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Black-legged Kittiwakes *Rissa tridactyla* are the most abundant gull species in the world but some populations have declined in recent years, apparently due to food shortage. Kittiwakes are surface feeders and thus can compensate for low food availability only by increasing their foraging range and/or devoting more time to foraging. The species is widely studied in many respects, but long-distance foraging and the limitations of conventional radio telemetry have kept this vital activity largely out of view. Development of GPS loggers is advancing rapidly. With devices as small as 8 g now available it is possible to use this technology for tracking relatively small species of oceanic birds like kittiwakes. Here we present the first results of GPS telemetry applied to Black-legged Kittiwakes in 2007 in the North Pacific. All but one individual foraged in the neritic zone north of the island. Three birds performed foraging trips only close to the colony (within 13 km), while six birds had foraging ranges averaging about 40 km. The maximum foraging range was 59 and the maximum distance traveled was 165 km. Maximum trip duration was 17 h (mean: 8 h). An apparently bimodal distribution of foraging ranges affords new insight on the variable foraging behaviour of Black-legged Kittiwakes. Successful deployment of GPS loggers on kittiwakes holds much promise for telemetry studies on many other species of similar size and encourages this new approache for further studies.

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

Seabirds spend most of their time at sea and are difficult to observe when not attending nests during breeding. Research is therefore biased toward land-based observations, with the at-sea biology of smaller species generally limited to counts of travelling and foraging birds from research vessels. Such studies are time- or area-restricted and unable to give detailed insights into the foraging behaviour of individuals (Weimerskirch et al. 2005). However, knowledge of foraging behaviour is essential to understanding both the ecological roles of seabirds and constraints acting upon them in marine ecosystems (Monaghan 1996; Wilson et al. 2002). The most productive and cost-effective way to study the flight and foraging behaviour of birds at sea employs electronic devices attached to individuals (Daunt et al. 2003; Garthe et al. 2007; Grémillet et al. 2004; Wilson et al. 2002). A variety of loggers and techniques have been developed in the last 40 years (Grémillet et al. 2000; Hamer et al. 2007; Weimerskirch and Wilson 2000). The newest tracking devices to come on line are GPS receivers, unlimited in range and capable of much higher resolution and accuracy than satellite transmitters or conventional radio telemetry (Hulbert and French 2001; Hünerbein et al. 2000). As with most new technologies, the first GPS data loggers were too heavy to deploy on all but very large-bodied seabirds such as albatrosses (Diomedeidae; (Waugh et al. 2005; Weimerskirch et al. 2002) and gannets (Sulidae; (Grémillet et al. 2004). The latest equipment, with package sizes in the range of 8-12 g, bring small and medium-sized seabirds (c. 300 g and larger) into the scope of possible applications.

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

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

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

Methods

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

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

Tracking devices were deployed between 1 July and 11 August 2007. We captured 14 adult kittiwakes and deployed GiPSy® data loggers (11 g; L 50 x W 22 x H 10 mm) manufactured by TechnoSmart. The loggers were programmed to use a 5-min sampling interval. GPS data stored in the device memory and used for the analysis included date, time, latitude, longitude and speed. The devices were attached to feathers in the middle of the back with TESA® tape (Wilson et al. 1997). Before deployment, each bird was weighed to the nearest 5 g using a spring balance. The loggers were 2-3% of mean body mass (397 g, range 345-500 g). Mass was the only measurement taken upon first capture to minimize handling time. Additional measurements (bill length, head-bill length, wing length) and banding were taken upon recapture if data were not already available from previous studies. Measurements were used to determine the sex of the birds (Jodice et al. 2000). Handling time (capture to release) was approximately 10 min for deployment and 3-15 min for logger removal, banding, and measurements as needed. In 28 captures and recaptures, 15 birds returned to their nest within 15 min (5 of them immediately), 4 birds within 31 min, and 3 birds more than 1 h after capture. Return time for 6 birds was undetermined due to a lack of nest observations. We deployed 12 of the 14 loggers in the late afternoon or evening, which allowed us potentially to capture information on nighttime foraging. We used 106 unmanipulated nests on the tower as a control group to compare breeding success between equipped and non-equipped birds.

