauss et al. 2012). In addition, recent studies suggest that many marine vertebrate
48 species show individual feeding specializations that are not sex-specific (Cherel et al. 2009;
49 Masello et al. 2013; Patrick et al. 2014). As central-place foragers during the breeding season,
50 seabirds have to adjust their feeding behavior to satisfy both their energetic requirements and
51 those of their offspring (Weimerskirch et al. 2000; Phillips et al. 2004b; McLeay et al. 2010). As
52 a result, within a single breeding season, foraging strategies may also vary in response to
53 fluctuations in prey availability, the switch from incubation to chick rearing, and changes in
54 nutritional demands of growing chicks (Shaffer et al. 2003; Hipfner et al. 2013).

55 The degree of plasticity in foraging behavior within individuals has important
56 implications, particularly when the distribution and abundance of different prey is highly
57 variable (Hamer et al. 2007). Generalist predators exhibit greater plasticity in their foraging
58 strategies when compared with specialists because they have the ability to exploit different
59 trophic resources (Christel et al. 2012). Amongst marine predators, skuas are a good example of
60 an opportunistic species with a high degree of flexibility in feeding tactics, enabling them to
61 exploit a wide range of food resources (Moncorps et al. 1998; Pezzo et al. 2001; Anderson et al.
62 2009). Skua populations are known to include both generalist scavengers, and individuals which
63 specialize on catching small petrels at night (Young et al. 1988; Mougeot et al. 1998; Bolnick et

64 al. 2003). Although skuas can switch between different prey types, buffering them against
65 changes in resources availability, this is not necessarily without a cost; Phillips et al. (2004a), for
66 example, showed that territorial attendance dropped substantially when skuas switched from seal
67 carrion to seabird prey.

68 Brown Skuas (*Stercorarius antarcticus lonnbergi*) are widely distributed on islands from
69 the sub-Antarctic to the Antarctic continent. They show clear reversed sexual size dimorphism,
70 with females ~5% larger and up to 16% heavier than males (Phillips et al. 2002; Hahn and Bauer
71 2008). During breeding, their diet can include seal carcasses, placentae and feces, or eggs,
72 chicks, adults or stomach contents of seabirds nesting in nearby colonies (Reinhardt et al. 2000;
73 Phillips et al. 2004a; Anderson et al. 2009). In several Antarctic populations, some birds
74 establish feeding territories in areas adjacent to penguin or petrel colonies, whereas others forage
75 over a wide area that they do not defend (Trivelpiece et al. 1980; Pietz 1987; Carneiro et al.
76 2010). Brown Skuas that defend feeding territories benefit from the predictability of resources;
77 their chicks show higher survivorship and fledge earlier than those of non-territorial pairs (Hahn
78 and Peter 2003; Hahn and Bauer 2008).

79 Although the diet of Brown Skuas has been characterized at a number of colonies
80 (Mougeot et al. 1998; Reinhardt et al. 2000; Phillips et al. 2004a; Ryan et al. 2009; Grilli and
81 Montalti 2012), little is known about other aspects of their foraging ecology (but see Carneiro et
82 al. 2014). This study examined the movements and foraging behavior of Brown Skuas during the
83 breeding season at a colony in the South Shetland Islands, using a combination of GPS and
84 immersion (activity) loggers, and behavioral observations from birds of known sex, body size
85 and condition. Foraging strategies were considered in the context of changing reproductive
86 constraints, and spatial and seasonal fluctuations in prey availability, to investigate the extent to

87 which the plasticity of Brown Skuas allows individuals to balance the intrinsic demands of
88 breeding with extrinsic environmental variation. To our knowledge, the only published study of
89 fine-scale foraging movements of Brown Skuas (using GPS loggers) is of adults breeding at
90 South Georgia where they feed mainly by scavenging seal carrion and placenta on beaches, and
91 to a lesser extent by predation of other seabirds (Phillips et al. 2004a; Anderson et al. 2009;
92 Carneiro et al. 2014). There are no published tracking studies of Brown Skuas breeding further
93 south, where their main food resources on land are usually penguin eggs and chicks. Hence, there
94 is no information on changes in foraging area or other aspects of feeding behavior in response to
95 the steep decline in terrestrial prey availability associated with the fledging of penguin chicks,
96 which precedes that of skua chicks by several weeks. We also investigated whether sexual size
97 dimorphism in this species was reflected in sexual differences in foraging, and whether this or
98 other factors contributed to variation in breeding success.

