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Original research article

Satellite tracking of red-listed nominate lesser black-backed gulls (*Larus f. fuscus*): Habitat specialisation in foraging movements raises novel conservation needs

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HIGHLIGHTS

- Individual gulls of a generalist species are highly specialised in their foraging.
- Differences in foraging behaviour may lead to differences in demographic trends.
- Local conservation problems such as shooting in birds visiting farms are identified.
- Problems need to be tackled by mere actions in the breeding period of the species.
- A novel threat having effect on breeding success is the predation by eagles.

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ABSTRACT

In contrast to many other gull species, nominate lesser black-backed gulls (*Larus fuscus fuscus*, nLBBG) have shown generally decreasing population trends throughout their breeding area in northern and eastern Fennoscandia over the past decades and are now red-listed. Interspecific competition, predation, increased disturbance, organochlorine poisoning and food shortages were suggested as main reasons for the overall decrease. Here we contribute to a better understanding of population declines by comparing foraging movements of satellite tracked adult gulls in three geographical areas of Finland (West, South, and East) that differ in their population trends. Our analysis examines potential

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Foraging movement
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differences and preferences in the feeding site behaviour of adult gulls. Our comparison of the three geographical areas showed that nLBBGs preferred feeding at fur farms in West Finland, waste dumps in South Finland, and lakes and fields in East Finland. We found individual gulls of this purportedly generalist species to be highly specialised in their foraging behaviour, particularly those that might be associated with their survival probabilities. We hypothesise that differences in foraging behaviour and food availability during the breeding season are partially responsible for differences in demographic trends between populations. Specifically, we identify potential local conservation problems such as shooting in birds visiting fur farms. Our data suggest that the effective conservation and management of endangered nLBBGs could be aided by simple actions in the breeding areas in addition to better protection throughout the annual movement cycle.

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1. Introduction

In recent years, satellite tracking with radio transmitters fitted to large and successively smaller birds, including raptors, gulls, seabirds or cuckoos, have revealed exciting and often unexpected results of these migratory journeys (Jouventin and Weimerskirch, 1990; Kjellén et al., 1997; Meyburg et al., 2003; Thorup et al., 2003; Pütz et al., 2007, 2008; Klaassen et al., 2012; Willemoes et al., 2014; Kays et al., 2015; Wikelski et al., 2015). While many satellite telemetry studies primarily emphasise migration periods with large distances covered, long-range foraging movements during the breeding seasons have been investigated very prominently in seabirds (Prince et al., 1992; Weimerskirch et al., 1993; Weimerskirch and Robertson, 1994; Brothers et al., 1998; Wood et al., 2000; Hamer et al., 2000; Burger and Shaffer, 2008) but also within shorter ranges (Camphuysen, 2013). Other observational methods for long-range foraging movements such as visual observation by the use of colour or regular ringing have also produced a wealth of data of migratory and foraging movements of many bird groups, gulls in particular (Ens et al., 2009; Helberg et al., 2009; Marques et al., 2009, 2010; Shamoun-Baranes et al., 2011; Camphuysen, 2013; Valkama et al., 2014). However, such traditional methods do not allow for the quantification of habitat use in gulls that cover large distances during daily foraging trips and may change their foraging sites daily, weekly or seasonally.

According to OSPAR (2009) the global population of lesser black-backed gulls (*Larus fuscus*, hereafter as LBBG) (all subspecies) is about 680 000–750 000 pairs and the European breeding population is considered large with over 300 000 pairs. However, the global estimates for the *L.f. fuscus* subspecies (hereafter as nLBBG) by national surveys are 18 000–19 000 pairs. A national survey carried out in Finland in 2013 by BirdLife Finland, gave a total population estimate of 7300 pairs, representing around 40% of the world population (Hario, 2014). According to the Red List of Finnish Bird Species, the nLBBG is classified as endangered (EN) (Tiainen et al., 2016). It is listed in the Red Data books also in Sweden, Norway, Estonia and Russian Karelia.

In Finland, nominate *fuscus* has been decreasing in numbers over the past decades, following a numerical increase between 1930 and 1960 (Bergman, 1982; Kilpi, 1983). Nominate *fuscus* has also declined dramatically in numbers in northern Norway, and it is now generally considered to be threatened (Strann and Vader, 1992; OSPAR, 2009). In Sweden, nLBBGs have shown decreasing population trends from the late 1970s to late 1990s, but have then slightly recovered (Lif et al., 2005). On the other hand, the increase of the White Sea population in Russia contrasts with a strong decline of the Baltic population (Cherenkov et al., 2007), though the western populations of Lake Onega and Lake Ladoga have also decreased in the 2000s, showing low production partly due to egg harvesting (2000–2015 yearly counts by R. Juvaste, pers. comm.).

The causes of the decline are unknown but were expected to be related to food shortages during the breeding season and high chick mortality caused by elevated levels of DDE and other pollutants picked up by adults in their wintering areas in East Africa (Strann and Vader, 1992; Anker-Nilssen et al., 2000; Bakken et al., 2003; Hario et al., 2004). Interspecific competition and predation by herring gulls (*Larus argentatus*) and greater black-backed gulls (*Larus marinus*) are possible reasons for low production of nLBBG fledglings (Hario, 1994; Capandegui, 2006). Also predation by minks (*Neovison vison*), goshawks (*Accipiter gentilis*), common crows (*Corvus corone cornix*) and white-tailed eagles (*Haliaeetus albicilla*) may have notable effects on breeding success (R. Juvaste, pers. comm.; see Blight et al., 2015).

The foraging movements and the ecology of LBBG *graellsii* subspecies at the North Sea have been well studied by counting gulls feeding at sea and on land, by determining diet composition from pellets and feces, and by radio and GPS tagging (Camphuysen, 1995; Noordhuis and Spaans, 1992; Schwemmer and Garthe, 2005; Kim and Monaghan, 2006; Camphuysen, 2011, 2013). However, foraging movements and feeding behaviour of nominate *fuscus*, especially at lake areas, are not well known. Here we used satellite GPS telemetry to determine the daily foraging movements of three populations of nominate LBBGs in Finland that were selected to represent differing population trends within a small geographical area in Central Finland (Table 1). Based on satellite tracking data at lake and coastal areas in Finland, we estimated the distances and directions of foraging trips of marked individuals as a function of status (location of origin) and sex of the birds. We expected the different population trends in the study areas to be partly influenced by foraging habits of breeding LBBGs.

Table 1

Estimated breeding numbers of Finnish nLBBGs given by the local bird associations in 2003 and 2013. Data from Hario (2014), Hannila et al. (2008)¹, and Hannila & Hongell (unpublished)².