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

Loggers were switched on at deployment — no delayed start was possible — and due to battery depletion or occasional large gaps in data collection, not all foraging trips were well documented from start to finish. In calculating the mean maximum range, mean distance to colony and mean trip duration we included only complete trips, but estimated values are also reported for individual trips that were incomplete. The missing portion of a track line was extrapolated directly back to the colony, which underestimates the distance travelled by an unknown, but probably modest amount. Extrapolated track lines were then used to correct the trip duration of incomplete trips using a mean flight speed of 33 km/h (as measured in this study; see below). Statistical analyses were carried out in R 2.8.0. and SPSS 11.5.

Results

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

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

The main foraging area was north of the colony, encompassing the continental shelf area between Middleton Island and Prince William Sound (Fig. 2). Birds stayed mostly over waters less than 200 m deep. One bird made repeated visits to the shelf slope south and east of the island but did not access the abyssal zone beyond (Fig. 2a, 2c). One bird visited the nearshore area of Hinchinbrook Island at the entrance to Prince William Sound (92 km from Middleton).

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

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

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

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

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

Discussion

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

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

Foraging ranges of breeding kittiwakes are variable from one location to another. Ranges (± SE) of 41 ± 3 km (Shoup Bay), 26 ± 5 km (Icy Bay), and 21 ± 5 km (Eleanor Island) were reported for three colonies in Prince William Sound (Ainley et al. 2003). The maximum foraging distance from the Shoup Bay colony was 120 km (Suryan et al. 2000). Values reported here for Middleton Island (mean range of all trips: 26 km, maximum: 59 km) are intermediate relative to Prince William Sound, whereas radio telemetry in Great Britain (Sumburgh Head, Shetland) found that kittiwakes usually travelled more than 40 km from the colony in 1990, beyond the range of receiving equipment (Wanless et al. 1992). In the following year, more than 95% of foraging trips stayed within 5 km of the Sumburgh Head colony, a reversal attributed to improved food availability (Hamer et al. 1993). Elsewhere in Britain, maximum ranges of 73 ± 9 km from the Isle of May and 55.5 km from the Farne Islands were estimated from flight duration and speed (Daunt et al. 2002; Pearson 1968). Kittiwakes breeding at Helgoland in the German Bight were seen at a distance of 10-35 km from the colony (aerial and ship based transect counts). Only single birds were observed at distances up to 70-80 km (Dierschke et al. 2004). Those relatively short foraging distances may be explained by low competition for prey — good feeding conditions around the island, small size of the colony, and its isolation from other colonies of the same species

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

With one exception, kittiwakes foraged only in a northerly direction from the colony, over the continental shelf and within the 200-m depth contour. We expected the shelf edge, a potentially rich feeding habitat close to the island, to be a greater attraction than it was. However, upwelling along the shelf edge is not as strong in summer as in winter (Weingartner et al. 2005), which may explain the absence of kittiwakes in that area during July and August. Observations on diet suggest a different situation in April, prior to egg-laying. Prey regurgitated by kittiwakes in the first several weeks after returning to Middleton Island in spring consist mostly of lanternfishes (Myctophidae) and small squids (S. A. Hatch, unpubl. data). The birds presumably obtain this prey from deep ocean habitat of the continental slope and abyssal ocean south of the island. Myctophids and squids are important components of the mesopelagic community that migrate vertically to the ocean surface at night (Beamish et al. 1999; Sinclair and Stabeno 2002). Myctophids, in particular, are high-energy prey (Van Pelt et al. 1997) whose availability to kittiwakes before and during early breeding stages on Middleton is thought to influence breeding success (Gill and Hatch 2002). Such prey are seen also during incubation in some years (Gill and Hatch 2002). In this study we sampled two birds late in incubation, one of which went to the shelf edge east of Middleton while the other made the most distant foraging trip observed, on a northwesterly heading to Hinchinbrook Island. More sampling is needed to clarify the relative importance and seasonality of deep ocean versus neritic foraging by kittiwakes from Middleton.

