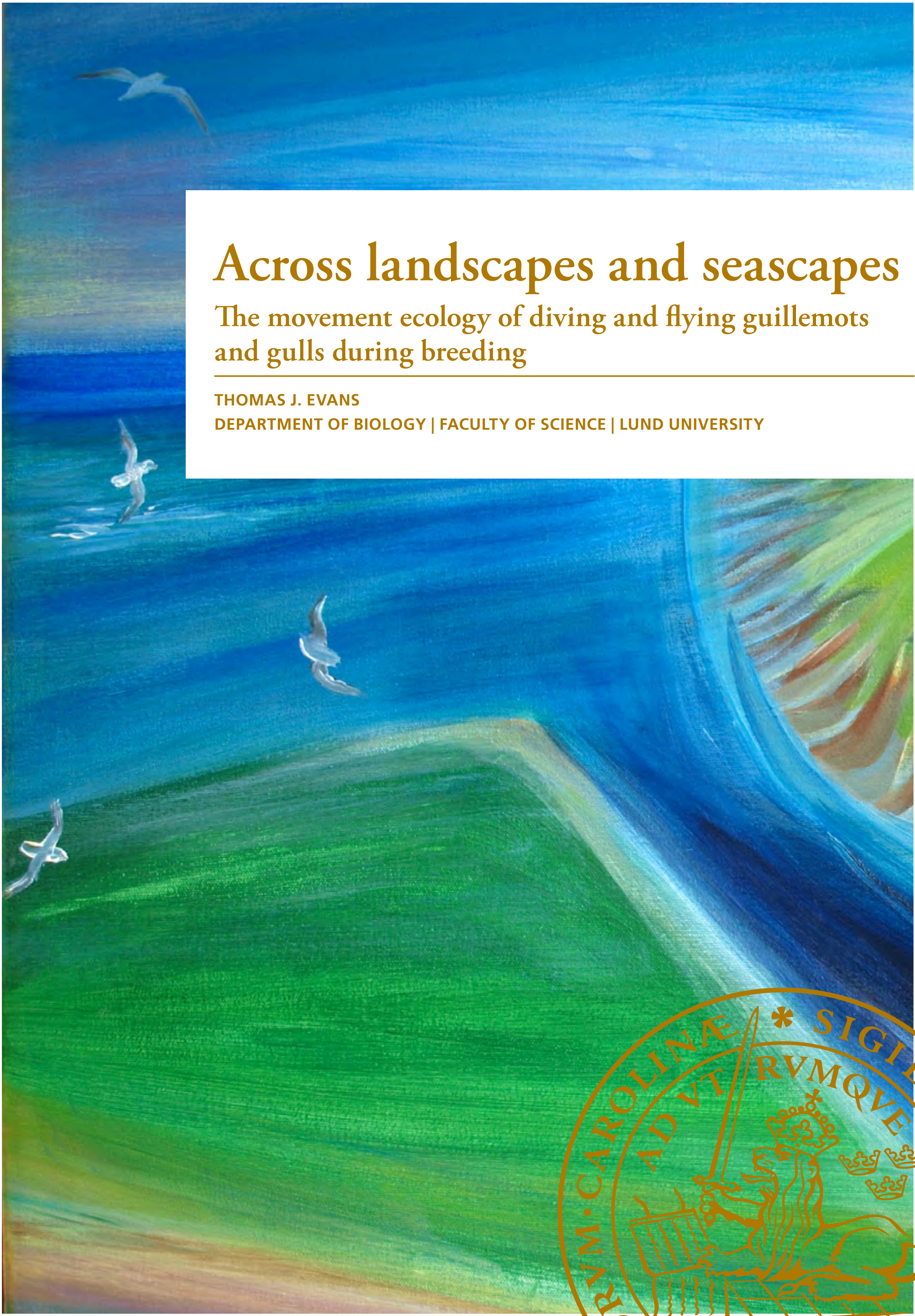

# Across landscapes and seascapes

## The movement ecology of diving and flying guillemots and gulls during breeding

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Thomas Jude Evans

LUND
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Abstract

Most seabirds breed colonially, at which time they make central-place foraging trips. Parents must collect food both for themselves and for egg production/chick-rearing. How should they forage? I followed five species across two sites in Sweden in the Baltic Sea using GPS and time-depth recorder (TDR) devices, giving information on both flight and diving activity. I use a movement ecology approach, asking questions about which spatiotemporal aspects determine these species' movement activities and on how species differ in their foraging activity. Further, I test theories of how birds should optimally vary their flight behaviour in response to winds, and of how individual birds collect information on alternative breeding sites, i.e. prospecting.

Chick-rearing Common Murre (CM, *Uria aalge*) from the island of Stora Karlsö (SK; 17.97°E, 57.29°N), foraged most around sunset and sunrise, when they made more frequent and shallower dives compared to at midday. They made longer distance and duration overnight trips where they visited more distant foraging areas than during daytime trips. In a following study I showed that the GPS device deployed had little measurable effect on the CMs activity, though murres did lose body mass which remains to be explained.

During flights returning from foraging sites to their colony at SK, both CM and Lesser Black-backed Gull (LG, *Larus fuscus*) optimally adjust their airspeeds to minimise their costs of transport, increasing airspeed under headwinds and cross-winds, but reducing airspeed under tailwinds. While the gulls also adjusted their altitude, increasing altitude under tailwinds, thus benefiting from the faster winds higher up, but flying low, where wind is slower, under headwinds and crosswinds; the murres though always fly low, close to the sea surface.