99

100 **Methods**

101 Fieldwork was carried out on Brown Skuas at the Antarctic Specially Managed Area No. 128
102 (Site of Special Scientific Interest No. 8) located on the western shore of Admiralty Bay, King
103 George Island, South Shetland Islands (62°10'S, 58°27'W) during the austral summer of
104 2012/13. The island is separated by c. 100 km from the Antarctic Peninsula by the Bransfield
105 Strait. Brown Skuas breeding at Admiralty Bay feed mainly on penguins (Trivelpiece et al.
106 1980). Most of the breeding population defends combined feeding-breeding territories around
107 colonies of pygoscelid penguins (*Pygoscelis adeliae* and *P. papua*). Other pairs have some
108 penguin or petrel prey nearby, but subsist primarily by feeding at sea on fish and crustaceans. A

109 total of 29 deployments of GPS loggers (IgotU; Mobile Action Technology Inc., Taiwan) and
110 immersion (activity) loggers (Mk 18L; British Antarctic Survey, Cambridge) were made on
111 breeding adults for 2-3 days during early or late chick rearing (chicks aged <29 days, and >32
112 days, respectively), with some birds tracked in both periods. Early and late chick rearing
113 deployments were made in January or February, respectively. GPS loggers weighed 25 g
114 including waterproof packing and were attached to the dorsal feathers with TESA® tape.
115 Immersion loggers weighed 1.5 g and were fitted with a cable-tie to standard metal rings. Total
116 instrument load including the tape was ca. 32 g, equivalent to 1.7% of the mean body mass,
117 which was well below the threshold of 3% at which device effects tend to become apparent in
118 other flying seabirds (Phillips et al. 2003). Only birds with a dual-purpose feeding and breeding
119 territory were tracked, as most non-territorial pairs that had bred previously in the study area
120 deferred breeding in the 2012/13 season.

121 The GPS loggers were programmed to acquire a fix every 30 seconds. For each GPS
122 track, the following information was derived: 1) duration (elapsed time from the beginning to
123 end of the trip); 2) total distance (summed great circle distances between fixes) and 3) maximum
124 range (great circle distance to the furthest location). Foraging trips on land, especially those
125 targeting penguin colonies, were indistinguishable from time spent on territory because birds
126 defended a combined nesting and feeding territory. Consequently, as a conservative approach,
127 track statistics were derived only for trips to the ocean. The activity loggers tested for saltwater
128 immersion every three seconds, and logged the number of positive tests at the end of each 10 min
129 period, i.e. values from 0 (continuously dry) to 200 (continuously wet). These data were used to
130 calculate the duration and proportion of time spent on the water, and the interval between the
131 start of civil twilight in the morning (hereafter, sunrise) and that of the trip (Harris et al. 2013).

132 To examine differences in morphology of the sexes, a full set of measurements was taken
133 from each captured bird, following the approaches of Pennycuick (1989), Shaffer et al. (2001)
134 and Phillips et al. (2004b). Tarsus length, head plus culmen length, and culmen depth were
135 measured to the nearest 0.1 mm using vernier calipers. Wing length (maximum flattened chord)
136 was measured to the nearest 1 mm. A tape was used to measure maximum body circumference,
137 shoulder width, wing width and wing span. Wing was extended to a flat position, photographed
138 with a digital camera, and the area calculated subsequently from the image using ImageJ
139 software (Schneider et al. 2012). Total wing area was estimated by doubling the area of the
140 photographed wing and adding the area between the shoulders, the latter equal to the product of
141 root chord (wing width at the junction with the body, measured in the field) and shoulder width.
142 Maximum body frontal area, representing the cross-sectional area of a bird at its widest point,
143 was calculated as the square of the maximum body circumference measured in the field divided
144 by 4π . Wing chord (mean wing width) was the wing area over wing span, wing loading (an index
145 of force per unit wing area) as Newtons per wing area, assuming $g = 9.8 \text{ ms}^{-2}$, and aspect ratio (an
146 index of wing shape) as wing span² over wing area. Study birds were sexed by behavioral
147 observations as part of a long term project carried out over the last 30 years.