Area	Population estimate 2003, pairs	Population estimate 2013, pairs	Percentage change
Whole country, total	8790	7330	–17
Coastal, total	5670	4600	–19
Inland, total	3120	2730	–13
W Central Ostrobothnia	1310	1320	+1
S Pirkanmaa+Valkeakoski	435	421	–3
E Southern Savonia	450	384	–15
E North Karelia	255	232	–9
W Kokkola	250 ¹	235 ²	–6

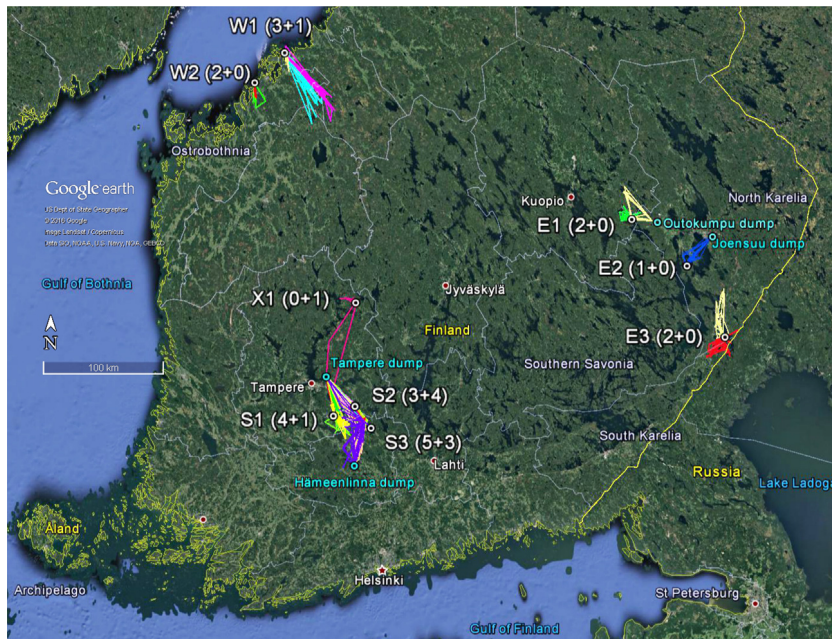


Fig. 1. Histories of tagged nominate lesser black-backed gulls from the Finnish breeding sites together with some additional nLBBGs that were caught at Tampere waste dump. The first number in brackets refers to year 2009, the second one refers to years 2010–2011. The areas are W1 Kokkola, W2 Uusikaarlepyy, S1 Pälkäne and Valkeakoski, S2 Pälkäne, S3 Hauho, E1 Outokumpu, E2 Liperi and E3 Kesälahti. The breeding site W2 of about 180 pairs was the biggest breeding site in Finland. W1 Kokkola breeding site had about 30 pairs and the other study breeding sites about 15–20 pairs.

2. Materials and methods

Between 24 May and 2 June 2009, 25 breeding adult nLBBGs were trapped from nest-sites at three geographical areas (Fig. 1): (1) western Finland (W), two sites at the coast of the Bothnian Bay, near the cities of Kokkola and Uusikaarlepyy; (2) southern Finland (S), including three sites near the city of Tampere (Hauho, Pälkäne and Valkeakoski); and (3) eastern Finland (E), including three sites in North Karelia (Kesälahti, Liperi and Outokumpu). The breeding sites were typical Finnish lake and sea breeding sites, with the size of 15–30 pairs, except one which was one of the largest breeding sites in Finland (180 pairs) (Fig. 1). In the breeding sites, walk-in nest traps were set just above the egg nest during the late phase of incubation and adjusted to launch automatically when a bird entered the trap.

After trapping, the gulls were measured (wing length, tarsus, bill, weight), ringed (metal ring, read ring), and photographed. Birds were sexed using the measurements (Coulson et al., 1983) and checked later by DNA-analyses from the blood samples (Arriero et al., 2015). The satellite transmitters, 30 g Microwave solar powered GPS-PTT (Microwave Telemetry Inc., Maryland, USA), were attached using a backpack-style Teflon harness, a method used before with good success (e.g. Ens et al., 2008; Roshier and Asmus, 2009; Beason et al., 2010; Pavón et al., 2010; Takekawa et al., 2010). Harnesses were adjusted such as to minimally bother or harm the birds. Gulls were released immediately after conducting the measurements, blood sampling and the attachment of transmitters.

Nominate LBBGs weighed between 580 g and 880 g (average 733 g, females 653 g and males 804 g). Therefore, birds that carried the PTT transmitters in this study received slightly more than the recommended 3% of their body mass. However, if the harness is well adjusted, this may be acceptable (Vandenabeele et al., 2012; O'Mara et al., 2014).

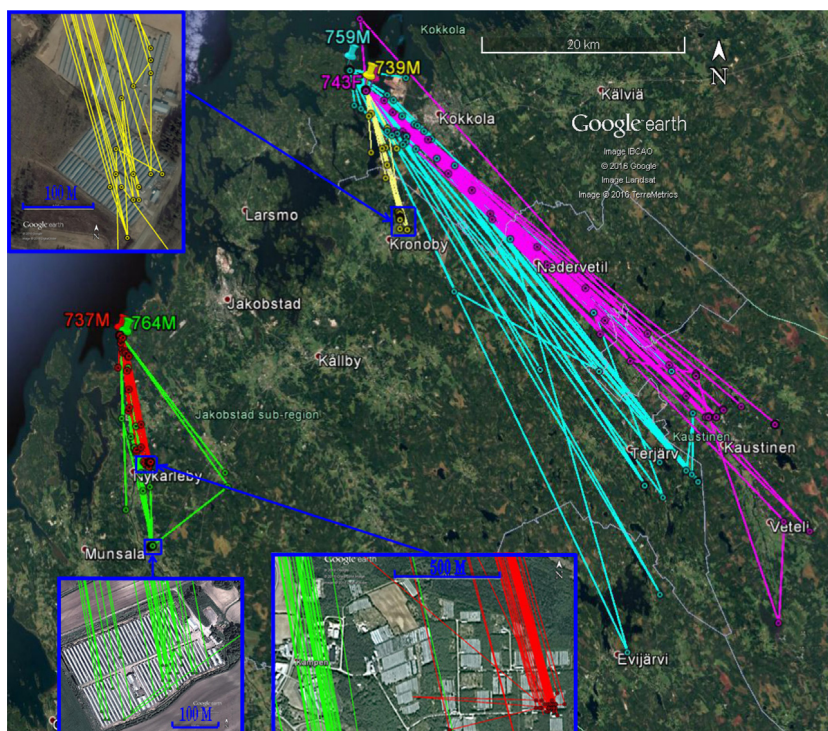


Fig. 2. GPS locations of nominate lesser black-backed gulls during the study period 8 June–7 July 2009 in the areas W1 (F743, M739, M759) and W2 (M737, M764). Photo magnifications inside denote locations in and over different fur farms.

The GPS-PTT satellite transmitters had duty cycles of 4 fixes per day at 0500, 0800, 1400 and 2000 GMT (+2 h Finnish time). These transmitters measure location, flight heading and instantaneous speed with a fair degree of accuracy. PTTs sent their data via the ARGOS system, Toulouse, France. The data were downloaded automatically from the ARGOS server to the MOVEBANK data base. All data are stored in MOVEBANK and are freely available ([doi:10.5441/001/1.q986rc29](https://doi.org/10.5441/001/1.q986rc29); Movebank Data Repository).