LG are generalist foragers, at SK they feed both on land and at sea. How do they choose between these? LG were followed with GPS and observations were made at arable fields on nearby Gotland. The gulls foraged most on land early in the breeding season, and during early mornings especially on cool and cloudy days, while they foraged mostly at sea later in the season, and later in the day. They foraged most on fields with short vegetation and low ground-cover, presumably where soil living invertebrates and earthworms are more available.

Following four *Larus* gull species with GPS during the peak breeding period at the Björn Archipelago at Fågelsundet (FS; 17.72°E, 60.63°N), I show using an information reduction and clustering method how different gull species overlap in the types of foraging trip they use, while also using distinct types of foraging trip. Some species used just a couple of types of trip (specialist), while others used several types quite equally (generalists), this variation was also present within species when comparing between individuals.

LG from both SK and FS, followed with GPS, made very long-distance return movements away from their colonies, mostly after failed breeding attempts. On the majority of these movements, gulls visited multiple coastal sites, likely prospecting at alternative breeding colonies. The gulls from FS travelled furthest, visiting many of the same coastal sites as the SK gulls with no difference between sexes.

Key words *Uria aalge*, *Larus fuscus*, Laridae, animal flight, foraging ecology, movement ecology, seabirds

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"How good, how good does it feel to be free?"

And I answer them most mysteriously

"Are birds free from the chains of the skyway?"

*Bob Dylan*

# Contents

# List of Papers

I. Evans, T.J., Kadin, M., Olsson, O., and Åkesson, S. (2013). Foraging behaviour of common murres in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices. *Marine Ecology Progress Series* **475**, 277–289.[1]

II. Evans, T.J., Young, R.C., Watson, H., Olsson, O., Åkesson, S. Back-mounted tags have limited effects on a flying and diving seabird. (Manuscript, unsubmitted).

III. Evans, T.J., Hedenström, A., Hentati-Sundberg, J., Shamoun-Baranes, J., Åkesson, S. Adaptive adjustment of flight height and airspeed in relation to winds in two morphologically distinct seabird species (Manuscript, submitted).