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

In conclusion, we affirm the utility of GPS data loggers in elucidating the movements and marine habitat use of seabirds previously excluded from such investigations because of their small body size. Kittiwakes exhibited flexible foraging behaviour—short and long foraging trips that appeared to change in relative frequencies over the course of chick rearing. Although the sample was limited to 16 foraging trips, seven of them complete, we gained much insight into the foraging behaviour of Black-legged Kittiwakes from Middleton Island. Nearly all foraging trips were over the continental shelf, in northerly direction of the colony. Thus, we believe the sample typifies the behaviour of most birds in this colony, but further investigations are desirable. Interannual and within-season variation have yet to be fully investigated.

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

Zusammenfassung

GPS-Logger offenbaren Nahrungssuchstrategien der Dreizehenmöwen

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

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

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References

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

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

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

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

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

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

Coulson JC and Johnson MP (1993) The attendance and absence of adult Kittiwakes *Rissa tridactyla* from the nest site during the chick stage. Ibis 135: 372-378

Daunt F, Benvenuti S, Harris MP, Dall'Antonia L, Elston DA and Wanless S (2002) Foraging strategies of the black-legged kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. Mar Ecol Prog Ser 245: 239-247

Daunt F, Peters G, Scott B, Grémillet D and Wanless S (2003) Rapid-response recorders reveal interplay between marine physics and seabird behaviour. Mar Ecol Prog Ser 255: 283-288

Dierschke V, Garthe S and Markones N (2004) Aktionsradien Helgoländer Dreizehenmöwen *Rissa tridactyla* und Trottellummen *Uria aalge* während der Aufzuchtphase. Vogelwelt 125: 11-19

Frederiksen M, Mavor RA and Wanless S (2007) Seabirds as environmental indicators: the advantages of combining data sets. Mar Ecol Prog Ser 352: 205-211

Frederiksen M, Jensen H, Daunt F, Mavor RA and Wanless S (2008) Differential effects of a local industrial sand lance fishery on seabird breeding performance. Ecol Appl 18: 701-710

Furness RW and Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar Ecol Prog Ser 202: 253-264

Garthe S, Montevecchi WA and Davoren GK (2007) Flight destinations and foraging behaviour of northern gannets (*Sula bassana*) preying on a small forage fish in a low-arctic ecosystem. Deep Sea Res Part II 54: 311-320

Gill VA and Hatch SA (2002) Components of productivity in Black-legged Kittiwakes *Rissa tridactyla*: response to supplemental feeding. J Avian Biol 33: 113-126

Gill VA, Hatch SA and Lanctot RB (2002) Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes *Rissa tridactyla*. Ibis 144: 268-283

Götmark F (1980) Foraging flights of Kittiwakes-some functional aspects. Vår Fågelvärld 39: 65-74

Grémillet D, Storch S and Peters G (2000) Determining food requirements in marine top predators: a comparison of three independent techniques in Great Cormorants, *Phalacrocorax carbo carbo*. Can J Zool 78: 1567-1579

Grémillet D, Omo GD, Ryan PG, Peters G, Ropert-Coudert Y and Weeks SJ (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape Gannets from neighbouring colonies. Mar Ecol Prog Ser 268: 265-279

Hamer KC, Monaghan P, Uttley JD, Walton P and Burns MD (1993) The influence of food supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. Ibis 135: 255-263

Hamer KC, Humphreys EM, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips RA, Harris MP and Wanless S (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. Mar Ecol Prog Ser 338: 295-305

Harding AMA, Piatt JF, Schmutz JA, Shultz MT, Pelt TIV, Kettle AB and Speckman SG (2007) Prey density and the behavioral flexibility of a marine predator: the Common Murre (*Uria aalge*). Ecology 88: 2024-2033

Harris MP and Wanless S (1990) Breeding Success Of British Kittiwakes *Rissa tridactyla* In 1986-88 - Evidence For Changing Conditions In The Northern North Sea. J Appl Ecol 27: 172-187