We opted for rather few GPS fixes per day to ensure a long lifetime of the PTTs without draining the battery (Wikelski et al., 2015). When studying foraging or migratory flights ideally the tags should collect GPS fixes every few minutes, however far fewer fixes suffice for general route tracking (Ens et al., 2008; Kranstauber et al., 2012). For example, the average foraging flights of LBBGs at the North Sea took about 7.9 h (SD 9.0 h, $n = 78$) (Camphuysen, 2013).

The breeding period was determined on the basis of long-term ringing data and only transmitter locations between 8 June and 7 July 2009 were included in the analysis, because during the first days after attaching the transmitters the birds might have moved differently than they normally do and in July the unsuccessful breeders start to leave the breeding areas. Based on extensive previous observations on the behaviour of gulls in the breeding sites, we assumed that locations within 2 km from nest are “colonial”, i.e. not proper foraging flights. As proper foraging flights we selected the locations of more than 2 km from the breeding site, which is the typical distance that offers unobstructed viewing in a lake area.

Nominate LBBGs are “specialists” acting at two different levels. At the first level of specialisation, most individuals specialise to use large food supply such as waste dumps, fur farms, fish discards and spawning herrings if available, even from a far distance. We can call these sites as “hot spots”. Some individuals may, however, specialise to use scarce local food supply like worms, insects and fish carcasses. Secondly, individuals specialise to use only one or some of the available hot spots, for example just one out of dozens of fur farms, a special part of waste dump or compost pile, or fly recurrently to the same field, lake or summer cottage for fisher’s discard. This second level of specialisation inevitably helps to avoid inter- and intraspecific competition.

We defined “specialisation” as an individual bird’s recurrent foraging flights in specific direction(s) or place(s), where food preference is independent from its availability. In the three geographical areas, available foraging sites within a radius of 60 km around colony included fur farms (W1–2), coastal areas and sea (W1–2), inland lakes (W1–2, S1–3, E1–3), waste dumps (W1–2, S1–3, E1–3) and fields (W1–2, S1–3, E1–3). Although we collected few GPS fixes per day, these fixes represent a timed sample of the birds’ daily locations and we thus consider these locations a true representation of an individuals’ movement choices (Altmann, 1974). We focused our attention for the Google Map analysis of foraging habitat onto those areas that individual birds repeatedly visited. Fortunately, based on the natural history of the foraging flights of nLBBGs to fur farms and waste dumps, it was straightforward to determine where an individual foraged (Table 2; Figs. 2–4).

Table 2

Individual nLBBG data from the study period. Data year 2009 consists of 22 gull histories and the years 2010–2011 additional 3 + 7 gull histories. W = west (numbers 1, 2 and 3 refer to breeding areas); S = south; E = east; H = birds translocated to Heligoland, returned to S area (one to X1 area in Central Finland); F = Female; M = male; ID = transmitter number; N = total number of transmitter fixes; Col% = fixes from breeding site (<2 km); MaxD = maximum distance from breeding site (km); ForDM = mean distance of foraging sites (>2 km); sumForD = sum of foraging site distances (km); n = number of transmitter fixes at foraging sites (>2 km); vR(km) = length of foraging resultant vector; vRDir = mean direction of foraging sites (degrees); P95Dir = 95% confidence interval for the mean foraging direction (degrees); r = vector length, concentration parameter (0 = directions are random, 1 = directions are uniform); NoF/D = number of fixes in “hot spot” areas (fur farm or waste dump), n + n, where the first is the number of actual fixes, the second is the number of other fixes of the same direction; NoOther = number of fixes in other areas (lakes and fields); Pref% = percent of fixes in a “hot spot” preference area (fur farm or waste dump).

No	AreaSexID -(year)	N fix	Col %	MaxD km	ForDM km	sumForD km	n fix	vR km	vRdir deg	P95dir deg	r (0–1)	NoF/D fix	NoOther fix	Pref %
1	W1F743	71	44	65.9	34.9	1395	40	1381	133	5	0.954	10+28	2	95
2	W1M739	114	68	14.3	11.2	403	36	402	164	1	0.998	18+18	0	100
3	W1M759	114	59	63.0	29.1	1368	47	1359	141	3	0.978	22+21	4	91
4	W2M737	112	63	12.8	11.9	487	41	487	166	1	0.999	32+9	0	100
5	W2M764	113	64	20.9	18.1	742	41	738	170	2	0.994	29+10	2	95
6	S1F742	100	58	19.7	11.5	485	42	434	142	10	0.841	0+0	42	0
7	S1M734	100	49	31.3	9.7	496	51	368	119	11	0.759	1+2	48	6
8	S1M751	92	66	28.4	13.8	428	31	398	344	15	0.746	5+8	18	42
9	S1M761	108	73	31.5	26.8	777	29	740	347	13	0.823	20+5	4	86
10	S2F738	110	77	30.1	12.7	319	25	207	315	45	0.309	3+5	17	32
11	S2F762	112	71	30.0	19.5	643	33	632	315	10	0.874	11+14	8	76
12	S2M780	99	58	29.8	19.3	810	42	780	316	10	0.832	16+10	16	62
13	S3F735	108	35	46.2	16.3	1140	70	840	309	24	0.415	27+20	23	67
14	S3F758	111	63	50.4	17.8	730	41	624	201	10	0.832	15+10	16	61
15	S3F779	107	49	46.3	22.8	1255	55	852	220	13	0.692	21+16	18	67
16	S3M732	98	63	35.0	11.3	407	36	359	208	11	0.837	2+9	25	31
17	S3M781	111	32	46.3	7.1	533	75	488	303	5	0.922	5+7	63	16
18	E1F774	97	42	25.8	16.9	946	56	751	357	14	0.656	6+3	47	16
19	E1M749	112	41	11.6	8.0	531	66	494	268	5	0.927	0+0	66	0
20	E2M748	112	44	28.1	14.6	920	63	864	42	8	0.839	19+26	18	71
21	E3F740	111	73	39.7	16.4	493	30	470	353	10	0.886	0+0	30	0
22	E3F746	118	43	19.6	9.5	637	67	522	181	8	0.834	0+0	67	0
23	W1M739-10	119	50	24.1	13.1	775	59	773	165	1	0.998	35+21	3	95
24	S1M761-10	76	50	31.9	23.1	877	38	845	348	8	0.888	13+11	14	63
25	S3M732-10	98	81	19.0	5.5	105	19	29	151	39	0.531	0+0	19	0
26	HS2M864-10	80	85	30.1	14.7	177	12	159	318	51	0.289	2+1	9	25
27	HS2M864-11	110	79	29.8	16.3	375	23	348	317	21	0.465	2+8	13	43
28	HS2M916-10	116	76	30.3	22.9	642	28	630	315	8	0.920	17+9	2	93
29	HS2M916-11	112	79	30.2	20.3	487	24	475	314	9	0.915	11+9	4	83
30	HS3M823-10	119	66	41.6	29.2	1167	40	1164	303	2	0.990	19+19	2	95
31	HS3M823-11	117	64	44.6	28.1	1179	42	996	296	12	0.790	18+11	13	69
32	HX1F910-10	119	25	70.6	5.7	510	89	365	198	12	0.688	0+0	89	0

During the subsequent season (2010), three of the gulls returned to Finland from their wintering areas and could be tracked during the entire year, also during the arrival and pre-breeding phase within the general breeding area (Table 2; Fig. 1). Some additional gulls that were caught in the beginning of August 2009 at Tampere waste dump had been translocated to Heligoland as part of a navigation experiment (Wikelski et al., 2015). Four of them returned again to the breeding grounds after their migratory flights into Africa in 2010 and 2011 and were included in Table 2, Fig. 1 and Figs. A2–A5. The birds were tracked until their autumn migration started or up to 8 September. Long (>50 km) pre-migratory flights that are common in LBBGs (Camphuysen, 2013; data by S. Åkesson at CanMove, Lund University) could be easily distinguished from the local foraging flights and were thus excluded from the analysis.