IV. Isaksson, N., Evans, T.J., Shamoun-Baranes, J., and Åkesson, S. (2016) Land or sea? Foraging area choice during breeding by an omnivorous gull. *Movement Ecology* **4**, 11.[2]

V. Evans, T.J., Shiomi, K., Isaksson, N., Löteberg, U., Bouten, W., Åkesson, S. Niche sharing and partitioning during foraging among a quartet of coastal gulls. (Manuscript, unsubmitted).

VI. Åkesson, S., Evans, T.J., Shiomi, K., Shamoun-Baranes, J., Bouten, W., and Lötberg, U. On the move for food or a new home? Long-distance return movements by Lesser Black-backed Gull during breeding. (Manuscript, unsubmitted).

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# Author Contributions

I. T.E. O.O, and S.Å. conceived the study. T.E., M.K. performed the fieldwork. T.E. analysed the data with input from M.K. and S.Å. The initial manuscript was drafted by T.E. with input from M.K. and S.Å., and all authors contributed to and gave approval to the submission for publication of the final manuscript.

II. T.E. conceived the study with input from R.Y and S.Å. T.E. and R.Y. carried out the fieldwork. T.E., R.Y., and H.W. performed the lab work. T.E. analysed the data with input from R.Y., H.W. and S.Å. T.E. drafted the initial manuscript. All authors contributed to the final manuscript.

III. T.E., A.H., and S.Å. designed the study. T.E. carried out the fieldwork with guidance from J.H-S. and S.Å. T.E. analysed the data with input from A.H., S.Å., and J.S-B. T.E. drafted the initial manuscript. All authors contributed to and gave approval to the submission for publication of the final manuscript.

IV. N.I., T.E., and S.Å. designed the study. N.I. and T.E. carried out the fieldwork with the agricultural-field observations and the GPS-tracking components led by N.I. and T.E. respectively. N.I. and T.E. performed the statistical analysis, and co-drafted the manuscript with input from S.Å and J.S-B. All authors gave approval to the submission for publication of the final manuscript.

V. T.E., S.Å., U.L., and K.S. conceived the study. T.E., S.Å., U.L., and K.S carried out the fieldwork. T.E. analysed the data with input from K.S. and N.I. T.E. drafted the initial manuscript. All authors contributed to the final manuscript.

VI. S.Å., T.E., and K.S. conceived the study. S.Å., T.E., K.S. and U.L. performed the fieldwork. S.Å. and T.E. analysed the data. S.Å. drafted the initial manuscript with input from T.E. All authors contributed to the final manuscript.

A.H., Anders Hedenström; H.W., Hannah Watson; J.H-S., Jonas Hentati-Sundberg; J.S-B., Judy Shamoun-Baranes; M.K., Martina Kadin; N.I., Natalie Isaksson; O.O., Olof Olsson; R.Y., Rebecca C. Young; S.Å., Susanne Åkesson; T.E., Thomas J. Evans; U.L., Ulrik Lötberg; W.B., Willem Bouten

# Abstract

Most seabirds breed colonially, at which time they make central-place foraging trips. Parents must collect food both for themselves and for egg production/chick-rearing. How should they forage? I followed five species across two sites in Sweden in the Baltic Sea using GPS and time-depth recorder (TDR) devices, giving information on both flight and diving activity. I use a movement ecology approach, asking questions about which spatiotemporal aspects determine these species' movement activities and on how species differ in their foraging activity. Further, I test theories of how birds should optimally vary their flight behaviour in response to winds, and of how individual birds collect information on alternative breeding sites, i.e. prospecting.

Chick-rearing Common Murre (*Uria aalge*) from the island of Stora Karlsö (SK; 17.97°E, 57.29°N), foraged most around sunset and sunrise, when they made more frequent and shallower dives compared to at midday. They made longer distance and duration overnight trips where they visited more distant foraging areas than during daytime trips. In a following study I showed that the GPS device deployed had little measurable effect on the Common Murre's activity, though murres did lose body mass which remains to be explained.

