



**HAL**  
open science

## GPS tracking devices reveal foraging strategies of Black-legged Kittiwakes

Jana Kotzerka, Stefan Garthe, Scott A. Hatch

► **To cite this version:**

Jana Kotzerka, Stefan Garthe, Scott A. Hatch. GPS tracking devices reveal foraging strategies of Black-legged Kittiwakes. *Journal für Ornithologie = Journal of Ornithology*, 2009, 151 (2), pp.459-467. 10.1007/s10336-009-0479-y . hal-00568362

**HAL Id: hal-00568362**

**<https://hal.science/hal-00568362>**

Submitted on 23 Feb 2011

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Journal of Ornithology 00: 000-000, 2009**

2

3 **GPS tracking devices reveal foraging strategies of Black-legged Kittiwakes**

4

5 Jana Kotzerka, Stefan Garthe and Scott A. Hatch

6

7 *J. Kotzerka (correspondence) and S. Garthe, Research and Technology Center Westcoast*

8 *Büsum, University of Kiel, Hafentörn 1, 25761 Büsum, Germany, E-mail: [9 \*\[west.uni-kiel.de\]\(http://west.uni-kiel.de\), Phone: ++49-4834-604142, Fax: ++49-4834-604199\*](mailto:kotzerka@ftz-</a></i></p></div><div data-bbox=)*

10 *S. A. Hatch, U.S. Geological Survey, Alaska Science Center, 4210 University Drive,*

11 *Anchorage, Alaska 99508, USA*

12

13 Black-legged Kittiwakes *Rissa tridactyla* are the most abundant gull species in  
14 the world but some populations have declined in recent years, apparently due  
15 to food shortage. Kittiwakes are surface feeders and thus can compensate for  
16 low food availability only by increasing their foraging range and/or devoting  
17 more time to foraging. The species is widely studied in many respects, but  
18 long-distance foraging and the limitations of conventional radio telemetry  
19 have kept this vital activity largely out of view. Development of GPS loggers  
20 is advancing rapidly. With devices as small as 8 g now available it is possible  
21 to use this technology for tracking relatively small species of oceanic birds  
22 like kittiwakes. Here we present the first results of GPS telemetry applied to  
23 Black-legged Kittiwakes in 2007 in the North Pacific. All but one individual

24 foraged in the neritic zone north of the island. Three birds performed foraging  
25 trips only close to the colony (within 13 km), while six birds had foraging  
26 ranges averaging about 40 km. The maximum foraging range was 59 and the  
27 maximum distance traveled was 165 km. Maximum trip duration was 17 h  
28 (mean: 8 h). An apparently bimodal distribution of foraging ranges affords  
29 new insight on the variable foraging behaviour of Black-legged Kittiwakes.  
30 Successful deployment of GPS loggers on kittiwakes holds much promise for  
31 telemetry studies on many other species of similar size and encourages this  
32 new approach for further studies.

33

34 Key words: Black-legged Kittiwake, *Rissa tridactyla*, foraging, Gulf of Alaska,  
35 telemetry

36

37 Seabirds spend most of their time at sea and are difficult to observe when not  
38 attending nests during breeding. Research is therefore biased toward land-based observations,  
39 with the at-sea biology of smaller species generally limited to counts of travelling and  
40 foraging birds from research vessels. Such studies are time- or area-restricted and unable to  
41 give detailed insights into the foraging behaviour of individuals (Weimerskirch et al. 2005).  
42 However, knowledge of foraging behaviour is essential to understanding both the ecological  
43 roles of seabirds and constraints acting upon them in marine ecosystems (Monaghan 1996;  
44 Wilson et al. 2002). The most productive and cost-effective way to study the flight and  
45 foraging behaviour of birds at sea employs electronic devices attached to individuals (Daunt  
46 et al. 2003; Garthe et al. 2007; Grémillet et al. 2004; Wilson et al. 2002). A variety of loggers

47 and techniques have been developed in the last 40 years (Grémillet et al. 2000; Hamer et al.  
48 2007; Weimerskirch and Wilson 2000). The newest tracking devices to come on line are GPS  
49 receivers, unlimited in range and capable of much higher resolution and accuracy than  
50 satellite transmitters or conventional radio telemetry (Hulbert and French 2001; Hünerbein et  
51 al. 2000). As with most new technologies, the first GPS data loggers were too heavy to deploy  
52 on all but very large-bodied seabirds such as albatrosses (Diomedidae; (Waugh et al. 2005;  
53 Weimerskirch et al. 2002) and gannets (Sulidae; (Grémillet et al. 2004). The latest equipment,  
54 with package sizes in the range of 8-12 g, bring small and medium-sized seabirds (c. 300 g  
55 and larger) into the scope of possible applications.

56         Black-legged Kittiwakes (*Rissa tridactyla*), widely distributed in north temperate to  
57 arctic regions of the northern hemisphere, are the most abundant and one of the most  
58 thoroughly studied gull species in the world (Hatch et al. 2009). Detailed knowledge of  
59 foraging ecology is still lacking, however, as the species is highly pelagic, especially in  
60 winter, and foraging activity is difficult to observe. Kittiwakes stay closer to the coast while  
61 breeding, returning frequently to their nests to change incubation duties or deliver food to  
62 their chicks (Daunt et al. 2002; Hatch et al. 2009; Suryan et al. 2000), but even then their  
63 foraging trips often take them out of range of telemetry techniques that rely on fixed receiving  
64 equipment (Camphuysen 2005; Wanless et al. 1992). Kittiwake body mass averages about 430  
65 g (Pacific) or 390 g (Atlantic) (Hatch et al. 2009), thus telemetry devices exceeding 20 g (~ 5% of  
66 their body weight) are not recommended (Caccamise and Hedin 1985; Calvo and Furness 1992;  
67 Phillips et al. 2003).

68         Kittiwakes are regarded as useful indicators of marine environmental change in the  
69 North Atlantic and North Pacific oceans (Frederiksen et al. 2007; Gill et al. 2002; Wanless et

70 al. 2007). Many colonies have declined in numbers and productivity in the last 20-30 years  
71 (Daunt et al. 2002; Hatch et al. 2009), probably because of reduced availability of their  
72 principal food — small, schooling fish such as sand lance *Ammodytes* spp., capelin *Mallotus*  
73 *villosus*, and juvenile cods (Gadidae) (Frederiksen et al. 2008; Harris and Wanless 1990;  
74 Hatch et al. 1993b; Suryan et al. 2006), which they capture by dipping or surface plunging  
75 (Hatch et al. 2009; Hoyo et al. 1996). As obligate surface feeders, kittiwakes are affected by  
76 changes in both the abundance and vertical distribution of their food (Furness and Tasker  
77 2000; Hatch et al. 1993b). Breeding kittiwakes may compensate for food shortage by  
78 spending more time foraging and/or ranging farther from the colony, although this could have  
79 disadvantages like higher vulnerability to nest site competition and predation on eggs or  
80 chicks.