For statistical analyses, we used paired *t*-test for the habitat specialisation within each of the study areas and between the sexes. One-way ANOVA was used for measuring the differences between the three geographical areas. For the accuracy of foraging movements, we used circular statistics to calculate vector concentration parameters. SPSS Statistics 21 software package and Excel spreadsheet were used for the calculations (Table 2).

3. Results

Comparison of transmitter fixes and flight lines leading to different feeding sites showed that nLBBGs mostly fed at fur farms in West Finland, two large waste dumps (Tampere and Hämeenlinna) in South Finland, and lakes and fields in East Finland (Table 2; Figs. 2–4, A1–A6). According to the number of transmitter fixes per preference area, there were differences in the individual first-level specialisation between the areas (mean W = 96.2%, $n = 5$; mean S = 45.5%, $n = 12$; mean E = 17.4%, $n = 5$; $F = 12.081$, $df = 2, 19$, $p < 0.001$; Table 2). Most individuals used fur farms and waste dumps more than expected because they obviously are so-called “hot spots” relatively small in size.

In West Finland, nLBBGs visited mostly fur farms and hardly ever coastal sites (Fig. 2). All long flights were heading to different fur farms where gulls showed second-level specialisation (Fig. 2, Table 2). In South Finland, most of the birds'

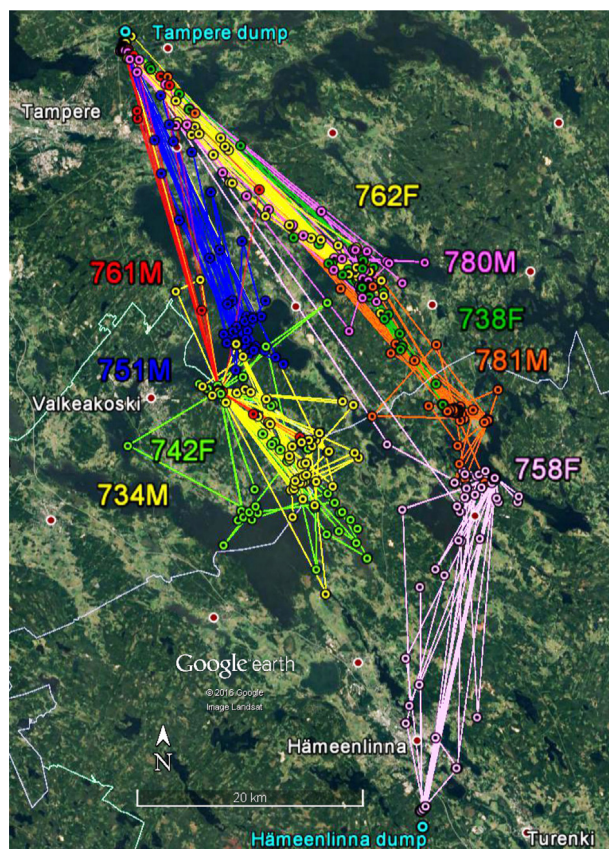


Fig. 3. GPS locations of n nominate lesser black-backed gulls during the study period 8 June–7 July 2009 in the areas S1 (F742, M734, M751, M761), S2 (F738, F762, M780) and S3 (F758, M781).

foraging flights focused on waste dumps, irrespective of the long distance from the breeding sites (maximum 30–50 km, Table 2, Fig. 3). Only 3 out of 16 individuals did not seem to visit regularly waste dumps, but instead fields or lakes nearby (Fig. A6). In East Finland (North Karelia), nLBBGs visited waste dumps less often, some of them (E3, Fig. 4) never, presumably because the breeding sites were far from the nearest waste dump in Savonlinna (approx. 52 km). Still the individuals in this area were specialised in getting food from a specific direction, one gull from the northern and another gull from the southern corridor. Similarly, the E1 birds were also specialised to fly within narrow directional corridors (W and N/E, Fig. 4).

There were no differences in the maximum distances of individual foraging flights between the three geographic areas (mean W = 35.4 ± 26.7 km, $n = 5$; mean S = 35.4 ± 9.5 km, $n = 12$; mean E = 25.0 ± 10.4 km, $n = 5$; $F = 0.934$, $df = 2, 19$, $p = 0.410$; Table 2). As expected, birds from all the areas showed intra-population variation. Some individuals (e.g. W2M737, W1M739, S1F742, and E1M749) generally stayed near the breeding site. On the other hand, some individuals (e.g. W1F743, W1M759, S3F735, and S3F779) undertook long foraging trips to a specific fur farm or waste dump.

According to the calculated concentration parameters, deviation from the mean direction of foraging movements (angle of deviation) was smallest in West Finland where the flight directions were highly consistent (Table 2), whereas the movements of the birds from East and South Finland were more scattered. N nominate LBBGs from all the three geographic areas did not appear to use habitat in proportion to its availability. Overall, only fur farms, waste dumps and lakes and fields were selected, whereas the open sea was the only habitat type that was avoided (Fig. 2, Table 2).

The proportion of time individuals spent around the breeding sites varied considerably between the birds, in males from 32% to 73% and in females from 35% to 77%, with an overall mean of 56% (Table 2). Birds mostly stayed at their breeding sites in the mornings and the evenings. The birds were most likely on the move away from the breeding sites during the afternoons, in fact twice as likely as during the other times. However, we did not find significant differences in the mean foraging distances ($t = -0.908$, $df = 10$, $p = 0.187$) or breeding site percentages ($t = 0.200$, $df = 10$, $p = 0.422$) between the sexes during the breeding period (Table 2).