During flights returning from foraging sites to their colony at Stora Karlsö, both Common Murre and Lesser Black-backed Gull (*Larus fuscus*) optimally adjust their airspeeds to minimise their costs of transport, increasing airspeed under headwinds and cross-winds, but reducing airspeed under tailwinds. While the gulls also adjusted their altitude, increasing altitude under tailwinds, thus benefiting from the faster winds higher up, but flying low, where wind is slower, under headwinds and crosswinds; the murres though always fly low, close to the sea surface.

Lesser Black-backed Gull are generalist foragers, at Stora Karlsö they feed both on land and at sea. How do they choose between these? Lesser Black-backed Gull were followed with GPS and observations were made at arable fields on nearby Gotland. The gulls foraged most on land early in the breeding season, and during early mornings especially on cool and cloudy days, while they foraged mostly at sea later in the season, and later in the day. They foraged most on fields with short vegetation and low ground-cover, presumably where soil living invertebrates and earthworms are more available.

Following four *Larus* gull species with GPS during the peak breeding period at the Björn Archipelago at Fågelsundet (FS; 17.72°E, 60.63°N), I show using an information reduction and clustering method how different gull species overlap in the types of foraging trip they use, while also using distinct types of foraging trip. Some species used just a couple of types of trip (specialist), while others used several types quite equally (generalists), this variation was also present within species when comparing between individuals.

Lesser Black-backed Gull from both Stora Karlsö and Fågelsundet, followed with GPS, made very long-distance return movements away from their colonies, mostly after failed breeding attempts. On the majority of these movements, gulls visited multiple coastal sites, likely prospecting at alternative breeding colonies. The gulls from Fågelsundet travelled furthest, visiting many of the same coastal sites as the Stora Karlsö gulls with no difference between sexes.

**Common Murre with time-depth recorder** (Photo: Tom Evans/CC BY-NC 4.0)

# Popular Science Summary

Some seabirds we encounter only fleetingly, as they fly by as we walk along the beach, or perhaps meet far out at sea when we take a boat trip. Others though we are more familiar with, such as the ‘seagulls’ that many will not even turn their head to appreciate. Yet, all seabirds have remarkable stories to tell, and we are fortunate now to live at a time where we can follow individual birds as they fly out to sea, and even as they dive down under the sea. So they can now tell their own stories through their movements. This is all thanks to small devices sharing much in common with the smartphone in your pocket. In this thesis I follow several species of seabird during the spring and early summertime, when they come to land to lay their eggs and raise chicks. I look at how they forage during this time and how they react and respond to the changing conditions around them both across the season, within days, and as the winds change.

In this thesis I study five species of seabird. The Common Guillemot (or Murre in North America, and the internationally accepted common name, hence Murre is used throughout the rest of this thesis), effectively a rather small flying penguin, the guillemots can fly out from the rock ledges on which they breed on sea cliffs where they lay their single egg and raise their chick, then land on the sea where they then proceed to dive deep down under the water (85 m is the record in this thesis, but they have been recorded to dive >200 m) to catch fish. On the same Swedish island as the guillemot, at Stora Karlsö, located in the western central Baltic Sea, I also followed Lesser Black-backed Gull. These make a nest where they raise up to three chicks. Like the guillemots, these gulls can feed out at sea, but they only catch prey at the surface, unlike the guillemots they also forage inland. The final three species are three further gull species, these studied further north, in eastern central Sweden, at the Björn Archipelago at Fågelsundet south of Gävle. The four gull species together range in body size from the small Common (or Mew) Gull, through to the Lesser Black-backed Gull, the Herring Gull, and up to the largest of all gulls, the Greater Black-backed Gull.

I used GPS devices to learn where the birds went and when. The GPS gives us more than just a location, it also tells us how fast, in what direction, and how high our birds fly. The GPS is a small match-box sized device that sits on the back of our birds, either attached by tape to feathers (on guillemots) or by a backpack type harness (the gulls). We learn how the guillemot dives thanks to water pressure increasing predictably with depth, thus by recording the pressure experienced by the guillemot over time we can observe their diving activity; this I did using a second device, a time-depth recorder or 'TDR'. The TDRs are much smaller than the GPS, and were attached on plastic rings to the guillemots' legs.