81         Here we report on the first use of miniature GPS data loggers to characterize the  
82 foraging behaviour of Black-legged Kittiwakes. The work was conducted during the breeding  
83 season of 2007 at Middleton Island in the north-central Gulf of Alaska, where population  
84 monitoring and studies of breeding ecology, behaviour, and physiology have occurred since  
85 the mid 1970s (Gill et al. 2002; Hatch et al. 1993b; Hatch et al. 1993a; Roberts and Hatch  
86 1993). Data on foraging trip durations from this colony are available from one prior study  
87 (Roberts and Hatch 1993) that employed direct observations of nest attendance in 1988, when  
88 the colony was much larger than at present. There is concern about the status and viability of  
89 this colony, which has declined more than 90% — from 83,000 pairs to 6,200 pairs — over  
90 the last 26 years (Hatch et al. 2009). Understanding the decline will require a thorough  
91 understanding of the birds' foraging habits, both during and outside the breeding season.  
92 Knowledge of their foraging habits could reveal possible food shortness caused for example

93 by competition with other seabird species, oceanographic anomalies, or fishing activities.

94

## 95 **Methods**

96

97 Middleton Island (59.4° N, 146.3° W) is close to the steep submarine terrain of the  
98 continental slope (about 10-15 km south) and faces a broad expanse of unsheltered continental  
99 shelf to the north (Fig. 1). Thus, both neritic and deep ocean habitats are readily available to  
100 breeding kittiwakes.

101 Kittiwakes sampled in the study nested on a U.S. Air Force radar tower,  
102 decommissioned and derelict since the 1960s, to which artificial nest sites have been added  
103 for research purposes. The tower supported 910 nesting pairs in 2007, most using wooden  
104 ledges viewable from inside the building through sliding panes of one-way mirror glass (Gill  
105 and Hatch 2002). Birds were snared around the leg with a wire hook passed through a slot in  
106 the wall beneath each window. Individuals chosen for logger deployment were actively  
107 incubating or rearing chicks. Chick-rearing birds had one or two chicks aged 1-40 days. All  
108 birds in the study were marked with a unique combination of steel and plastic colour bands  
109 for individual recognition. Every nest was checked each morning for egg or chick status and  
110 for the presence of adult birds.

111 Tracking devices were deployed between 1 July and 11 August 2007. We captured 14  
112 adult kittiwakes and deployed GiPSy<sup>®</sup> data loggers (11 g; L 50 x W 22 x H 10 mm)  
113 manufactured by TechnoSmart. The loggers were programmed to use a 5-min sampling  
114 interval. GPS data stored in the device memory and used for the analysis included date, time,  
115 latitude, longitude and speed. The devices were attached to feathers in the middle of the back

116 with TESA<sup>®</sup> tape (Wilson et al. 1997). Before deployment, each bird was weighed to the  
117 nearest 5 g using a spring balance. The loggers were 2-3% of mean body mass (397 g, range  
118 345-500 g). Mass was the only measurement taken upon first capture to minimize handling  
119 time. Additional measurements (bill length, head-bill length, wing length) and banding were  
120 taken upon recapture if data were not already available from previous studies. Measurements  
121 were used to determine the sex of the birds (Jodice et al. 2000). Handling time (capture to  
122 release) was approximately 10 min for deployment and 3-15 min for logger removal, banding,  
123 and measurements as needed. In 28 captures and recaptures, 15 birds returned to their nest  
124 within 15 min (5 of them immediately), 4 birds within 31 min, and 3 birds more than 1 h after  
125 capture. Return time for 6 birds was undetermined due to a lack of nest observations. We  
126 deployed 12 of the 14 loggers in the late afternoon or evening, which allowed us potentially to  
127 capture information on nighttime foraging. We used 106 unmanipulated nests on the tower as  
128 a control group to compare breeding success between equipped and non-equipped birds.

129 Flight paths were plotted in ArcView<sup>®</sup> 3.2 from the positional data obtained.  
130 Maximum foraging range was defined as the most distant position in a straight line from the  
131 colony. Distance travelled refers to the summed distances between positions from start to end  
132 locations of each foraging trip. Elapsed time from start to end of a trip is trip duration. Start  
133 and end of a trip were defined using GPS data. Trips started when a positional fix was 300 m  
134 away from the colony and subsequent positions were progressively farther away. In  
135 calculating mean velocity (ground speed), we used only flight speeds greater than 10 km h<sup>-1</sup>,  
136 excluding one outlier of 119 km h<sup>-1</sup>. Speeds less than 10 km h<sup>-1</sup> were probably associated with  
137 swimming or feeding (Weimerskirch et al. 2006).

138 Loggers were switched on at deployment — no delayed start was possible — and due

139 to battery depletion or occasional large gaps in data collection, not all foraging trips were well  
140 documented from start to finish. In calculating the mean maximum range, mean distance to  
141 colony and mean trip duration we included only complete trips, but estimated values are also  
142 reported for individual trips that were incomplete. The missing portion of a track line was  
143 extrapolated directly back to the colony, which underestimates the distance travelled by an  
144 unknown, but probably modest amount. Extrapolated track lines were then used to correct the  
145 trip duration of incomplete trips using a mean flight speed of 33 km/h (as measured in this  
146 study; see below). Statistical analyses were carried out in R 2.8.0. and SPSS 11.5.

147

## 148 **Results**

149

150 All 14 instrumented birds were recaptured after 1-7 days. Two birds had shed the  
151 logger by pulling out the feathers to which it was attached, although we did not observe birds  
152 pecking at or trying to remove the logger. Two loggers failed to record data for unknown  
153 reasons. Among the remaining sample of 10 kittiwakes, one bird incubated for nearly 2 days,  
154 thus depleting its logger battery before leaving the nest. We used data from 9 successful  
155 deployments (5 females, 4 males) for analysis of foraging patterns.

156 We obtained data for 16 foraging trips, 7 of which were complete (Table 1). Four birds  
157 made one foraging trip, three made two trips, and two birds made three foraging trips during  
158 the working period of the logger. Loggers recorded between 24 and 626 positional fixes  
159 within a foraging trip (mean 123, SD 144).

160 The main foraging area was north of the colony, encompassing the continental shelf  
161 area between Middleton Island and Prince William Sound (Fig. 2). Birds stayed mostly over



162 waters less than 200 m deep. One bird made repeated visits to the shelf slope south and east of  
163 the island but did not access the abyssal zone beyond (Fig. 2a, 2c). One bird visited the  
164 nearshore area of Hinchinbrook Island at the entrance to Prince William Sound (92 km from  
165 Middleton).

166 On 9 of the 16 foraging trips, which we categorize as “short” trips, kittiwakes stayed  
167 within 13 km of the breeding site, in contrast to the remaining 7 trips — “long” trips that  
168 exceeded 35 km from the colony (Fig. 3). Among the completed trips, the maximum range  
169 from the colony was 59 km, with a mean foraging range of 25.5 km (SD 22.2 km). However,  
170 one incomplete trip had a maximum range from the colony of at least 91.8 km (Table. 2). The  
171 maximum total distance travelled by a kittiwake on a completed trip was 164.7 km (mean  
172 72.5 km, SD 58.4 km). When incomplete trips are taken into account the total maximum  
173 distance travelled per trip was at least 306.3 km.