One of the tagged birds from West Finland (W1F743) was shot in a fur farm on 28 June 2009, about 60 km SE from the breeding site, and another bird (W765, not listed in Table 2), obviously shot on 31 May 2009, while its ring was later found in a red fox hole nearby. For six individuals we were able to compare foraging flights between the years 2009–2010 or 2010–2011 (W1M739, S1M761, S3M732, HS2M864, HS2M916 and HS3M823) as their tags were still transmitting. These comparisons

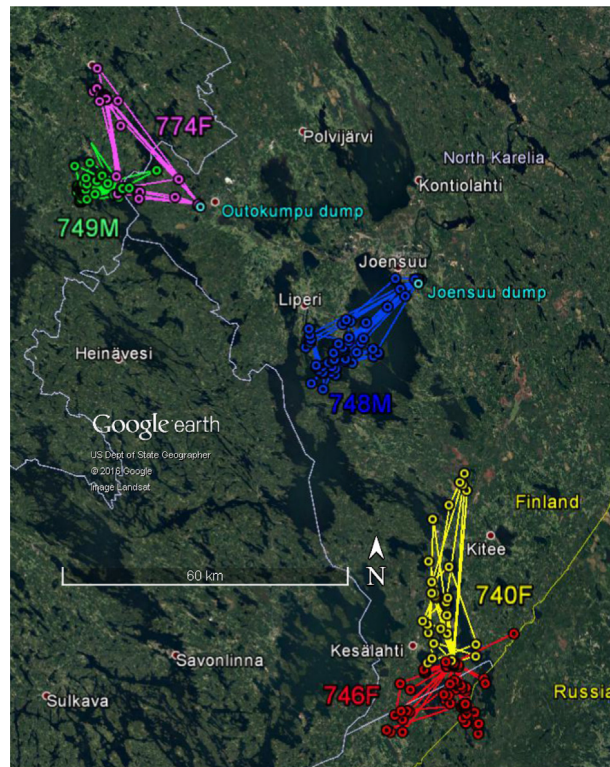


Fig. 4. GPS locations of nominate lesser black-backed gulls during the study period 8 June–7 July 2009 in the areas E1 (F774, M749), E2 (M748) and E3 (F740, F746).

for preferred foraging habits showed substantial similarities between the years (Table 2, Figs. A2–A4). For instance, when arriving in spring, the birds previously translocated to the West, to the island of Heligoland (see Wikelski et al., 2015), were heading straight to their previous year breeding sites and from then onward foraged at the waste dump as in the previous year. One Heligoland bird (HX1F910) returned in 2010 to breed in Central Finland, foraging mostly on nearby lakes and fields, but on 3–4 July made an exceptional trip to Tampere dump and Lake Vesijärvi colony (distance of 65 km) (Fig. A5).

4. Discussion

4.1. Generalisation –Specialisation

During the breeding season nLBBGs in Finland showed individual and location-dependent specialised foraging behaviour at two levels. Generalised feeding habits seemed to be rare. According to our satellite tracking data, feeding sites were located at waste dumps, fur farms, fields and lake areas, with individual birds specialising on any one of these potential foraging sites (first level of specialisation). The data highlights that urban resources were used by the majority of the individuals. Most individuals simply opportunistically or through learning utilised available and profitable foraging “hot spots”. Still, the nLBBG may well be considered generalist species feeding diverse food even though individuals demonstrate specialisation, i.e. individual specialisation. The findings are supported by the literature where the LBBG generally behaves as a specialist in lake and sea areas feeding on freshwater and marine fishes (e.g. Götmark, 1984; Noordhuis and Spaans, 1992; Strann and Vader, 1992; Bustnes et al., 2010; Camphuysen, 2013).

Nominate LBBGs from all three study areas showed intraspecific variability in the specialisation of habitat use. Some individuals never visited the waste dumps, whereas most made many journeys to these areas. For example, some South-individuals made intense use of the waste dump area of Tampere, while other individuals barely used that habitat type. At waste dumps, individuals were specialised to use compost piles (S1M761, S2M780), mixed waste banks (S2F738, S3M781) or bio-plant (S3F735) (second level of specialisation). Moreover, apart from getting food independently, some individuals were specialised to snatch food from other gulls. The West-birds appeared to be the most specialised gulls and – counter intuitively – they did not seem to search for food around the sea, i.e., within the Gulf of Bothnia, but almost solely visited fur farms for foraging. Nevertheless, nLBBGs are observed foraging at sea at least when herrings are spawning. The fur farms in Ostrobothnia area in western Finland are practising fox and mink farming for commercial use and provide the farm animals with food (fodder) that is also partially available to gulls (Fig. A7). On the individual level gulls became specialised to a small

number of fur farms (second level of specialisation). It is noteworthy that individuals from the same breeding sites preferred different fur farms, some even flew over the farms which were used by other birds.

Inter-individual variability in resource use has long been an active field in evolutionary research, and recent reviews and studies have identified several ecological causes of individual specialisation (Bearhop et al., 2006; Araújo et al., 2011; Moleón et al., 2012; Patrick et al., 2014; Warwick-Evans et al., 2016). Classic optimal foraging theory suggests that as the abundance of preferred resources diminishes, gulls among other birds need to include suboptimal resources. Depending on the level of resource availability in their diet, foraging activity normally decreases or increases. Intra- and inter-individual flexibility may also vary annually, corresponding with a lower or higher breeding success (Warwick-Evans et al., 2016).

4.2. Foraging flight characteristics – Distances and directions

There were no significant differences between the maximum foraging flight distances of birds, based on the locations of transmitter fixes. Distinct variation in flight corridors of foraging movements was still found between the geographic areas. In contrast with the West Finland birds, the nLBBGs from South and East Finland varied in their movements away from the breeding site. S-birds moved to three separate foraging areas at a maximum distance of 50 km away from the breeding site, whereas E-birds moved to four different foraging areas within a distance of 40 km from the breeding site. Individuals utilising waste dumps, fields and lakes still had reasonably narrow flyways, showing second-level specialisation with hardly any overlaps in their foraging movements.

Foraging flight corridors were mostly determined by the location of foraging area, but the existence of other gull breeding sites may have also influenced the movements. This is exemplified by the S2 and S3 birds that never foraged in the eastern areas (Fig. 3), where a large Kukkia breeding area of 100 pairs is to be faced. Even when the flight corridors of some individuals overlapped to a large extent, these individuals flying in the same direction did not necessarily forage at the same sites. Generally, individuals that flew over larger distances did not stop at the foraging sites of those individual foraging closer to the breeding sites, as exemplified by W1 (M739, M759) and W2 birds (M737, M764) (Fig. 2). Overall, the longest feeding trips performed by this species were to the waste dumps and fur farms and not to the coast or lakes.

4.3. GPS tag shortcomings

A more detailed spatial and temporal evaluation of the results was impaired by satellite transmitters being programmed to having duty cycles of only 4 fixes per day. During 3–6-hour periods between the fixes gulls have enough time to visit waste dumps and fly back as minimum foraging times may be very short, in biowaste areas only some tens of minutes at a time (Coulson et al., 1987; data by R. Juvaste and M. Kangasniemi). However, some studies have reported average foraging times offshore (including resting and sleeping) to last 8 h (Camphuysen, 2013; Shamoun-Baranes et al., 2011). We have also observations at the Tampere dump, where gulls seem to rest (digesting food) long times before returning to their breeding sites, often after sudden disturbances, e.g. patrolling goshawks (*Accipiter gentilis*) (data by R. Juvaste and M. Kangasniemi).