Hatch SA, Roberts BD and Fadely BS (1993a) Adult survival of Black-legged Kittiwakes *Rissa tridactyla* in a Pacific colony. Ibis 135: 247-254

Hatch SA, Byrd GV, Irons DB and G. L. Hunt J (1993b) Status and ecology of kittiwakes (Rissa tridactyla and R. brevirostris) in the North Pacific. Canadian Wildlife Service, Ottawa, ON

Hatch SA, Robertson GJ and Baird PH (2009) Black-legged Kittiwake (Rissa tridactyla). In: Poole A (ed) The Birds of North America Online. Cornell Lab of Ornithology, Ithaca

Hoyo Jd, Elliott A and Sargatal J (1996) Handbook of the Birds of the World. Vol. 3. Lynx Edictions, Barcelona

Hulbert IAR and French J (2001) The accuracy of GPS for wildlife telemetry and habitat mapping. J Appl Ecol 38: 869-878

Humphreys EM, Wanless S and Bryant DM (2006) Stage-dependent foraging in breeding black-legged kittiwakes *Rissa tridactyla*: distinguishing behavioural responses to intrinsic and extrinsic factors. J Avian Biol 37: 436-446

Hünerbein Kv, Hamann HJ, Ruter E and Wiltschko W (2000) A GPS-based system for recording the flight path of birds. Naturwissenschaften 87: 278-279

Jodice PGR, Lanctot RB, Gill VA, Roby DD and Hatch SA (2000) Sexing Adult Black-legged Kittiwakes by DNA, Behavior, and Morphology. Waterbirds 23: 405-415

Kitaysky AS, Jr GLH, Flint EN, Rubega MA and Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. Mar Ecol Prog Ser 206: 283-296

Monaghan P (1996) Relevance of the behaviour of seabirds to the conservation of marine environments. Oikos 77: 227-237

Pearson TH (1968) The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J Anim Ecol 37: 521-552

Pennycuick CJ (1987) Flight of Auks (Alcidae) and other northern seabirds compared with southern Precellariiformes: ornithodolite observations. J Exp Biol 128: 335-347

Pennycuick CJ (1997) Actual and 'optimum' flight speeds: field data reassessed. J Exp Biol 2000: 2355-2361

Phillips RA, Xavier JC and Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. Auk 120: 1082-1090

Roberts BD and Hatch SA (1993) Behavioral ecology of Black-legged Kittiwakes during chick rearing in a failing colony. Condor 95: 330-342

Sinclair EH and Stabeno PJ (2002) Mesopelagic nekton and associated physics of the southeastern Bering Sea. Deep Sea Res Part II 49: 6127-6145

Suryan RM, Irons DB and Benson J (2000) Prey switching and variable foraging strategies of Black-legged Kittiwakes and the effect on reproductive success. Condor 102: 374-384

Suryan RM, Irons DB, Brown ED, Jodice PGR and Roby DD (2006) Site-specific effects on productivity of an upper trophic-level marine predator: Bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. Prog Oceanogr 68: 303-328

Van Pelt TI, Piatt JF, Lance BK and Roby DD (1997) Proximate composition and energy density of some North Pacific forage fishes. Comp Biochem Physiol A-Mol Integr Physiol 118: 1393-1398

Wanless S, Monaghan P, Uttley JD, Walton P and Morris JA (1992) A radio-tracking study of kittiwakes (*Rissa tridactyla*) foraging under suboptimal conditions. In: Priede IG and Swift SM (eds) Wildlife telemetry. Remote monitoring and tracking of animals. Ellis Horwood, New York, pp 581-590

Wanless S, Frederiksen M, Daunt F, Scott BE and Harris MP (2007) Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. Prog Oceanogr 72: 30-38

Waugh S, Filippi D, Fukuda A, Suzuki M, Higuchi H, Setiawan A and Davis L (2005) Foraging of royal albatrosses, *Diomedea epomophora*, from Otago Peninsula and its relationships to fisheries. Can J Fish Aquat Sci 62: 1410-1421

Weimerskirch H and Wilson RP (2000) Oceanic respite for Wandering Albatrosses. Nature 406: 955-956