174 Trip duration varied from 1.5 h to 16.8 h (mean 7.9 h, SD 5.8 h) for complete trips,  
175 whereas one incomplete trip exceeded 33 h for incomplete trips. We found a positive  
176 relationship between trip duration and total distance travelled per foraging for complete trips  
177 trip (Spearman’s  $r_s = 0.835$ ,  $P < 0.01$ ) but no significant relationship between foraging trip  
178 duration and maximum distance to colony. Because of the small sample size of complete  
179 foraging trips, statistical tests between males and females were not applicable.

180 Most trips occurred solely during daylight, but overnight trips were conducted by one  
181 female and two males. In one instance the bird appeared to spend the night in or near another  
182 portion of the colony on Middleton, whereas two overnight trips likely entailed foraging, as  
183 the birds travelled far from the colony (Table 2). Nonetheless, the birds were mostly inactive  
184 at night as indicated by rates of movement  $< 10 \text{ km h}^{-1}$  (Fig. 2b).

185 Mean flight speed during foraging trips was 33 km h<sup>-1</sup> (maximum 87 km h<sup>-1</sup>, SD 13  
186 km h<sup>-1</sup>) (Fig. 4). Kittiwakes spent only about a third (35%) of their foraging trips engaged in  
187 sustained directional flight. The remaining 65% of the time budget consisted of periods of  
188 inactivity or other behaviours not characterized by directional flight (speeds < 10 km h<sup>-1</sup>).

189 We found no evidence that GPS loggers influenced breeding performance of the  
190 subjects. Breeding success (number of chicks fledged/number of eggs laid) of instrumented  
191 birds (0.5) was similar to that of controls (0.44) and there were no differences in mean chick  
192 mass between groups at three stages of development: newly hatched chicks, mid-chick stage  
193 or chicks near fledging (Table 3).

194

## 195 **Discussion**

196

197 Foraging patterns were highly variable among Black-legged Kittiwakes sampled on  
198 Middleton Island in 2007, with a tendency towards bimodality in the distances travelled on  
199 foraging trips. The longest and most far-ranging excursions were overnight trips, but even day  
200 trips tended to range either less than 10 km or more than 40 km from the island. It may be that  
201 shorter trips were used for chick-provisioning, while the longer trips were important for self-  
202 feeding by adults, as suggested for chick-rearing Procellariiformes (Congdon et al. 2005;  
203 Weimerskirch et al. 2001). Further study is needed to confirm that possibility in kittiwakes.  
204 The disjunct distribution of foraging distances could also reflect prey distribution, as the main  
205 prey of kittiwakes during chick rearing at Middleton, capelin and sand lance (Gill and Hatch  
206 2002), may be available at different distances from the island.

207 Foraging trips that included a night at sea generally lasted much longer than trips

208 performed only during daylight (Coulson and Johnson 1993; Hamer et al. 1993; Roberts and  
209 Hatch 1993). The importance of nighttime foraging was noted on Middleton in 1988, when  
210 62% of overnight trips resulted in chick feeding upon return of the adult, while 35% of  
211 daytime absences resulted in chick-feeding (Roberts and Hatch 1993). Overnight trips may in  
212 general access distant foraging areas. Two of three overnight trips recorded in 2007 were  
213 among the three most distant trips. Among birds tracked at night, the recorded flight speeds  
214  $<10 \text{ km h}^{-1}$  indicated that hours of darkness were often spent in relative inactivity, probably  
215 drifting on the surface, as was also observed by (Hamer et al. 1993) in Shetland. However,  
216 birds “on water” might also engage in feeding by picking up small prey items, such as  
217 euphausiids or polychaetes, likely available at the surface at night.

218 Foraging ranges of breeding kittiwakes are variable from one location to another.  
219 Ranges ( $\pm$  SE) of  $41 \pm 3$  km (Shoup Bay),  $26 \pm 5$  km (Icy Bay), and  $21 \pm 5$  km (Eleanor  
220 Island) were reported for three colonies in Prince William Sound (Ainley et al. 2003). The  
221 maximum foraging distance from the Shoup Bay colony was 120 km (Suryan et al. 2000).  
222 Values reported here for Middleton Island (mean range of all trips: 26 km, maximum: 59 km)  
223 are intermediate relative to Prince William Sound, whereas radio telemetry in Great Britain  
224 (Sumburgh Head, Shetland) found that kittiwakes usually travelled more than 40 km from the  
225 colony in 1990, beyond the range of receiving equipment (Wanless et al. 1992). In the  
226 following year, more than 95% of foraging trips stayed within 5 km of the Sumburgh Head  
227 colony, a reversal attributed to improved food availability (Hamer et al. 1993). Elsewhere in  
228 Britain, maximum ranges of  $73 \pm 9$  km from the Isle of May and 55.5 km from the Farne  
229 Islands were estimated from flight duration and speed (Daunt et al. 2002; Pearson 1968).  
230 Kittiwakes breeding at Helgoland in the German Bight were seen at a distance of 10-35 km

231 from the colony (aerial and ship based transect counts). Only single birds were observed at  
232 distances up to 70-80 km (Dierschke et al. 2004). Those relatively short foraging distances  
233 may be explained by low competition for prey — good feeding conditions around the island,  
234 small size of the colony, and its isolation from other colonies of the same species

235         Our mean trip duration (7.9 h) was longer than that observed by (Roberts and Hatch  
236 1993) on Middleton Island in 1988 (mean 4.1 h for daytime trips that culminated in chick-  
237 feeding). Shorter trips are also reported from other colonies in Alaska and in Great Britain.  
238 Mean trip durations of 3.4-6 h were found among kittiwakes in Prince William Sound (Ainley  
239 et al. 2003; Suryan et al. 2000). Kittiwakes from the Isle of May spent 6.1 h (Humphreys et al.  
240 2006) and 5.5 h (Daunt et al. 2002) at sea, and foraging trips were shorter still in two other  
241 Scottish colonies — 3.4 h (Hamer et al. 1993) and 2.8 h (Coulson and Johnson 1993).  
242 However, trip durations averaged more than 6 h during a year of reduced prey availability  
243 (Hamer et al. 1993; Wanless et al. 1992). Our mean trip duration of nearly 8 h therefore  
244 suggests poor food availability near Middleton Island in 2007. Flexible time budgets, as a  
245 means of coping with low food availability, are also known from other colonies of kittiwakes  
246 and murre (*Uria lomvia* and *U. aalge*) in Alaska (Harding et al. 2007; Kitaysky et al. 2000).

247         With one exception, kittiwakes foraged only in a northerly direction from the colony,  
248 over the continental shelf and within the 200-m depth contour. We expected the shelf edge, a  
249 potentially rich feeding habitat close to the island, to be a greater attraction than it was.  
250 However, upwelling along the shelf edge is not as strong in summer as in winter (Weingartner  
251 et al. 2005), which may explain the absence of kittiwakes in that area during July and August.  
252 Observations on diet suggest a different situation in April, prior to egg-laying. Prey  
253 regurgitated by kittiwakes in the first several weeks after returning to Middleton Island in

254 spring consist mostly of lanternfishes (Myctophidae) and small squids (S. A. Hatch, unpubl.  
255 data). The birds presumably obtain this prey from deep ocean habitat of the continental slope  
256 and abyssal ocean south of the island. Myctophids and squids are important components of  
257 the mesopelagic community that migrate vertically to the ocean surface at night (Beamish et  
258 al. 1999; Sinclair and Stabeno 2002). Myctophids, in particular, are high-energy prey (Van  
259 Pelt et al. 1997) whose availability to kittiwakes before and during early breeding stages on  
260 Middleton is thought to influence breeding success (Gill and Hatch 2002). Such prey are seen  
261 also during incubation in some years (Gill and Hatch 2002). In this study we sampled two  
262 birds late in incubation, one of which went to the shelf edge east of Middleton while the other  
263 made the most distant foraging trip observed, on a northwesterly heading to Hinchinbrook  
264 Island. More sampling is needed to clarify the relative importance and seasonality of deep  
265 ocean versus neritic foraging by kittiwakes from Middleton.