In paper I, I found that the guillemots mostly forage around sunset and sunrise, at these times they make more frequent and shallow dives compared to around midday. This likely reflects that the guillemots need light to forage, so can only forage deep down under the midday sun. More importantly though, maybe, the fish they eat spend most of the day in deeper water, but at night these come close the surface where they forage on smaller animals (zooplankton), thus the fish are then more assessable to the guillemots. The guillemots made two types of foraging trip, longer duration and distance overnight trips, and shorter daytime trips. On the long overnight trips they travelled further, potentially to more productive areas with more fish available, on the shorter trips they foraged relatively near to their nesting island. This may allow them to balance feeding for themselves (long trips) with catching fish for their chicks (short trips).

We assume that the stories told by the seabirds through their movements recorded with the electronic devices do not differ from that told by birds not carrying devices; in other words we assume the devices do not much affect the activity of the birds tracked. Following up from paper I, I set out to investigate this in paper II. I compared the activity of guillemots carrying both the GPS and TDR devices, and the same individuals with just the TDR. In this way I found that their foraging activity was little affected by carrying the GPS devices. However, whilst carrying GPS loggers, the guillemots lost more mass than when without, suggesting some effect of loggers on the guillemots' condition. This could suggest that the guillemots used more energy to maintain the same activity levels, or that the extra weight and drag from the device reduced their success in catching their prey fish.

For birds flying through the air, wind has a large influence on how quickly they can travel, and how much energy they must use to travel, it can be both beneficial and a negative influence depending on the direction of the wind relative to where the bird wishes to travel. Therefore, we expect birds to change their flight behaviour as wind conditions change. This I investigated in paper III. During their flights returning from foraging sites out at sea back to their colony at Stora Karlsö, both the guillemots and gulls adjusted their speed of flight relative to the air around them (airspeed) to minimise their energy use for a given distance travelled. They increased their airspeed under headwinds and cross-winds, but reduced their airspeed under tailwinds. While the gulls also adjusted how high they flew, flying higher under tailwinds, thus benefiting from the faster winds higher up, but flying low, where wind is slower, under headwinds and crosswinds. The guillemots always flew low, close to the sea surface.

Gulls are flexible foragers, able to use a wide range of prey found in different habitats, both on land and at sea. I investigate how they vary their foraging activity across habitats, over time, and between species in papers IV and V.

The Lesser Black-backed gulls at Stora Karlsö feed both out at sea and on arable fields on nearby Gotland. In paper IV, I followed individual gulls with GPS and complemented this with observations on the arable fields they visit. The gulls foraged most on land early in the breeding season, and during early mornings especially on cool and cloudy days, while they foraged mostly at sea later in the season, and later in the day. When on land, they foraged most on fields with short vegetation and low ground-cover. Together this suggests the gulls are feeding on soil living invertebrates and earthworms especially; for earthworms come more to the soil surface at night (continuing into the early morning) especially under damp conditions. The seasonal changes may either come about through the gulls having different food requirements through the season, for themselves or their eggs/chicks, or through changes in the availability of different prey. The study suggests that availability may play a role, for the most suitable arable fields (short vegetation with bare soil) were more available early in the season.