Weimerskirch H, Chastel O, Cherel Y, Henden J-A and Tveraa T (2001) Nest attendance and foraging movements of northern fulmars rearing chicks at Bjørnøya Barents Sea. Polar Biol 24: 83-88

Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G and Lipp H-P (2002) GPS tracking of foraging Albatrosses. Science 295: 1259

Weimerskirch H, Corre ML, Jaquemet S and Marsac F (2005) Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. Mar Ecol Prog Ser 288: 251-261

Weimerskirch H, Corre ML, Ropert-Coudert Y, Kato A and Marsac F (2006) Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. Oecologia 146: 681-691

Weingartner TJ, Danielson SL and Royer TC (2005) Freshwater variability and predictability in the Alaska Coastal Current. Deep Sea Res Part II 52: 169-191

Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin J-B and Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildl Soc Bull 25: 101-106

Wilson RP, Grémillet D, Syder J, Kierspel MAM, Garthe S, Weimerskirch H, Schaefer-Neth C, Scolaro JA, Bost C-A, Plötz J and Nel D (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar Ecol Prog Ser 228: 241-261

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

				Date		No. of trips	
Bird no.	**Nest**	**Sex**	**Brood stage**	**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

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

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
			33.0	91.8	306.3	incomplete	n
6	female	chick rearing	2.5	3.8	9.7	incomplete	d
			12.8	59.0	164.7	complete	n
			4.6	47.2	100.5	incomplete	d
8	male	chick rearing	16.8	35.2	92.5	complete	n
9	male	chick rearing	7.2	49.5	129.7	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

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

	Logger birds	**Non-equipped birds**	**Statistics (GLM)**
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

Figure Legends

Figure 1. Study area in the Gulf of Alaska showing the locations of Middleton Island and Prince William Sound (PWS). Middleton lies about 80 km south of the Alaska mainland. Depth contours indicate the position of the continental slope.

Figure 2. Foraging tracks of Black-legged Kittiwakes from Middleton Island during the breeding season in 2007. Maps show Middleton Island (MDO), the entrance to Prince William Sound (PWS), Hinchinbrook Island (HI), and bathymetry in meters. (a) All foraging trips (16) performed by nine instrumented birds. (b) Two long-distance, overnight trips (two different birds) shown in more detail. Circles indicate resting areas at night, white dots are positional fixes obtained by the GPS logger, and arrows indicate direction of movement. (c) Two examples of shorter trips shown in more detail. Symbology as in (b).

Figure 3. Maximum foraging distances (km) for all recorded foraging trips from Middleton Island in 2007, sorted chronologically.

Figure 4. Flight speeds of Black-legged Kittiwakes from Middleton Island recorded by GPS-data loggers during the breeding season in 2007. Flight speeds ≤ 10 km h^{-1} are not depicted for reasons explained in the text.