266 Pennycuick (1987; 1997) and Götmark (1980) observed air speeds for kittiwakes of  
267 about 47 and 54 km h<sup>-1</sup>, respectively. Our observed mean flight speed of 33 km h<sup>-1</sup> was lower  
268 than those speeds and matches better with the minimum power speed of Pennycuick (1987;  
269 1997). But flight speeds varied greatly during foraging trips. Speed of flight to and from  
270 foraging areas ranged from about 20-60 km h<sup>-1</sup>, while birds searching for food had flight  
271 speeds up to 20 km h<sup>-1</sup>. It seems that birds changed between minimum power and maximum  
272 range speeds (Pennycuick 1987, 1997) while flying to and coming back from foraging areas.  
273 Whether this behaviour was weather dependent should be investigated.

274 In conclusion, we affirm the utility of GPS data loggers in elucidating the movements  
275 and marine habitat use of seabirds previously excluded from such investigations because of  
276 their small body size. Kittiwakes exhibited flexible foraging behaviour—short and long

277 foraging trips that appeared to change in relative frequencies over the course of chick rearing.  
278 Although the sample was limited to 16 foraging trips, seven of them complete, we gained  
279 much insight into the foraging behaviour of Black-legged Kittiwakes from Middleton Island.  
280 Nearly all foraging trips were over the continental shelf, in northerly direction of the colony.  
281 Thus, we believe the sample typifies the behaviour of most birds in this colony, but further  
282 investigations are desirable. Interannual and within-season variation have yet to be fully  
283 investigated.

284         Future applications of this powerful new technology promise many valuable insights  
285 on the foraging strategies of kittiwakes and other oceanic birds of similar size. GPS data  
286 loggers are able to track seabirds at distances from the colony that are out of range of  
287 conventional radio telemetry. In addition, they are unaffected by weather conditions, an  
288 important constraint on ship or aerial transect counts.

289

290

## 291 **Zusammenfassung**

292

293 GPS-Logger offenbaren Nahrungssuchstrategien der Dreizehenmöwen

294

295 Die Dreizehenmöwe (*Rissa tridactyla*) ist die weltweit häufigste Möwenart, aber viele  
296 Populationen haben in den letzten Jahren abgenommen, was vermutlich auf  
297 Nahrungsverknappung zurückzuführen ist. Dreizehenmöwen suchen ihre Nahrung an der  
298 Wasseroberfläche und können deshalb geringe Nahrungsverfügbarkeit nur durch ein  
299 Ausweiten ihres Nahrungssuchgebietes und / oder einen erhöhten Zeitaufwand kompensieren.

300 Diese Möwenart ist schon in vielen Aspekten ihrer Biologie untersucht wurden, aber durch  
301 ihre weiten Nahrungssuchflüge und die Einschränkungen durch die konventionelle  
302 Radiotelemetrie konnten diesen Aktivitäten bisher nur wenig untersucht werden. Die  
303 Entwicklung von GPS-Loggern schreitet schnell voran. Mit neuen Geräten, die nur noch 8 g  
304 wiegen, ist es jetzt auch möglich relativ kleine Seevogelarten, wie die Dreizehenmöwe, mit  
305 dieser Technologie auszustatten und zu untersuchen. Hier präsentieren wir erste Ergebnisse  
306 der GPS-Loggereinsätze auf Dreizehenmöwen aus dem Jahr 2007 aus dem Nordpazifik. Mit  
307 Ausnahme von einem Tier sind alle Vögel in der neritischen Zone nördlich der Insel auf  
308 Nahrungssuche gegangen. Drei Vögel suchten nur in unmittelbarer Nähe zur Kolonie (<  
309 13 km) nach Nahrung, während sechs weitere Tiere eine durchschnittliche Entfernung von  
310 40 km zeigten. Die maximale Entfernung zur Kolonie betrug 59 km und die maximale  
311 zurückgelegte Distanz während eines Nahrungssuchfluges betrug 165 km. Der längste  
312 Nahrungssuchflug dauerte 17 h (Mittelwert: 8 h). Die maximalen Distanzen zur Kolonie der  
313 Nahrungssuchflüge machen eine bimodale Verteilung sichtbar, was neue Einsichten in das  
314 variable Nahrungssuchverhalten von Dreizehenmöwen liefert. Die erfolgreiche Ausstattung  
315 von Dreizehenmöwen mit GPS-Loggern verspricht auch Erfolg mit Telemetriestudien bei  
316 vielen anderen Arten ähnlicher Größe und gibt neue Ansätze für weitere Untersuchungen.

317

### 318 **Acknowledgements**

319

320 This project was funded by the German Science Foundation (DFG GA 617/5-1). We thank  
321 Hilger Lemke for major assistance with the field work and all others who helped us during the  
322 study on Middleton Island. Nele Markones, Philipp Schwemmer, and four anonymous

323 reviewers made useful comments on an earlier draft of the manuscript. Haglöfs® sponsored  
324 some of the equipment for this study. Mention of trade names is for descriptive purposes only  
325 and does not imply endorsement by the U.S. Government. The study was approved and  
326 carried out under Alaska State and U.S. Federal Fish and Wildlife permits.

327

## 328 **References**

329

330 Ainley DG, Ford RG, Brown ED, Suryan RM and Irons DB (2003) Prey resources,  
331 competition, and geographic structure of Kittiwake colonies in Prince William Sound.  
332 Ecology 84: 709-723

333 Beamish RJ, Leask KD, Ivanov OA, Balanov AA, Orlov AM and Sinclair B (1999) The  
334 ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres.  
335 Prog Oceanogr 43: 399-442

336 Caccamise DF and Hedin RS (1985) An Aerodynamic Basis For Selecting Transmitter Loads  
337 In Birds. Wilson Bull 97: 306-318

338 Calvo B and Furness RW (1992) A review of the use and the effects of marks and devices on  
339 birds. Ring Migr 13: 129-151

340 Camphuysen CJ (2005) Understanding marine foodweb processes: An ecosystem approach to  
341 sustainable sandeel fisheries in the North Sea. Impress Final Report. Royal  
342 Netherlands Institute for Sea Research, Texel

343 Congdon BC, Krockenberger AK and Smithers BV (2005) Dual-foraging and co-ordinated  
344 provisioning in a tropical Procellariiform, the wedge-tailed shearwater. Mar Ecol Prog  
345 Ser 301: 293-301