148 For each sex, a separate principal component analysis incorporating the variables wing,
149 tarsus length, and head plus culmen length was used to produce single factor scores (PC1 scores)
150 representing a composite index of body size (Catry et al. 1999; Phillips et al. 2002). The
151 standardized residuals obtained by regressing the mass of the birds against the PC1 scores were
152 used as a measure of body condition. An additional principal component analysis including all
153 birds was also run to produce single factor scores (PC1b) used in the calculation of a pair

154 dimorphism index for body size (Phillips et al. 2002). The dimorphism index was computed as:
155 $(\text{female size} - \text{male size}) / (\text{female size} + \text{male size})$ (Catry et al. 1999; Phillips et al. 2002).

156 *T*-tests were used to compare mean time spent on land and at sea during early and late
157 chick rearing, and male and female body measurements. The influence of sex on foraging trip
158 characteristics was assessed using linear mixed-effect models with sex as a fixed factor, and bird
159 identity as a random effect. To investigate possible relationships between breeding success, and
160 female, male and pair dimorphism, Spearman rank-order correlations were performed between
161 the number of chicks hatched and fledged, and male and female body size (PC1 scores) and
162 condition, the degree of dimorphism within pair, laying dates and number of penguins defended
163 per territory. The total number of penguins controlled by (i.e. in the territory of) each pair was
164 estimated from tracking data and field observations. Laying dates were determined by visiting
165 territories daily or on alternate days early in the season. In order to exclude first-time breeders
166 and pairs breeding together for the first time, which tend to have lower success in skuas (Davis
167 1976), only birds with at least two years of prior breeding experience, and that had the same
168 mate in 2011/12 and 2012/13 were included in the analysis. This analysis also excluded the
169 single pair that did not defend a feeding territory with penguins, and instead fed on another
170 resource (storm petrels). Data were logarithmic, square root or arcsine square-root transformed if
171 necessary to achieve normality. Mixed-effect models were built using lme4, and Spearman rank-
172 order correlation using Hmisc packages in R (Bates et al. 2013; Harrell 2013). Unless indicated
173 otherwise, all data are presented as means \pm SE.

174

175 **Results**

176 GPS tracks were obtained for 24 deployments on 16 different birds (Fig. 1). We were unable to
177 download data from two GPS loggers, one bird failed breeding and disappeared from the study
178 area before the logger could be retrieved, and two loggers were detached by the birds. Eight birds
179 were tracked both during early and late chick rearing, four birds only during early chick rearing,
180 and another four birds only during late chick rearing. Birds were tracked on average for $49.4 \pm$
181 5.7 hr on each deployment. Out of the 24 deployments, 12 birds (7 females and 5 males)
182 travelled to the ocean, mostly during late chick rearing (Fig. 1). Members of just one breeding
183 pair travelled to the ocean during early chick rearing; however, these trips represented only 1.0
184 hr ($\sim 2\%$) and 0.6 hr ($\sim 3\%$) out of 54.7 hr and 21.6 hr of tracking, respectively, of these two
185 individuals, and the distances covered were much smaller than in foraging trips during late chick
186 rearing (Fig. 1). During late chick rearing, trips to the ocean lasted on average 3.5 ± 0.4 hr (range
187 = 0.6 – 7.4), covered a travel distance of 91.1 ± 9.9 km (range = 17.0 – 163.2) and were to a
188 maximum range of 36.7 ± 3.8 km (range = 3.9 – 56.8). The proportion of time spent at sea was
189 much higher during late chick rearing (9.2 ± 2.3 %, range = 0.1 – 26.4%) than early chick rearing
190 (0.1 ± 0.1 %, range = 0.0 – 0.9%) (2-sample *t*-test, $t_{22} = -6.2$, $P < 0.001$).