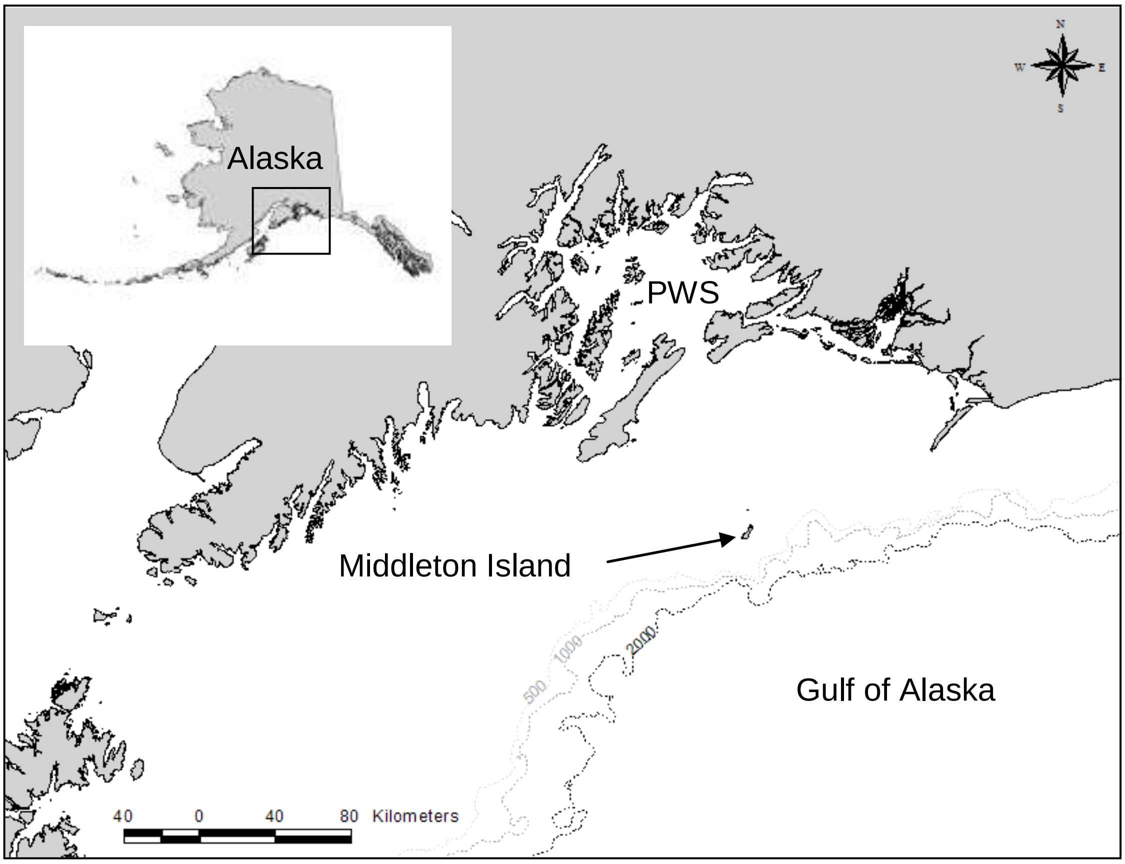

Alaska
PWS
Middleton Island
Gulf of Alaska
500
1000
2000
40 0 40 80 Kilometers
N
W
E
S