- 346 Coulson JC and Johnson MP (1993) The attendance and absence of adult Kittiwakes *Rissa*  
347 *tridactyla* from the nest site during the chick stage. *Ibis* 135: 372-378
- 348 Daunt F, Benvenuti S, Harris MP, Dall'Antonia L, Elston DA and Wanless S (2002) Foraging  
349 strategies of the black-legged kittiwake *Rissa tridactyla* at a North Sea colony:  
350 evidence for a maximum foraging range. *Mar Ecol Prog Ser* 245: 239-247
- 351 Daunt F, Peters G, Scott B, Grémillet D and Wanless S (2003) Rapid-response recorders  
352 reveal interplay between marine physics and seabird behaviour. *Mar Ecol Prog Ser*  
353 255: 283-288
- 354 Dierschke V, Garthe S and Markones N (2004) Aktionsradien Helgoländer Dreizehenmöwen  
355 *Rissa tridactyla* und Trottellummen *Uria aalge* während der Aufzuchtphase.  
356 *Vogelwelt* 125: 11-19
- 357 Frederiksen M, Mavor RA and Wanless S (2007) Seabirds as environmental indicators: the  
358 advantages of combining data sets. *Mar Ecol Prog Ser* 352: 205-211
- 359 Frederiksen M, Jensen H, Daunt F, Mavor RA and Wanless S (2008) Differential effects of a  
360 local industrial sand lance fishery on seabird breeding performance. *Ecol Appl* 18:  
361 701-710
- 362 Furness RW and Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of  
363 seabirds to reductions in sandeel abundance, and identification of key areas for  
364 sensitive seabirds in the North Sea. *Mar Ecol Prog Ser* 202: 253-264
- 365 Garthe S, Montevecchi WA and Davoren GK (2007) Flight destinations and foraging  
366 behaviour of northern gannets (*Sula bassana*) preying on a small forage fish in a low-  
367 arctic ecosystem. *Deep Sea Res Part II* 54: 311-320

- 368 Gill VA and Hatch SA (2002) Components of productivity in Black-legged Kittiwakes *Rissa*  
369 *tridactyla*: response to supplemental feeding. *J Avian Biol* 33: 113-126
- 370 Gill VA, Hatch SA and Lanctot RB (2002) Sensitivity of breeding parameters to food supply  
371 in Black-legged Kittiwakes *Rissa tridactyla*. *Ibis* 144: 268-283
- 372 Götmark F (1980) Foraging flights of Kittiwakes-some functional aspects. *Vår Fågelvärld* 39:  
373 65-74
- 374 Grémillet D, Storch S and Peters G (2000) Determining food requirements in marine top  
375 predators: a comparison of three independent techniques in Great Cormorants,  
376 *Phalacrocorax carbo carbo*. *Can J Zool* 78: 1567-1579
- 377 Grémillet D, Omo GD, Ryan PG, Peters G, Ropert-Coudert Y and Weeks SJ (2004) Offshore  
378 diplomacy, or how seabirds mitigate intra-specific competition: a case study based on  
379 GPS tracking of Cape Gannets from neighbouring colonies. *Mar Ecol Prog Ser* 268:  
380 265-279
- 381 Hamer KC, Monaghan P, Uttley JD, Walton P and Burns MD (1993) The influence of food  
382 supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. *Ibis* 135:  
383 255-263
- 384 Hamer KC, Humphreys EM, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips RA, Harris  
385 MP and Wanless S (2007) Annual variation in diets, feeding locations and foraging  
386 behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Mar*  
387 *Ecol Prog Ser* 338: 295-305
- 388 Harding AMA, Piatt JF, Schmutz JA, Shultz MT, Pelt TIV, Kettle AB and Speckman SG  
389 (2007) Prey density and the behavioral flexibility of a marine predator: the Common  
390 Murre (*Uria aalge*). *Ecology* 88: 2024-2033

- 391 Harris MP and Wanless S (1990) Breeding Success Of British Kittiwakes *Rissa tridactyla* In  
392 1986-88 - Evidence For Changing Conditions In The Northern North Sea. *J Appl Ecol*  
393 27: 172-187
- 394 Hatch SA, Roberts BD and Fadely BS (1993a) Adult survival of Black-legged Kittiwakes  
395 *Rissa tridactyla* in a Pacific colony. *Ibis* 135: 247-254
- 396 Hatch SA, Byrd GV, Irons DB and G. L. Hunt J (1993b) Status and ecology of kittiwakes  
397 (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. Canadian Wildlife Service,  
398 Ottawa, ON
- 399 Hatch SA, Robertson GJ and Baird PH (2009) Black-legged Kittiwake (*Rissa tridactyla*). In:  
400 Poole A (ed) *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca
- 401 Hoyo Jd, Elliott A and Sargatal J (1996) *Handbook of the Birds of the World*. Vol. 3. Lynx  
402 Edicions, Barcelona
- 403 Hulbert IAR and French J (2001) The accuracy of GPS for wildlife telemetry and habitat  
404 mapping. *J Appl Ecol* 38: 869-878
- 405 Humphreys EM, Wanless S and Bryant DM (2006) Stage-dependent foraging in breeding  
406 black-legged kittiwakes *Rissa tridactyla*: distinguishing behavioural responses to  
407 intrinsic and extrinsic factors. *J Avian Biol* 37: 436-446
- 408 Hünnerbein Kv, Hamann HJ, Ruter E and Wiltshcko W (2000) A GPS-based system for  
409 recording the flight path of birds. *Naturwissenschaften* 87: 278-279
- 410 Jodice PGR, Lanctot RB, Gill VA, Roby DD and Hatch SA (2000) Sexing Adult Black-  
411 legged Kittiwakes by DNA, Behavior, and Morphology. *Waterbirds* 23: 405-415

- 412 Kitaysky AS, Jr GLH, Flint EN, Rubega MA and Decker MB (2000) Resource allocation in  
413 breeding seabirds: responses to fluctuations in their food supply. *Mar Ecol Prog Ser*  
414 206: 283-296
- 415 Monaghan P (1996) Relevance of the behaviour of seabirds to the conservation of marine  
416 environments. *Oikos* 77: 227-237
- 417 Pearson TH (1968) The feeding biology of sea-bird species breeding on the Farne Islands,  
418 Northumberland. *J Anim Ecol* 37: 521-552
- 419 Pennycuik CJ (1987) Flight of Auks (Alcidae) and other northern seabirds compared with  
420 southern Procellariiformes: ornithodolite observations. *J Exp Biol* 128: 335-347
- 421 Pennycuik CJ (1997) Actual and 'optimum' flight speeds: field data reassessed. *J Exp Biol*  
422 2000: 2355-2361
- 423 Phillips RA, Xavier JC and Croxall JP (2003) Effects of satellite transmitters on albatrosses  
424 and petrels. *Auk* 120: 1082-1090
- 425 Roberts BD and Hatch SA (1993) Behavioral ecology of Black-legged Kittiwakes during  
426 chick rearing in a failing colony. *Condor* 95: 330-342
- 427 Sinclair EH and Stabeno PJ (2002) Mesopelagic nekton and associated physics of the  
428 southeastern Bering Sea. *Deep Sea Res Part II* 49: 6127-6145
- 429 Suryan RM, Irons DB and Benson J (2000) Prey switching and variable foraging strategies of  
430 Black-legged Kittiwakes and the effect on reproductive success. *Condor* 102: 374-384
- 431 Suryan RM, Irons DB, Brown ED, Jodice PGR and Roby DD (2006) Site-specific effects on  
432 productivity of an upper trophic-level marine predator: Bottom-up, top-down, and  
433 mismatch effects on reproduction in a colonial seabird. *Prog Oceanogr* 68: 303-328