4.4. Time budgets and seasonal changes in flight characteristics

Our data suggest that gulls faced a trade-off between the time spent at the breeding site and time investment in foraging behaviour, which in turn resulted in differences in food quality (cf. Harding et al., 2007). We hypothesise that birds that forage in the distant areas will get plenty of food easily, however at the expense of either some food risks from foraging on waste sites or the risk of being shot at fur farms. It is important to mention that many of the long feeding trips are assumed to be performed during the fledging period of the breeding season. Because older chicks need more energy, parents have to be more flexible in their time budgets. The risk of leaving the chicks unprotected for long time periods and fly long distances to feed from waste dumps or fur farms shows the importance of these food sources in the diet of nLBBGs. Moreover, birds normally come back to their breeding sites even if their nests have been destroyed or nesting has been unsuccessful due to another cause such as rainstorms (pers. obs., R. Juvaste). The importance of waste dumps and fur farms in the gulls' diet during the non-reproductive season is already known (e.g. in the Ostrobothnia area), but the use of these food sources during the breeding period might also indicate that 'fast food' is even preferred over food in the nearby lake/sea areas during the breeding season.

4.5. Conservation implications of food specialisations

During the migration periods and at wintering sites the LBBG is considered as generalist in its feeding habits (Klaassen et al., 2012). However, if birds arrive in spring when ice is still covering the lakes, waste dumps and fur farms may play important roles in the diet of birds as well as in the development of eggs or during recovery from migration. The possible food types individual gulls may specialise in during different time periods include biowaste, high-energy feed for domestic animals such a food pellets, fish, fish wastes and earthworms. Unfortunately, as seen during this study and also known from anecdotal information (pers. obs. by J. Hannila, H. Hongell and Finnish Food Safety Authority Evira), individual specialisation on food pellets often leads to a high mortality risk because gulls and many other birds are driven away from farms by shooting or poisoning, even during the preserved breeding periods. In this study, two out of five satellite tracked gulls from the coast

of West Finland (Kokkola, Uusikaarlepyy) were evidently shot by fur farmers. Furthermore, in Eastern Finland, four satellite-tagged birds (2/5 adults, and 2/7 juveniles not listed in Table 2) disappeared in August, coinciding with the onset of the duck hunting period but also with the end of the conservation period of herring gulls (HG) and great black-backed gulls (GBBG), which allows shooting again from 1st of August. At the time the shooting period starts, juveniles of any of the large gull species are hard or impossible to distinguish from each other; even adult nLBBGs and GBBGs look very similar. When visiting the sites where the satellite tags provided the last locations, we determined one adult and one juvenile as being shot (one of the tags was in fact returned later by a local hunter). The other two birds disappeared on 24 August and 5 September from Joensuu waste dump, where shooting of crows is a common phenomenon.

This alarming situation of high human-caused mortality (25%–40%) also in adult birds may well explain a part of the population decrease of LBBGs in recent years (Hannila et al., 2008; Hario, 2014; Hario and Rintala, 2014). Exceptional shooting permits additionally allow farmers to shoot HGs and GBBGs at fur farms and waste dumps. Particularly in the West Coast Game Districts, where our Western birds were tagged, GBBGs have been shot in high numbers (some 800 individuals) in relation to the existing population of the species (~300 pairs during 2010). For example, in the Stormossen waste dump area, the proportion of HG–GBBG shooting has been 1.8:1, in comparison to the 26:1 ratio of breeding pairs (R. Juvaste, pers. obs.). We believe that shooting must have had effect on the production and population of nLBBG, but then again the population decrease is compensated by recruits to these very attractive sites with plenty of food.

4.6. Suggesting solutions to the negative population trend

From the 1970s to the 1990s nLBBG populations largely collapsed particularly in the Gulf of Finland due to the widespread occurrence of environmental toxins (PCB, dioxins) in the food web, e.g. in Baltic herrings (Hario et al., 2004). The development of gull populations along the coast of West Finland (Ostrobothnia) was much more positive until recently (Hannila et al., 2008), perhaps due to the consumption of pure, unpolluted food dropped off by fur farmers. However, the reduction of fur farms and fisheries in West Finland has probably led to a decline in feeding opportunities both at farms and near the coast, with negative consequences for local nLBBG populations. At the same time, gull populations in interior Finland especially near waste dumps have remained unchanged (pers. data by R. Juvaste; Hario, 2014). This trend is going to change due to the closing of biowaste dump areas starting in 2016 according to the strict EU legislation on landfill waste. We expect the foraging behaviour of such nLBBGs specialised on landfill waste to include anthropogenic waste near towns and city centres.

Alarming is also the general misidentification of gull species during the official shooting period, especially near the fur farms in the Ostrobothnia area. In light of this problem, the practice of exceptional shooting permits needs to be discussed. Furthermore, the duration of safe (non-shooting) breeding period of nLBBG should be extended until the middle of September when most of the nLBBGs have embarked on their migration. This extension would also ensure that during the duck shooting period no gulls are shot, thus avoiding the misidentification of young nLBBG versus HGs (which are currently allowed to be shot).

Our results have provided a case to prove that illegal shooting at fur farms and waste dumps is of considerable importance in explaining different population trends, given the endangered status and breeding numbers of the species. At the same time, artificial food sources such as fur farms and waste dumps have so far kept the population closer to the natural carrying capacity. In terms of changing climate, species gaining suitable climate or other environmental conditions can be termed “winners”, whereas species losing suitable conditions can be termed “losers” (Araújo et al., 2011). Bird and mammal species are projected to have greater proportions of losers than winners in all scenarios by 2080. To examine potential net effect of human-caused mortality, fur farming, waste dumps, and other artificial food sources on conservation concern of the LBBG, we recommend urgent actions since our findings highlight the importance of these “hot spots” to explore individual responses to environmental changes.

On a more general level, the spatiotemporal dynamics of nLBBG populations should be taken into account in conservation planning (Virkkala, 2006). Site protection should be based on information of both breeding and visiting gulls over several years, so that a major proportion of the breeding red-listed gulls might be kept inside the protected areas. Therefore, areas to be protected should cover a large proportion of a lake or a coast but also the most important foraging and wintering sites.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2017.03.009>.