Figure 1

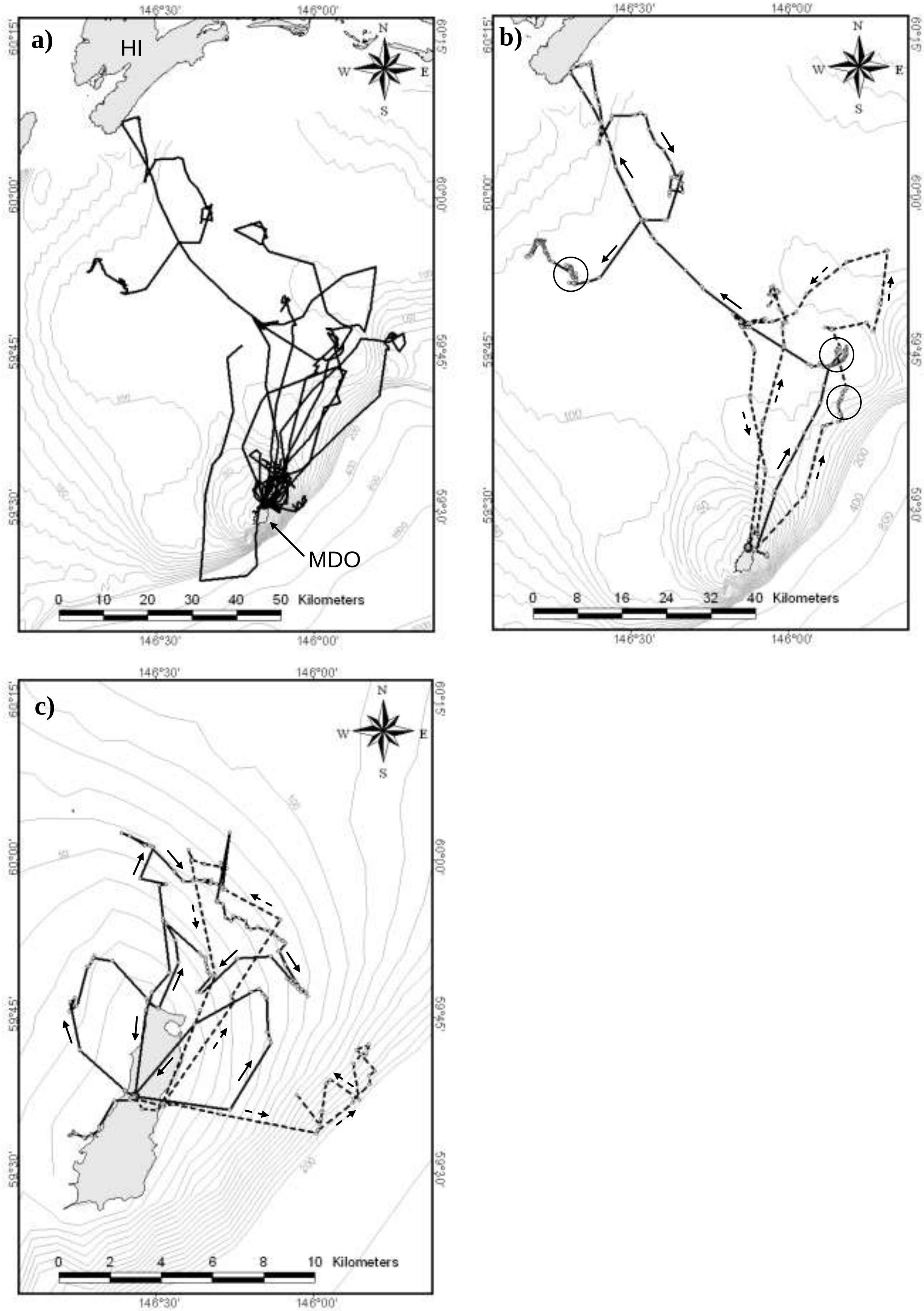

a)
HI
MDO
0 10 20 30 40 50 Kilometers
b)
0 8 16 24 32 40 Kilometers
c)
0 2 4 6 8 10 Kilometers
146°30'
146°00'
60°15'
60°00'
59°45'
59°30'
N
S
E
W

Figure 2

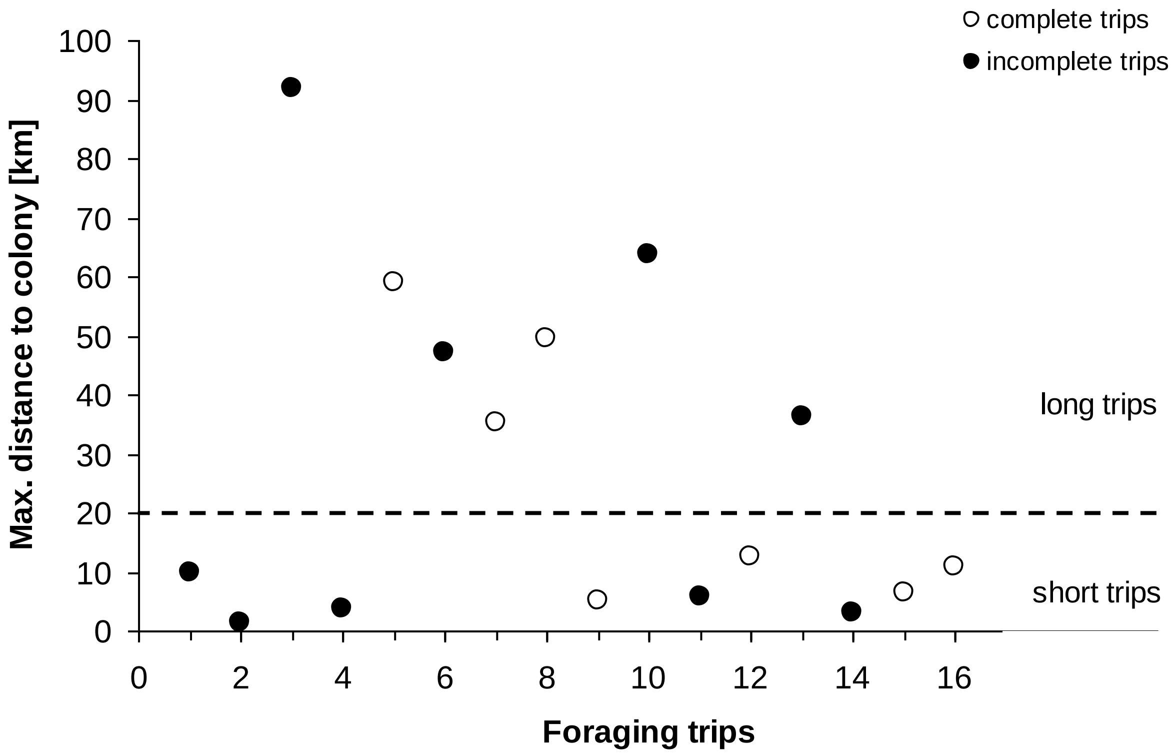
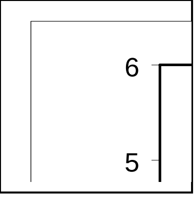