- 434 Van Pelt TI, Piatt JF, Lance BK and Roby DD (1997) Proximate composition and energy  
435 density of some North Pacific forage fishes. *Comp Biochem Physiol A-Mol Integr*  
436 *Physiol* 118: 1393-1398
- 437 Wanless S, Monaghan P, Uttley JD, Walton P and Morris JA (1992) A radio-tracking study of  
438 kittiwakes (*Rissa tridactyla*) foraging under suboptimal conditions. In: Priede IG and  
439 Swift SM (eds) *Wildlife telemetry. Remote monitoring and tracking of animals*. Ellis  
440 Horwood, New York, pp 581-590
- 441 Wanless S, Frederiksen M, Daunt F, Scott BE and Harris MP (2007) Black-legged kittiwakes  
442 as indicators of environmental change in the North Sea: Evidence from long-term  
443 studies. *Prog Oceanogr* 72: 30-38
- 444 Waugh S, Filippi D, Fukuda A, Suzuki M, Higuchi H, Setiawan A and Davis L (2005)  
445 Foraging of royal albatrosses, *Diomedea epomophora*, from Otago Peninsula and its  
446 relationships to fisheries. *Can J Fish Aquat Sci* 62: 1410-1421
- 447 Weimerskirch H and Wilson RP (2000) Oceanic respite for Wandering Albatrosses. *Nature*  
448 406: 955-956
- 449 Weimerskirch H, Chastel O, Cherel Y, Henden J-A and Tveraa T (2001) Nest attendance and  
450 foraging movements of northern fulmars rearing chicks at Bjørnøya Barents Sea. *Polar*  
451 *Biol* 24: 83-88
- 452 Weimerskirch H, Bonadonna F, Bailleul F, Mabile G, Dell'Omo G and Lipp H-P (2002) GPS  
453 tracking of foraging Albatrosses. *Science* 295: 1259
- 454 Weimerskirch H, Corre ML, Jaquemet S and Marsac F (2005) Foraging strategy of a tropical  
455 seabird, the red-footed booby, in a dynamic marine environment. *Mar Ecol Prog Ser*  
456 288: 251-261

- 457 Weimerskirch H, Corre ML, Ropert-Coudert Y, Kato A and Marsac F (2006) Sex-specific  
458 foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed  
459 booby. *Oecologia* 146: 681-691
- 460 Weingartner TJ, Danielson SL and Royer TC (2005) Freshwater variability and predictability  
461 in the Alaska Coastal Current. *Deep Sea Res Part II* 52: 169-191
- 462 Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin J-B and Ropert-Coudert Y  
463 (1997) Long-term attachment of transmitting and recording devices to penguins and  
464 other seabirds. *Wildl Soc Bull* 25: 101-106
- 465 Wilson RP, Grémillet D, Syder J, Kierspel MAM, Garthe S, Weimerskirch H, Schaefer-Neth  
466 C, Scolaro JA, Bost C-A, Plötz J and Nel D (2002) Remote-sensing systems and  
467 seabirds: their use, abuse and potential for measuring marine environmental variables.  
468 *Mar Ecol Prog Ser* 228: 241-261  
469  
470

471 Table 1. Summary of deployments of GPS data loggers attached to Black-legged Kittiwakes on Middleton Island, Alaska during the breeding  
 472 season in 2007.

473  
 474

475

476

477

478

479

480

481

482

483

484

485

486

487

488

489

490

Bird no.	Nest	Sex	Brood stage	Date		No. of trips	
				deployment	recapture	complete	incomplete
1	D-15	female	incubating	02 Jul	04 Jul	battery empty before left the nest	
2	B-10	male	incubating	05 Jul	10 Jul	0	1
3	B-6	male	incubating	08 Jul	10 Jul	0	2
4	D-15	male	incub./chick rear.	11 Jul	14 Jul	no data recorded	
5	B-14	female	chick rearing	11 Jul	14 Jul	no data recorded	
6	D-17	female	chick rearing	14 Jul	16 Jul	1	2
7	B-16	female	chick rearing	14 Jul	17 Jul	logger lost	
8	D-4	male	chick rearing	17 Jul	01 Jul	1	0
9	D-13	male	chick rearing	19 Jul	20 Jul	1	0
10	B-4	female	chick rearing	21 Jul	23 Jul	1	1
11	D-3	female	chick rearing	25 Jul	27 Jul	1	1
12	D-2	female	chick rearing	27 Jul	28 Jul	0	1
13	B-4	male	chick rearing	29 Jul	05 Aug	logger lost	
14	C-1	female	chick rearing	08 Aug	11 Aug	2	1

491 Table 2. Foraging behaviour of Black-legged Kittiwakes from Middleton Island, Alaska during the breeding season in 2007. Range indicates  
 492 maximum straight-line distance from the colony. Total distance travelled is distance covered during one foraging trip. Complete/incomplete  
 493 indicates whether the whole trip was recorded from nest-leaving through return to the colony. Diel period distinguishes overnight and day  
 494 trips.

495

Bird no.	Sex	Brood stage	Trip duration (h)	Range (km)	Total dist. travelled (km)	Complete/ incomplete	Diel period of trip	
							day only (d)	overnight (n)
2	male	incubating	6.5	9.8	51.2	incomplete	d	
3	male	incubating	2.1	1.4	3.9	incomplete	d	
6	female	chick rearing	33.0	91.8	306.3	incomplete	n	
			2.5	3.8	9.7	incomplete	d	
			12.8	59.0	164.7	complete	n	
8	male	chick rearing	4.6	47.2	100.5	incomplete	d	
			16.8	35.2	92.5	complete	n	
			7.2	49.5	129.7	complete	d	
9	male	chick rearing	7.2	49.5	129.7	complete	d	
			2.1	4.9	14.7	complete	d	
10	female	chick rearing	2.1	4.9	14.7	complete	d	
			8.8	63.6	179.0	incomplete	d	
11	female	chick rearing	3.8	5.6	18.7	incomplete	d	
			4.2	12.5	35.0	complete	d	
12	female	chick rearing	6.9	36.1	121.4	incomplete	d	
14	female	chick rearing	4.1	3.0	6.7	incomplete	d	
			1.5	6.4	15.5	complete	d	
			10.4	10.9	55.4	complete	d	



496 Table 3. Comparison of breeding success (number of chicks/number of eggs laid) and chick  
 497 growth at three stages of development between logger birds and non equipped Black-legged  
 498 Kittiwakes in 2007 on Middleton Island, Alaska. Numbers in parentheses are sample sizes.