191 Brown Skuas equipped with immersion loggers that travelled to sea in late chick rearing
192 spent on average 58.6 ± 15.6 min (range = 0.0 – 306.4 min) on the water, representing a mean of
193 21.2 ± 3.8 % (range = 0.0 – 69.0) of the total trip duration (3.5 ± 0.4 hr, range = 0.6 – 7.4 hr).
194 Although the proportion of time spent on saltwater by females was higher than by males ($25.5 \pm$
195 6.7 % vs. 18.5 ± 4.5 %, respectively), this difference was not significant (Likelihood ratio test,
196 $\chi^2_1 = 0.9$, $P = 0.34$). One skua from the breeding pair that travelled to the ocean during early chick
197 rearing did not land on the water, and the partner spent only ca. 0.1 min (0.1% of the trip) in
198 saltwater. Almost all marine trips started and finished in daylight; three trips (12%) began just 2

199 to 12 min before the start of morning twilight, and 16 (64%) within the following three hours
200 (overall mean: 2.3 ± 0.5 hr, range = $-0.2 - 8.6$ hr). No difference was found between males ($2.6 \pm$
201 0.9 hr, range = $-0.2 - 8.6$ hr) and females (1.9 ± 0.5 hr, range = $-0.1 - 5.0$ hr) in trip start times
202 relative to the onset of civil twilight (Likelihood ratio test, $\chi^2_1 = 0.5$, $P = 0.48$).

203 Males and females differed significantly in most morphological characters; values for
204 females were all higher than those for males, except for wing width (Table 1). There was no
205 significant difference in foraging trip characteristics between males and females (Table 2). In the
206 2012/13 breeding season, out of the total of 39 pairs that occupied territories, 21 laid eggs, from
207 which 18 chicks hatched and 11 fledged. The average laying date was December 7. Mean
208 number of penguins defended per territory was 725 ± 111 (range = $71 - 1,546$, $n =$ nine breeding
209 pairs and two single birds); there were no areas within penguin colonies that were not defended
210 by a skua pair. There was a negative correlation between laying date in 2012/13 and the number
211 of chicks hatched (Spearman rank-order correlation, $r_s = -0.8$, $P = 0.002$), but no significant
212 correlation between laying date and the number of chicks that fledged (Spearman rank-order
213 correlation, $r_s = -0.3$, $P = 0.33$). There were no significant correlations between the number of
214 chicks hatched or fledged, and body size, condition, number of penguins or the dimorphism
215 indices (Table 3).

216

217 **Discussion**

218 Analysis of the GPS data indicated a high degree of plasticity in foraging behavior of individual
219 Brown Skuas at our study site. Three strategies were identified, of which two were common
220 (defense of a feeding territory with penguins, or trips to sea to access marine resources), and one

221 was uncommon (targeting of storm petrels). Out of the eight birds that were tracked both during
222 early and late chick rearing, only three were consistent in their choice of prey, and this included
223 one pair that fed on storm petrels. Individual specialization within localities is especially strong
224 for skuas that target petrels (Mougeot et al. 1998; Ryan et al. 2009). Moreover, storm petrels
225 were available for skuas throughout the whole study period; first eggs are laid from mid-
226 December and fledging starts in mid March (Quillfeldt et al. 2005). Although most skuas were
227 flexible in their feeding tactics, this was not enough to ensure a successful breeding season.
228 Breeding success at Admiralty Bay in 2012/13 was low (0.52 chicks fledged per pair) in
229 comparison with studies of this species elsewhere (see Reinhardt 1997).

230 Brown Skuas at Admiralty Bay spent most of their time on land during early chick
231 rearing. During this time, the tracked birds fed almost exclusively on penguin chicks (one pair
232 specialized on storm petrels); just two birds spent very little time (<3% of the tracking period) at
233 sea. Although the breeding cycle of Brown Skuas at Admiralty Bay is largely matched to the
234 cycle of their penguin prey, ensuring plentiful food for much of the season, the availability of
235 penguins diminishes before the skua chicks have fledged (Burton 1968; Trivelpiece and
236 Volkman 1982; Pietz 1987). Adélie Penguins usually fledge in the first week of February, and
237 although the final dispersal of Gentoo Penguins is potentially a few weeks later, most gentoo
238 penguin fledglings are well-grown and difficult for skuas to kill. By late chick rearing, the
239 tracked skuas were supplementing the food obtained on land by foraging outside the bay in the
240 Bransfield Strait. The latter is considered to be a highly productive region, providing abundant
241 prey at all trophic levels (Zhou et al. 2006). Although several studies have suggested that Brown
242 Skuas eat fish during the breeding season, there are few quantitative data (Fraser 1984; Ryan and
243 Moloney 1991; Malzof and Quintana 2008). In addition, use of marine resources may have been