complete trips
incomplete trips
Max. distance to colony [km]
100
90
80
70
60
50
40
30
20
10
0
long trips
short trips
0
2
4
6
8
10
12
14
16
Foraging trips

Figure 3


6
5

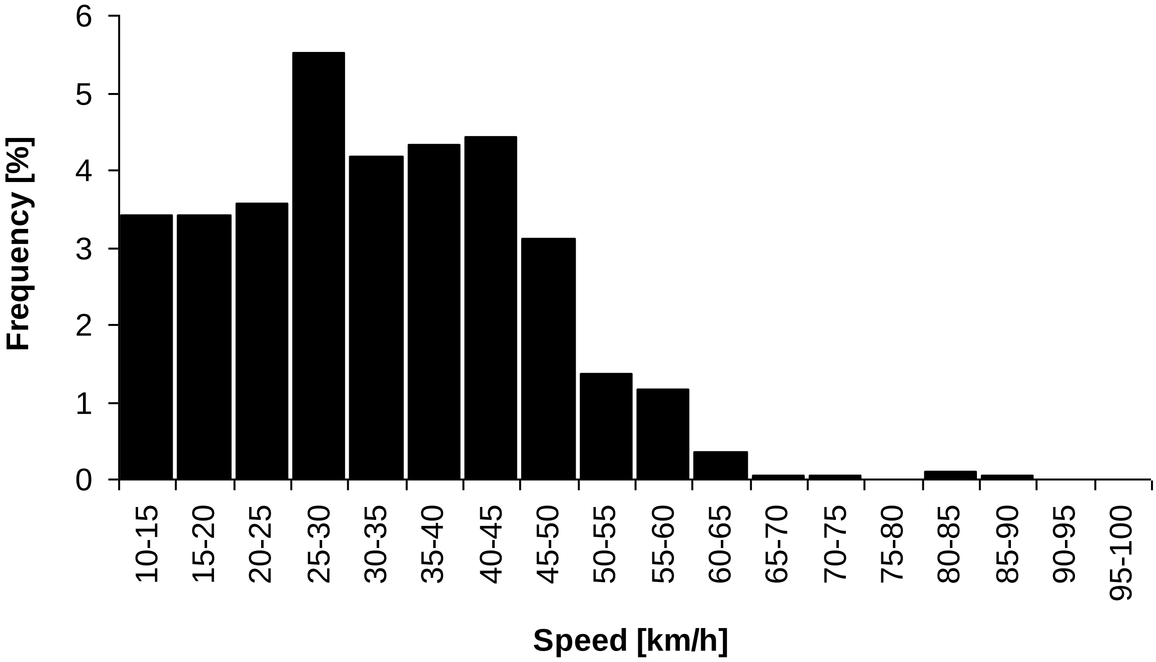

Frequency [%]
0
1
2
3
4
5
6
10-15
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
60-65
65-70
70-75
75-80
80-85
85-90
90-95
95-100
Speed [km/h]

Figure 4