	<b>Logger birds</b>	<b>Non-equipped birds</b>	<b>Statistics (GLM)</b>
no. chicks / no. eggs laid	0.5 (n=13)	0.4 (n=95)	$t = 0.617, P = 0.538$
mean chick mass in g (0 days)	36.5 (n=16)	35.7 (n=85)	$t = 0.664, P = 0.508$
mean chick mass in g (20 days)	300.3 (n=12)	319.3 (n=75)	$t = 1.107, P = 0.271$
mean chick mass in g (35 days)	413.9 (n=8)	422.0 (n=69)	$t = -0.538, P = 0.592$

499

500

501

502

503

504

505

506

507

508 Figure Legends

509

510 Figure 1. Study area in the Gulf of Alaska showing the locations of Middleton Island and

511 Prince William Sound (PWS). Middleton lies about 80 km south of the Alaska mainland.

512 Depth contours indicate the position of the continental slope.

513

514 Figure 2. Foraging tracks of Black-legged Kittiwakes from Middleton Island during the

515 breeding season in 2007. Maps show Middleton Island (MDO), the entrance to Prince

516 William Sound (PWS), Hinchinbrook Island (HI), and bathymetry in meters. (a) All foraging

517 trips (16) performed by nine instrumented birds. (b) Two long-distance, overnight trips (two

518 different birds) shown in more detail. Circles indicate resting areas at night, white dots are

519 positional fixes obtained by the GPS logger, and arrows indicate direction of movement. (c)

520 Two examples of shorter trips shown in more detail. Symbology as in (b).

521

522 Figure 3. Maximum foraging distances (km) for all recorded foraging trips from Middleton

523 Island in 2007, sorted chronologically.

524

525 Figure 4. Flight speeds of Black-legged Kittiwakes from Middleton Island recorded by GPS-

526 data loggers during the breeding season in 2007. Flight speeds  $\leq 10 \text{ km h}^{-1}$  are not depicted

527 for reasons explained in the text.