At the Björn Archipelago, at Fågelsundet, five different species of gull breed alongside each other across a range of small islands. In paper V, I followed four of these species with GPS to compare how they each forage in this common area. I got data for nearly 800 foraging trips made by these species. To find out whether individual gulls across species used similar types of foraging trip I used an analytical method where similar trips were grouped together, clustering. This suggested seven main types of foraging trip used across all the species. Some of these were used by multiple species, such as foraging on landfill/refuse sites, which both Herring and Great Black-backed gulls did. While, others were nearly unique to one species, this was the case for long distance foraging trips travelling out to sea, used nearly exclusively by the Lesser Black-backed gulls. Species also varied in how many different types of trip they performed, with Common Gull using mostly five different types of trip, whereas the Lesser Black-backed gulls mostly used just two types of trip. Patterns also varied within species, though overall a species might use several different foraging trips types, any given individual within the species might only use a subset of these. This was the case for the Great Black-backed gulls. Conversely, by following just one Herring Gull we would observe the majority of the types of trips this species uses, for all individuals were similar in their foraging patterns.

In the final study, paper VI, we leave the immediate area around the study islands, as Lesser Black-backed gulls travel widely across the Baltic Sea. Following breeding failure, or under poor local conditions birds may choose to move to a new breeding site. They could do this through random dispersal, but more effectively they may visit a range of potential sites to find which are best. Following breeding failure, many of the Lesser Black-backed gulls followed by GPS at both study sites made long distance return movements lasting up to 27 days. On some trips they remained at sea, visiting more distant, but likely more productive, foraging areas. On the majority though they would visit multiple coastal sites around the Baltic Sea islands and coasts, this suggests prospecting at alternative breeding colonies. The gulls from Björn Archipelago travelled furthest, both to the north and visiting many of the same coastal sites as the Stora Karlsö gulls across the south-central Baltic Sea.

**Fig. 1. Seabirds at Bempton Cliffs, England** (Photo: Tom Evans/CC BY-NC 4.0)

# Introduction and background

As thousands of individuals get on with their daily lives around you, going in their different directions, all apparently so busy, one cannot help but wonder, what are they are all up to? Initially a seabird colony seems an impossibly disordered explosion of life (Fig. 1.), yet soon one starts to notice common scenes across the colony. A Common Murre (*Uria aalge*, *Pontoppidan, 1763*) or guillemot (*hereafter bird species common and scientific names and authorities follow IOC convention,* Gill & Donsker 2015) flies towards a cliff ledge with a fish in its bill (Fig. 2.), it greets its partner, then feeds their hungry chick. Where has it been? How far did it travel? How deep did it have to dive to catch the fish? How did it cope with the wind during its flight back to the island?

**Fig. 2. Common Murre with a clupeid fish to feed its chick** (Photo: ©Aron Hejdström)

Seabirds have long fascinated people, with their seemingly mystical lives connecting land, sea, and sky (e.g. Savage 1987). Scientists have also long been interested in seabirds owing to their special biology, superficially familiar with their late breeding maturity, long life-spans, and monogamy. Yet, also unfamiliar with their foraging in an alien water world, and their leaving land for months, even years at a time. In a classic book on seabird natural history written by James Fisher and Ronald Lockley in the 1950s (Fisher and Lockley 1954), it is clear that some of the general themes of seabird research were already much developed. They write about: demography, how large populations of seabirds are sustained; breeding behaviour; and movement and migration. Yet, the last of these subjects would remain largely in the dark until the final years of the 20th century, when the seabirds' lives at sea were revealed in the brilliant light of biologging.

Far offshore there are no obvious landmarks, yet seabirds perform long migrations and foraging trips over these open oceans and seas making them an obvious focus for researchers interested in how animals find their way. Ringing recoveries of Manx Shearwater (*Puffinus puffinus, Brünnich, 1764*) on the coast of Argentina from shearwaters breeding on Skokholm Island in the western British Isles demonstrated that this species migrate thousands of kilometres across a large part of the Atlantic (Fisher and Lockley 1954). This led to several long-distance displacement experiments where breeding shearwaters from the island were transported up to 5,500 km to sites including Boston and Venice (Matthews 1953) then released. These same birds were then re-sighted at their colony under three weeks later, demonstrating the remarkable navigational abilities of seabirds.