References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–267.
- Anker-Nilssen, T., Bakken, V., Strøm, H., Golovkin, A.N., Bianki, V.V., Tatarinkova, I.P., 2000. The Status of Marine Birds Breeding in the Barents Sea Region. Norwegian Polar Institute Report No. 113. p. 213.
- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. *Ecol. Lett.* 14, 484–492.
- Arriero, E., Müller, I., Juvaste, R., Martínez, F.J., Bertolero, A., 2015. Variation in immune parameters and disease prevalence among lesser black-backed gulls (*Larus fuscus* sp.) with different migratory strategies. *PLoS One* 10 (2), e0118279. <http://dx.doi.org/10.1371/journal.pone.0118279>.
- Bakken, V., Runde, O., Tjorve, E., 2003. In: *Norwegian Bird Ringing Atlas, Volume 1*, Stavanger Museum, Stavanger, pp. 338–346.
- Bearhop, S., Phillips, R.A., McGill, R., Cherel, Y., Dawson, D.A., Croxall, J.P., 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar. Ecol. Prog. Ser.* 311, 157–164.
- Beason, R.C., Humphrey, J.S., Myers, N.E., Avery, M.L., 2010. Synchronous monitoring of vulture movements with satellite telemetry and avian radar. *J. Zool.* 282, 157–162.
- Bergman, G., 1982. Population dynamics, colony formation and competition in *Larus argentatus*, *fuscus* and *marinus* in the archipelago of Finland. *Ann. Zool. Fenn.* 19, 143–164.
- Blight, L.K., Drever, M.C., Arcese, P., 2015. A century of change in Glaucous-winged Gull (*Larus glaucescens*) populations in a dynamic coastal environment. *Condor* 117, 108–120.
- Brothers, N., Gales, R., Hedd, A., Robertson, G., 1998. Foraging movements of the Shy Albatross *Diomedea cauta* breeding in Australia; implications for interactions with longline fisheries. *Ibis* 140, 446–457.
- Burger, A.E., Shaffer, S.A., 2008. Perspectives in ornithology: application of tracking and data-logging technology in research and conservation of seabirds. *Auk* 125, 253–264.
- Bustnes, J.O., Barrett, R.T., Helberg, M., 2010. Northern Lesser Black-Backed Gulls: what do they eat? *Waterbirds* 33, 534–540.
- Camphuysen, C.J., 1995. Herring gull *Larus argentatus* and Lesser Black-backed Gull *L. fuscus* feeding at fishing vessels in the breeding season: Competitive scavenging versus efficient flying. *Ardea* 83, 365–380.
- Camphuysen, C.J., 2011. Lesser Black-backed Gulls at Texel. In: NIOZ Report 2011-05.
- Camphuysen, C.J., 2013. A Historical Ecology of Two Closely Related Gull Species (*Laridae*): Multiple Adaptations To a Man-Made Environment. (Ph.D. thesis), University of Groningen, The Netherlands.
- Capandegui, E., 2006. Factors Influencing the Breeding Success of Two Ecologically Similar Gulls, the Lesser Black-Backed Gull *Larus F. Fuscus* and Herring Gull *Larus Argentatus* At Stora Karlsö. (M.Sc. thesis), University of Stockholm, Sweden.
- Cherenkov, A., Semashko, V., Tertitski, G., 2007. Current status and population dynamics of nominate subspecies of Lesser Black-backed Gull *Larus fuscus fuscus* in the White Sea. *Ornis Svec.* 17, 29–36.
- Coulson, J.C., Butterfield, J., Duncan, N., Thomas, C., 1987. Use of refuse tips by adult British Herring Gulls *Larus argentatus* during the week. *J. Appl. Ecol.* 24, 789–800.
- Coulson, J.C., Thomas, C.S., Butterfield, J.E.L., Duncan, N., Monaghan, P., Shedden, C., 1983. The use of head and bill length to sex live gulls Laridae. *Ibis* 125, 549–557.
- Ens, B.J., Bairlein, F., Camphuysen, C.J., Boer, P. de, Exo, K.-M., Gallego, N., Hoye, B., Klaassen, R., Oosterbeek, K., Shamoun-Baranes, J., Jeugd, H. van der, Gasteren, H. van, 2008. Tracking of individual birds. In: Report on WP 3230 (Bird Tracking Sensor Characterization) and WP 4130 (Sensor Adaptation and Calibration for Bird Tracking System) of the FlySafe Basic Activities Project. SOVON- Onderzoeksrapport 2008/10. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Ens, B.J., Bairlein, F., Camphuysen, K., Boer, P.de., Exo, K.-M., Gallego, N., Klaassen, R.H.G., Oosterbeek, K., Shamoun-Baranes, J., 2009. Onderzoek aan Meeuwen met satellietzenders. *Limosa* 82, 33–42.
- Götmark, F., 1984. Food and foraging in five European *Larus* gulls in the breeding season: a comparative review. *Ornis Fenn.* 61, 9–18.
- Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., Wood, A.G., 2000. Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. *Mar. Ecol. Prog. Ser.* 200, 257–264.
- Hannila, J., Hongell, H., Wistbacka, R., 2008. Selkä- ja harmaalokki - Pohjanmaan rannikon kannankehitys. Saaristolintusymposio, Kokkola, Finland, 15.11.2008 (in Finnish). <http://www.birdlife.fi/suojelu/lajit/saaristolintuseminaari/Hannila-selkalokki-harmaalokki.pdf>. Accessed 1 November 2016.
- Hannila, J. and Hongell, H., Selkä- ja harmaalokkiseuranta Kokkolan saaristossa 2016. Tankarin lintuasema, Kokkola, 2016, 1–11 (in Finnish).
- Harding, A.M.A., Piatt, J.F., Schmutz, J.A., Shultz, M.T., Van Pelt, T.I., Kettle, A.B., Speckman, S.G., 2007. Prey density and the behavioral flexibility of a marine predator: the Common Murre (*Uria aalge*). *Ecology* 88, 2024–2033.
- Hario, M., 1994. Reproductive performance of the nominate Lesser Black-backed Gull under the pressure of Herring Gull predation. *Ornis Fenn.* 71, 1–10.
- Hario, M., 2014. The occurrence of the nominate Lesser Black-backed Gull in Finland in 2003 and 2013. *Linnut-Vuosikirja* 2013, 24–31 (in Finnish with English summary).
- Hario, M., Hirvi, J.-P., Hollmén, T., Rudbäck, E., 2004. Organochlorine concentrations in diseased vs. healthy gull chicks from the northern Baltic. *Environ. Pollut.* 127, 411–423.
- Hario, M., Rintala, J., 2014. Population trends of archipelago birds along Finnish coasts during 1986–2013. *Linnut-Vuosikirja* 2013, 46–53.
- Helberg, M., Systad, G.H., Birkeland, I., Lorentzen, N.H., Bustnes, J.O., 2009. Migration patterns of adult and juvenile Lesser Black-backed Gulls *Larus fuscus* from northern Norway. *Ardea* 97, 281–286.
- Jouventin, P., Weimerskirch, H., 1990. Satellite tracking of wandering albatrosses. *Nature* 343, 746–748.
- Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. *Science* 348. <http://dx.doi.org/10.1126/science.aaa2478>.
- Kilpi, M., 1983. Population trends and selection of nest-sites in *Larus argentatus* and *L. fuscus* on the Finnish coast. *Ornis Fenn.* 60, 45–50.
- Kim, S.Y., Monaghan, P., 2006. Interspecific differences in foraging preferences, breeding performance and demography in herring (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) at a mixed colony. *J. Zool.* 270, 664–671.
- Kjellén, N., Hake, M., Alerstam, T., 1997. Strategies of two ospreys *Pandion haliaetus* migrating between Sweden and tropical Africa as revealed by satellite tracking. *J. Avian Biol.* 28, 15–23.
- Klaassen, R.H.G., Ens, B.J., Shamoun-Baranes, J., Exo, K.-M., Bairlein, F., 2012. Migration strategy of a flight generalist, the Lesser Black-backed Gull *Larus fuscus*. *Behav. Ecol.* 23, 58–68.
- Kranstauber, B., Kays, R., LaPoint, S.D., Wikelski, M., Safi, K., 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *J. Anim. Ecol.* 81, 738–746.
- Lif, M., Hjernquist, M., Olsson, O., Österblom, H., 2005. Long-term population trends in the Lesser Black-backed Gull *Larus f. fuscus* at Stora Karlsö and Lilla Karlsö, and initial results on breeding success. *Ornis Svec.* 15, 105–112.
- Marques, P.A.M., Costa, A.M., Rock, P., Jorge, P.E., 2009. Age-related migration patterns in *Larus fuscus* spp. *Acta Ethol.* 12, 87–92.
- Marques, P.A.M., Sowter, D., Jorge, P.E., 2010. Gulls can change their migratory behavior during lifetime. *Oikos* 119, 946–951.