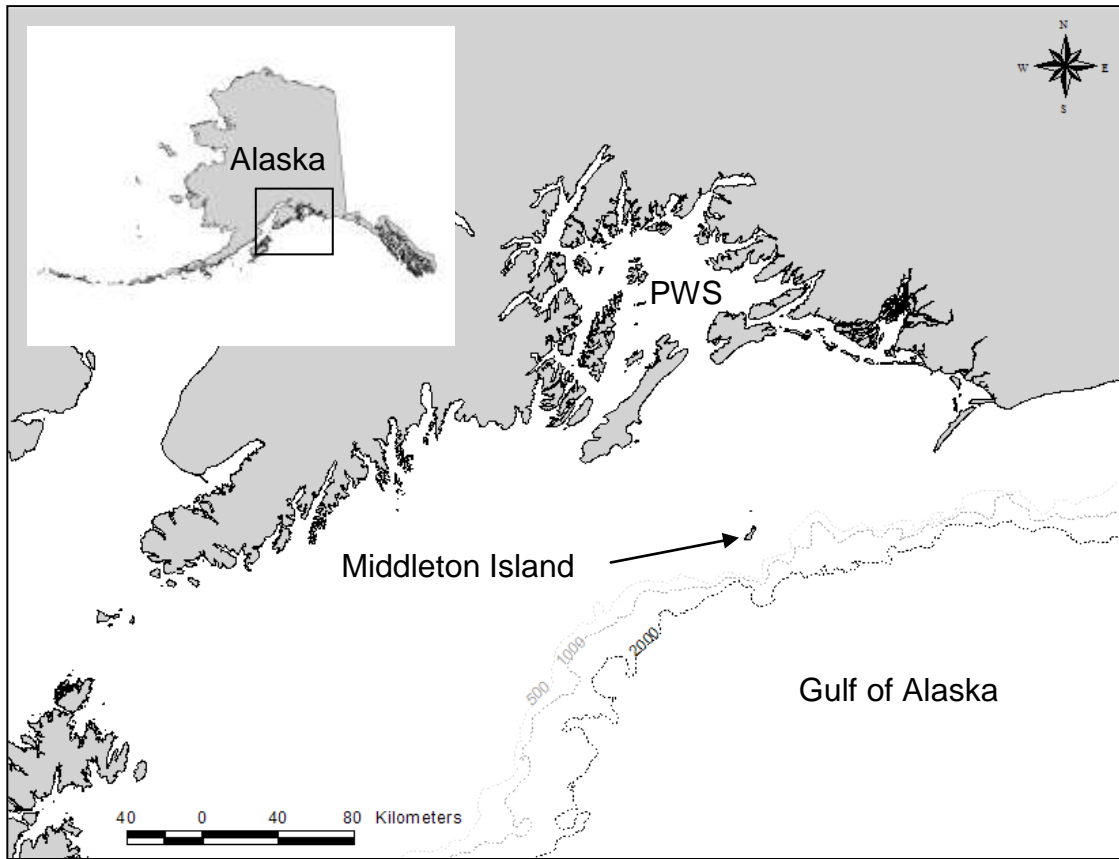


Figure 1

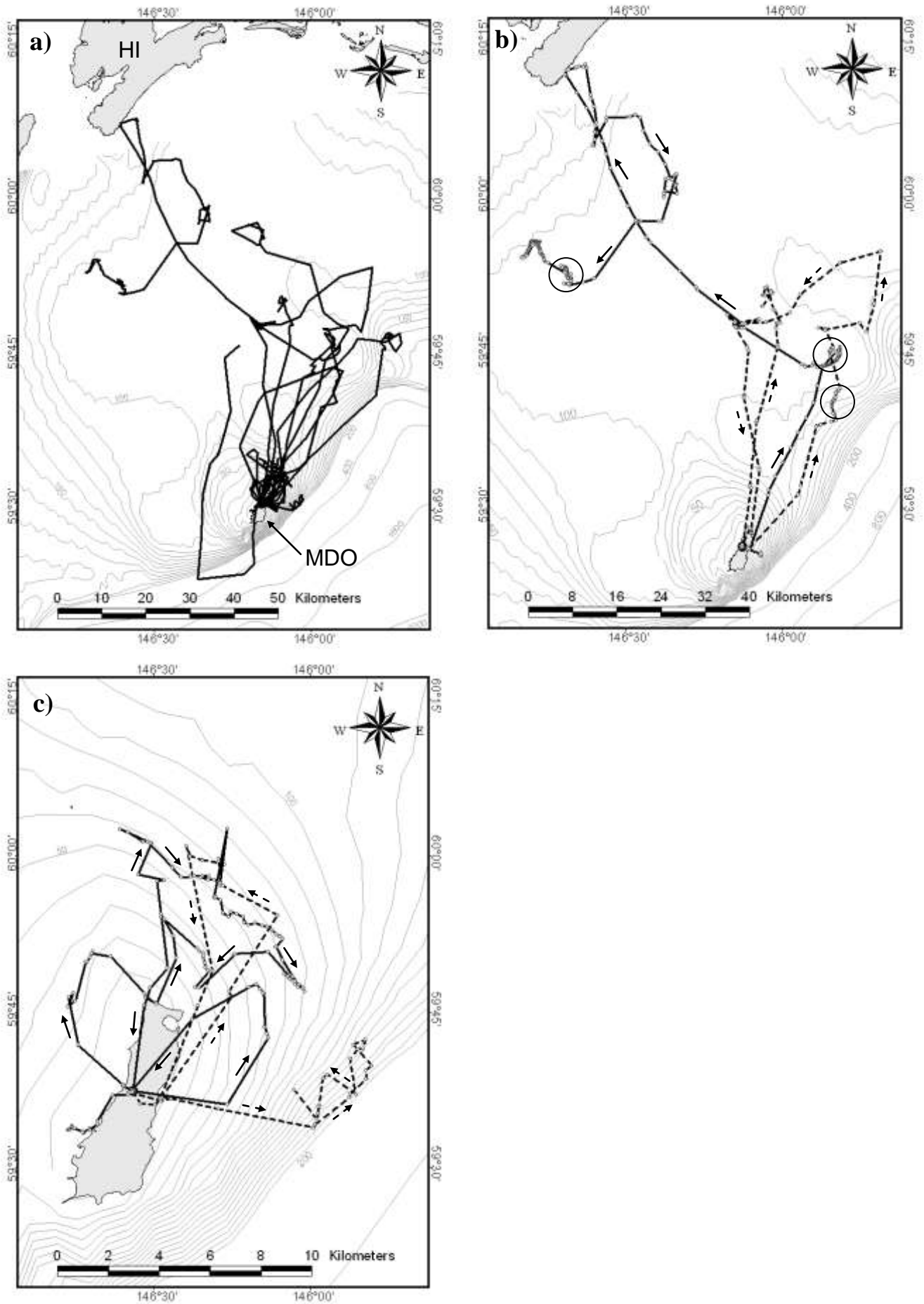


Figure 2

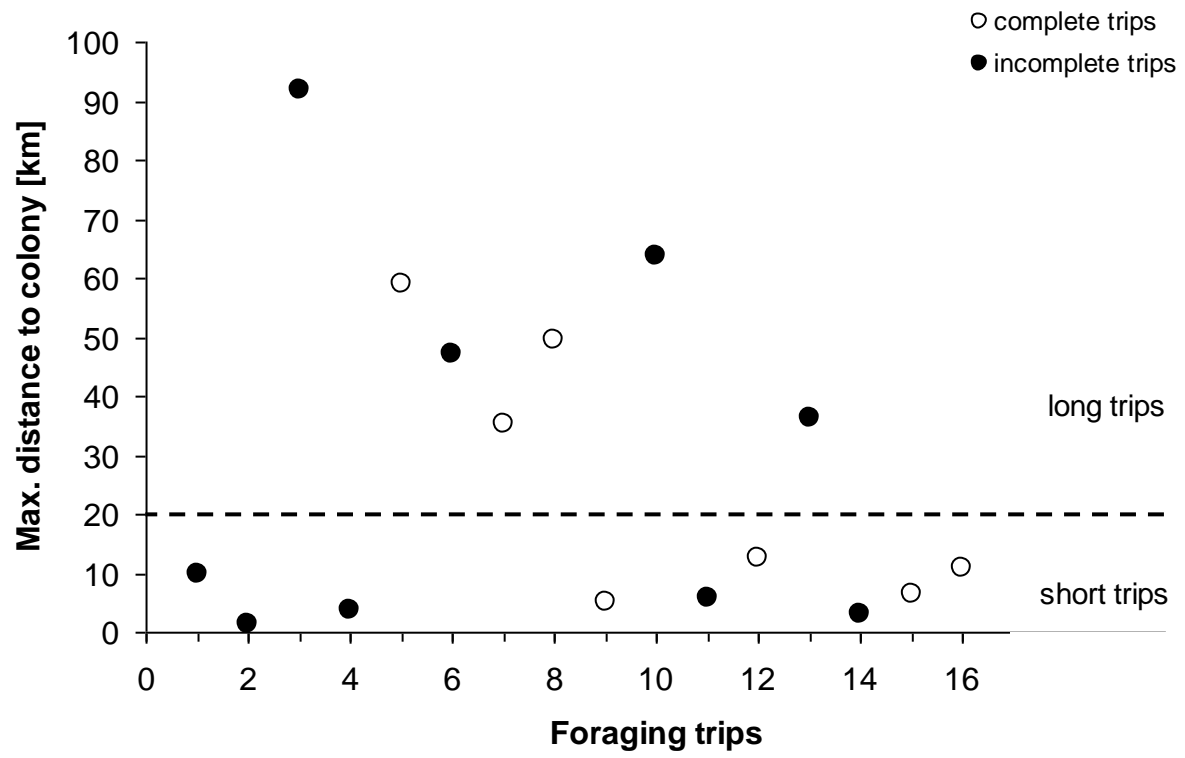


Figure 3

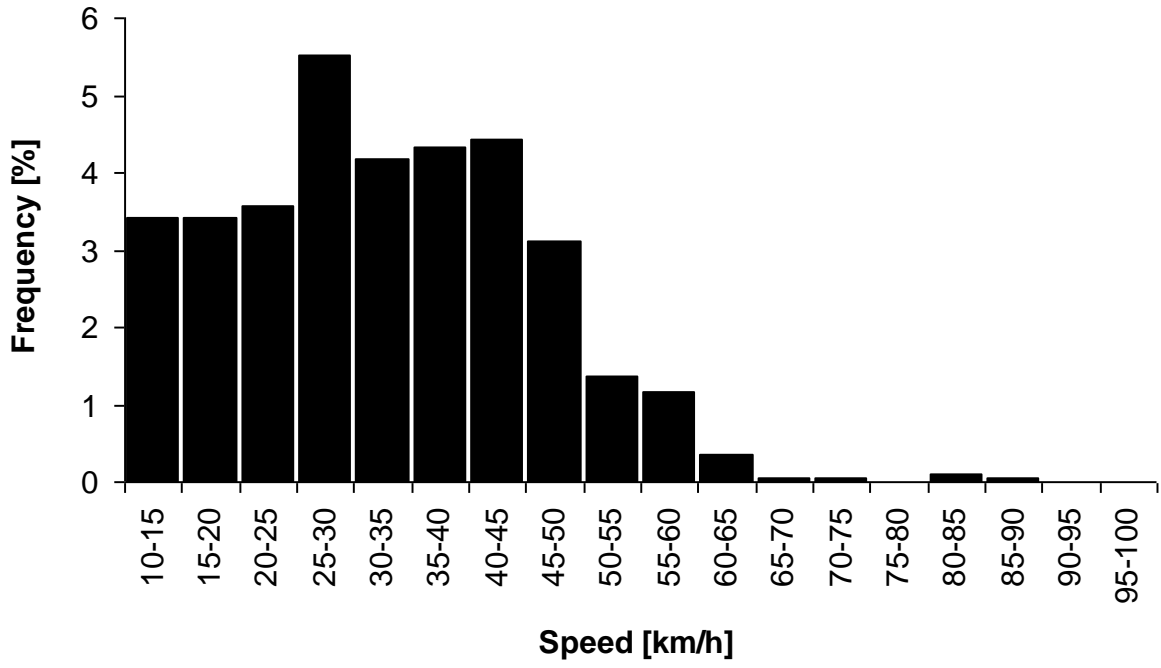


Figure 4