244 underestimated previously because many diet studies of skuas are based on pellets, and at sub-
245 Antarctic and Antarctic colonies, fish or crustaceans may be digested more rapidly than avian or
246 mammalian prey, leaving few remains (Ryan and Moloney 1991; Malzof and Quintana 2008).
247 Moreover, the majority of studies of skua diet have been conducted in incubation or early chick
248 rearing when most terrestrial resources are still available, and skuas do not need to forage at sea.

249 Dietary switches in response to changes in temporal and spatial availability of prey, or
250 triggered by the onset of hatching, have been reported for other seabirds (Annett and Pierotti
251 1989). For breeding Brown Skuas, seasonal variation in diet seems to reflect relative prey
252 abundance or availability, as well as ease of capture (Ryan and Moloney 1991; Phillips et al.
253 2004a; this study). Indeed, there is little requirement for skuas at Admiralty Bay to consume
254 marine resources during the early breeding season. Pairs defended territories that held a mean of
255 725 penguin nests (range 71 – 1,546 nests; see results), which is comparable to numbers
256 defended by skuas elsewhere in the South Shetlands: 90 to 2,011 penguin nests at Point Thomas,
257 King George Island (Trivelpiece et al. 1980; Carneiro et al. 2010), and; from 48 to >3,000
258 penguin nests at Potter Peninsula, but with the majority of territories containing <1,000 nests
259 (Hahn and Peter 2003).

260 A direct comparison of feeding trip characteristics of Brown Skuas breeding at Admiralty
261 Bay with colonies elsewhere is to some extent confounded by the considerable spatial and
262 seasonal variation in diet and foraging strategies. Nevertheless, the mean trip duration of Brown
263 Skuas at Admiralty Bay during late chick rearing (3.5 ± 0.4 hr; this study) was similar to that of
264 birds breeding around Palmer Station on Anvers Island, Antarctic Peninsula after all penguin
265 fledglings had departed (3.0 ± 0.5 hr; Pietz 1986). By comparison, foraging trips at Admiralty
266 Bay during late chick rearing were over twice as long as at Bird Island, South Georgia during

267 incubation and early to mid chick rearing (1.5 ± 0.1 hr; Carneiro et al. 2014). This seems likely
268 to reflect a difference in the main food resources, which at Bird Island were mainly seal carrion
269 and placentae on beaches, at a maximum foraging distance of 3.3 ± 0.7 km (Carneiro et al.
270 2014). There is no evidence that birds at South Georgia feed at sea; a very small percentage of
271 regurgitates collected in later chick rearing consisted of squid, but this could have been obtained
272 by kleptoparasitism (Phillips et al. 2004a). Hence, the comparison in trip characteristics among
273 sites suggests that birds which feed away from their territories at sea require substantially more
274 time to find prey than those that feed on terrestrial resources.

275 The immersion data indicated that unlike other seabirds, Brown Skuas do not spend time
276 foraging or resting at sea in darkness during the chick rearing period. Compared with other
277 seabirds, skuas seem therefore to use the ocean only as a supplementary source of food during
278 breeding. The percentage of daylight spent on water by Brown Skuas from Admiralty Bay
279 during the breeding season is similar to that of small albatrosses *Thalassarche* spp., White-
280 chinned Petrels *Procellaria aequinoctialis* and gadfly petrels *Pterodroma* spp. (Phalan et al.
281 2007; Mackley et al. 2011; Pinet et al. 2012). Similar activity patterns during daylight have been
282 recorded for Falkland Skuas (*S. a. antarcticus*) between the time they fail breeding and final
283 departure on migration (8-27% of time spent on the water; Phillips et al. 2007). However, the
284 foraging trips of skuas from Admiralty Bay during breeding are much shorter than procellariids;
285 this eliminates the need to spend part of the night resting on the sea surface, which is considered
286 to be a response to reduced aerial detectability of prey at low light levels (Phalan et al. 2007;
287 Mackley et al. 2011; Navarro et al. 2013). The timing by skuas of most trips to sea to coincide
288 with the first hours of daylight, suggest that they may adjust their activities to that of diel
289 (vertical) migration of certain prey (which tends to peak at dawn and then again at dusk).