- Meyburg, B.-U., Paillat, P., Meyburg, C., 2003. Migration routes of Steppe Eagles between Asia and Africa: a study by means of satellite telemetry. *Condor* 105, 219–227.
- Moleón, M., Sebastián-González, E., Sánchez-Zapata, J.A., Real, J., Pires, M.M., Gil-Sánchez, J.M., Bautista, J., Palma, L., Bayle, P., Guimarães Jr, P.R., Beja, P., 2012. Changes in intrapopulation resource use patterns of an endangered raptor in response to a disease-mediated crash in prey abundance. *J. Anim. Ecol.* 81, 1154–1160.
- Noordhuis, R., Spaans, A.L., 1992. Interspecific competition for food between Herring *Larus argentatus* and Lesser Black-Backed Gulls *L. fuscus* in the Dutch Wadden Sea Area. *Ardea* 80, 115–132.
- O'Mara, M.T., Wikelski, M., Dechmann, D.K.N., 2014. 50 years of bat tracking: device attachment and future directions. *Methods Ecol. Evol.* 5, 311–319. <http://dx.doi.org/10.1111/2041-210X.12172>.
- OSPAR, 2009. Background document on the Lesser Black-backed Gull. *Biodiversity Series*. 409.
- Patrick, S.C., Bearhop, S., Grémillet, D., Lescroëil, A., Grecian, W.J., Bodey, T.W., Hamer, K.C., Wakefield, E., Le Nuz, M., Votier, S.C., 2014. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* 123, 33–40.
- Pavón, D., Limiñana, R., Urrios, V., Izquierdo, A., Yáñez, B., Ferrer, M., de la Vega, A., 2010. Autumn migration of juvenile Short-toed Eagles *Circus gallicus* from Southeastern Spain. *Ardea* 98, 113–117.
- Prince, P.A., Wood, A.G., Barton, T., Croxall, J.P., 1992. Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarct. Sci.* 4, 31–36.
- Pütz, K., Helbig, A.J., Pedersen, K.T., Rahbek, C., Saurola, P., Juvaste, R., 2008. From fledging to breeding: long-term satellite tracking of the migratory behaviour of a Lesser Black-backed Gull *Larus fuscus intermedius*. *Ringing Migr.* 24, 7–10.
- Pütz, K., Rahbek, C., Saurola, P., Pedersen, K.T., Juvaste, R., Helbig, A.J., 2007. Satellite tracking of the migratory pathways of first-year Lesser Black-backed Gulls *Larus fuscus* departing from the breeding grounds of different subspecies. *Vogelwelt* 128, 67–78.
- Roshier, D.A., Asmus, M.W., 2009. Use of satellite telemetry on small-bodied waterfowl in Australia. *Mar. Freshwater Res.* 60, 299–305.
- Schwemmer, P., Garthe, S., 2005. At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull *Larus fuscus*, and its association with different prey. *Mar. Ecol. Prog. Ser.* 285, 245–258.
- Shamoun-Baranes, J., Bouten, W., Camphuysen, C.J., Baaij, E., 2011. Riding the tide: intriguing observations of gulls resting at sea. *Ibis* 153, 411–415.
- Strann, K.-B., Vader, W., 1992. The nominate Lesser Black-backed Gull *Larus fuscus fuscus*, a gull with a tern-like feeding biology, and its recent decrease in northern Norway. *Ardea* 80, 133–142.
- Takekawa, J.Y., Newman, S.H., Xiao, X., Prosser, D.J., Spragens, K.A., Palm, E.C., Yan, B., Li, T., Lei, F., Zhao, D., Douglas, D.C., Muzaffar, S.B., Ji, W., 2010. Migration of waterfowl in the East Asian Flyway and spatial relationship to HPAI H5N1 outbreaks. *Avian Dis.* 54, 466–476.
- Thorup, K., Alerstam, T., Hake, M., Kjellén, N., 2003. Can vector summation describe the orientation system of juvenile ospreys and honey buzzards? – An analysis of ring recoveries and satellite tracking. *Oikos* 103, 350–359.
- Tiainen, J., Mikkola-Roos, M., Below, A., Jukarainen, A., Lehtiniemi, T., Pessa, J., Rajasärkkä, A., Rintala, J., Sirkiä, P., Valkama, J., 2016. Suomen lintujen uhanalaisuus 2015 – The 2015 Red List of Finnish Bird Species. Ympäristöministeriö & Suomen Ympäristökeskus, 49 p.
- Valkama, J., Saurola, P., Lehtikoinen, A., Lehtikoinen, E., Piha, M., Sola, P., Velmala, W., 2014. The Finnish bird ringing atlas Vol. II. Finnish Museum of Natural History and Ministry of Environment, Helsinki, pp. 89–103.
- Vandenabeele, S.P., Shepard, E.L., Grogan, A., Wilson, R.P., 2012. When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Mar. Biol.* 159, 1–14.
- Virkkala, R., 2006. Spatiotemporal variation of breeding gull species in a boreal lake complex in Finland: Implications for conservation. *Biol. Conserv.* 128, 447–454.
- Warwick-Evans, V., Atkinson, P.W., Arnould, J.P.Y., Gauvain, R., Soanes, L., Robinson, L.A., Green, J.A., 2016. Changes in behaviour drive inter-annual variability in the at-sea distribution of northern gannets. *Mar. Biol.* 163, 156.
- Weimerskirch, H., Robertson, G., 1994. Satellite tracking of light-mantled sooty albatrosses. *Polar Biol.* 14, 123–126.
- Weimerskirch, H., Salamolard, M., Sarrazin, F., Jouventin, P., 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110, 325–342.
- Wikelski, M., Arriero, E., Gagliardo, A., Holland, R., Huttunen, M.J., Juvaste, R., Mueller, I., Tertitski, G., Thorup, K., Wild, M., Alanko, M., Bairlein, F., Cherenkov, A., Cameron, A., Flatz, R., Hannila, J., Hüppop, O., Kangasniemi, M., Kranstauber, B., Penttinen, M.-L., Safi, K., Semashko, V., Schmid, H., Wistbacka, R., 2015. True navigation in migrating gulls requires intact olfactory nerves. *Sci. Rep.* 5, 17061. <http://dx.doi.org/10.1038/srep17061>.
- Willemoes, M., Strandberg, R., Klaassen, R.H.G., Tøttrup, A.P., Vardanis, Y., Howey, P.W., Thorup, K., Wikelski, M., Alerstam, T., 2014. Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. *PLoS ONE* 9 (1), e83515. <http://dx.doi.org/10.1371/journal.pone.0083515>.
- Wood, A.G., Naef-Daenzer, B., Prince, P.A., Croxall, J.P., 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *J. Avian Biol.* 31, 278–286.