290 Alternatively, adult skuas may be taking advantage of first light to meet the demands of growing
291 chicks after many hours without being fed. If birds use the ocean as a supplementary source of
292 food, leaving early in the morning would allow them to search for other resources on land later in
293 the day. Having said that, the variation in proportion of time spent on the water (0-69%) in trips
294 to sea by different individuals in our study, despite broad overlap in foraging ranges (Fig. 1),
295 suggests either considerable variation in feeding success (reflecting the patchiness of marine
296 prey), or a degree of specialization in feeding behavior. Potentially, some individuals may rely
297 on scavenging of large prey and so spend more time on the water, whereas others may feed more
298 actively on small prey, or obtain food by kleptoparasitism.

299 Although considerable sexual size dimorphism was apparent, foraging parameters of
300 males and females breeding at Admiralty Bay were comparable in most respects, suggesting
301 broadly similar feeding strategies. No relationships were found between breeding success and the
302 indices of male and female body size, condition, or degree of size dimorphism. Although this
303 may reflect the small sample sizes, previous attempts to relate breeding success to body size and
304 condition have produced mixed results. In northern hemisphere skuas in particular, there are few
305 effects of male and female body size on breeding parameters (Catry et al. 1999). By comparison
306 clutch volume was related positively to size and condition of females, and negatively to
307 condition of males in southern hemisphere skuas (Phillips et al. 2002). Mean laying dates at
308 Admiralty Bay were similar to those recorded for Brown Skuas at Fildes and Potter peninsulas,
309 King George Island, in austral summers 1983/84 to 2003/04 (Hahn and Peter 2003; Hahn et al.
310 2007), and laying date showed a significant negative relationship with number of chicks hatched,
311 i.e., earlier pairs were more successful. Similarly, at other sites, earlier hatching is often
312 associated with increased reproductive output (Pezzo et al. 2001; Phillips et al. 2004a; Anderson

313 et al. 2009); however, number of chicks that fledged in our study was not correlated with earlier
314 laying dates. Although Brown Skuas with better access to penguin colonies are expected to be
315 more successful, there was no significant correlation between number of skua chicks hatched or
316 fledged and the number of penguins defended within the territory. Hahn and Peter (2003)
317 showed that Brown Skuas with feeding territories in penguin colonies finished breeding earlier,
318 and had higher offspring survivorship, but, similarly, there was no correlation between number
319 of penguins defended and overall breeding success (although this was probably due to lower
320 hatching success in territorial pairs). In the present study, the only pairs from previous years that
321 bred were territorial birds with direct access to penguin colonies. Hence, our sample probably
322 represents the pool of high quality parents which have good territories and are able to provide
323 adequate support for their chicks throughout the breeding season. The average number of
324 penguin nests defended (725 per skua pair) is only slightly smaller than the range considered by
325 Trivelpiece et al. (1980) to be optimal (766 to 2,011 penguin nests); therefore, it might be that
326 after achieving this threshold, additional penguin nests would not improve skua breeding
327 success.

328 In conclusion, Brown Skuas breeding at Admiralty Bay have access to penguin prey until
329 the mid chick-rearing period, but thereafter have to switch increasingly to resources obtained
330 from the ocean. Our study demonstrates the effectiveness of tracking as a tool for examining
331 prey switching by skuas; further work could usefully apply the same approach, potentially in
332 conjunction with direct or indirect diet estimation (e.g., stable isotope ratios, fatty acid analysis),
333 to investigate flexibility in foraging strategies of skuas during the early breeding season and at
334 other sites where there is marked seasonality in the abundance of different resources.

335

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344 **Conflict of Interest** The authors declare that they have no conflict of interest.

345

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- 485

486 List of figures

487 **Fig. 1** GPS tracking data obtained from 24 deployments on 16 different Brown Skuas during (a)
488 early chick rearing and (b) late chick rearing at Admiralty Bay, King George Island, during the
489 austral summer of 2012/13

490

491 Table 1: Pair dimorphism index and body measurements of male and female Brown Skuas
 492 breeding at Admiralty Bay, King George Island in austral summer 2012/13. Values are the mean
 493 \pm standard error, with sample size in parentheses. *T*-tests compare values for males and females.

494

Parameter	Male	Female	<i>t</i> -test	<i>P</i>
Pair dimorphism	-1.4 \pm 1.6 (9)			
Mass (g)	1,685.4 \pm 32.2 (13)	1,912.0 \pm 37.2 (15)	$t_{26} = -4.5$	< 0.001*
Tarsus (mm)	72.7 \pm 0.8 (14)	74.2 \pm 0.7 (15)	$t_{27} = -1.4$	0.18
Culmen length (mm)	55.2 \pm 0.7 (13)	56.0 \pm 0.5 (15)	$t_{26} = -0.8$	0.41
Culmen depth (mm)	19.8 \pm 0.2 (13)	20.4 \pm 0.1 (15)	$t_{26} = -3.0$	0.006*
Head length (mm)	117.8 \pm 1.2 (13)	118.6 \pm 1.1 (15)	$t_{26} = -0.5$	0.62
Wing	40.7 \pm 0.1 (14)	41.8 \pm 0.3 (15)	$t_{27} = -3.2$	0.003*
Wing area (cm ²)	1,967.1 \pm 49.5 (13)	1,998.2 \pm 30.3 (14)	$t_{25} = -0.5$	0.59
Wing span (cm)	141.8 \pm 1.4 (14)	149.7 \pm 0.9 (15)	$t_{27} = -4.6$	< 0.001*
Wing width (cm)	13.9 \pm 0.5 (13)	13.3 \pm 0.2 (14)	$t_{25} = 1.1$	0.30
Maximum body circumference (cm)	42.5 \pm 0.4 (14)	44.5 \pm 0.3 (15)	$t_{27} = -3.8$	< 0.001*
Maximum body frontal area (cm ²)	143.6 \pm 2.9 (14)	157.6 \pm 2.3 (15)	$t_{27} = -3.8$	< 0.001*
Aspect ratio	10.4 \pm 0.4 (13)	11.3 \pm 0.2 (14)	$t_{25} = -2.1$	0.044*
Wing loading	84.6 \pm 2.6 (13)	94.5 \pm 2.6 (14)	$t_{25} = -2.7$	0.01*

* Significant differences

495

496

497 Table 2: Foraging parameters of male and female Brown Skuas breeding at Admiralty Bay, King
 498 George Island in the austral summer 2012/13 during late chick rearing. Values are the mean \pm
 499 standard error, with sample size in parentheses. Likelihood ratio tests were used to compare
 500 estimates for males and females within a mixed model framework, correcting for the repeated
 501 sampling of individual birds.

502

Parameter	Male	Female	Likelihood ratio test	<i>P</i>
Trip duration (hr)	3.3 \pm 0.5 (13)	3.8 \pm 0.6 (10)	$\chi^2_1 = 0.6$	0.42
Travel distance (km)	90.9 \pm 15.9 (13)	95.9 \pm 13.2 (10)	$\chi^2_1 = 0.4$	0.55
Maximum range (km)	34.1 \pm 5.2 (13)	41.0 \pm 5.0 (10)	$\chi^2_1 = 1.0$	0.31

503

504

505 Table 3: Effects of male and female size, condition, pair dimorphism, laying dates and number of
 506 penguins on hatching success (number of eggs hatched) and breeding success (number of chicks
 507 fledged) in Brown Skuas breeding at Admiralty Bay, King George Island in the austral summer
 508 2012/13. *P* values are from Spearman rank-order correlations.

509

	Hatching success (r_s)	<i>P</i>	Breeding success (r_s)	<i>P</i>
Dimorphism index	-0.1	0.83	0.4	0.26
Number of penguins	0.5	0.13	0.6	0.08
Laying dates	-0.8	0.002*	-0.3	0.33
PC1 male	-0.2	0.66	-0.4	0.33
Condition male	-0.4	0.24	0.2	0.69
PC1 female	-0.1	0.73	-0.5	0.17
Condition female	-0.1	0.76	0.1	0.78

* Significant differences

510