Commonly seabirds form dense breeding aggregations, or colonies, with often thousands of birds. During the breeding period seabirds must continue to forage, yet are restricted in how far they may travel because of the need to return to incubate their clutch or feed their chicks. This situation makes breeding seabirds an interesting study system for studies of foraging ecology in animals, for the birds have a very small 'breeding territory', usually just the nest, but a large common foraging area shared with others breeding nearby. This raises many questions: do seabirds deplete prey near the colony? How do they locate their food? How do they trade-off caring for their brood while maintaining their own condition? How do they compete with other species of seabird nesting nearby; do they forage at the same sites on the same prey?

Though I here talk of seabirds as a single discreet group of birds, the label is problematic. Birds are traditionally classified into three discreet groups according to their foraging habitat, being either seabirds, those foraging exclusively at sea and only returning to land to breed; shorebirds, those birds that forage mostly at the waters' edge in the inter-tidal zone; and terrestrial birds which use neither sea nor shore, but forage on land. These classifications fit well for some groups, such as the petrels and albatrosses (Procellariiformes) for which all species forage nearly exclusively at sea (though still with an exception in giant petrels, *Macronectes spp., Richmond, 1905*), but less well for gulls and terns (Laridae and Sternidae) for instance, where individual gulls may forage on both land and at sea within a breeding season (e.g. Lesser Black-backed Gull, *Larus fuscus, L., 1758*, Camphuysen *et al.* 2015) or use both marine and terrestrial habitats across their annual cycle (e.g. Caspian Tern, *Hydroprogne caspia, Pallas, 1770,* Shiomi, Lötberg & Åkesson 2015). In the end the label 'seabird' is just a useful shorthand for a group of birds (for species usually included see: Brooke 2002) that have a reasonably common ecology. Schreiber and Burger (2001) summarised this succinctly; "the one common characteristic that all seabirds share is that they feed in saltwater, but, as seems to be true with any statement in biology, some do not".

Many seabird species' populations are in decline, with a ca. 70% decline in those that have been well monitored since 1950 (Paleczny et al. 2015), and a high-proportion are classified as near-threatened or threatened on the IUCN Red List (Croxall et al. 2012). Threats to seabirds include: climate change (Grémillet and Boulinier 2009, Frederiksen and Haug 2015), nest predation by invasive species (Jones et al. 2008), and industrial fisheries reducing prey availability (Cury et al. 2011). Given these threats, understanding the basic ecology of the group is essential for their effective conservation. For example to protect the key foraging grounds of seabirds through protected areas it is necessary to understand both the inter-annual and inter-individual variation in foraging site use (Soanes et al. 2013, Bogdanova et al. 2014), though general guidelines may still be drawn from colony locations and species-specific foraging ranges (Thaxter et al. 2012). Beyond the intrinsic value of conserving seabirds, research increasingly suggests that megafauna and predators may play important roles in nutrient transfer, linking ecosystems, and ecosystem functioning (Doughty et al. 2016). Even apparently purely academic questions, such as whether there are sex and age differences in foraging behaviour may have conservation implications, such as for why in Wandering Albatross (*Diomedea exulans, L., 1758*) there are sex and age specific rates of fisheries' bycatch (Weimerskirch et al. 2006, 2014, Jiménez et al. 2015).

Many seabirds spend a long time away from land over the non-breeding period, often thousands of kilometres away from their breeding grounds and during which time they will moult. During breeding they will often be based on an offshore island or coastal cliffs. Most species follow an annual cycle of breeding and migration, though some follow multi-year cycles with 'sabbatical years' such as Wandering Albatross (Weimerskirch et al. 2014). This thesis will focus on the breeding period, discussing the foraging ecology of seabirds in this critical period. I will consider the wider ecological theory relating to foraging and how this applies to seabirds. Much seabird foraging ecology can be explained in the context of their life-history strategy and their colonial nesting, thus I start with these two points, then go on to discuss optimal-foraging theory, central-place foraging, and diet and niche partitioning within and between populations. At the end of this introduction and background section I discuss how new technologies are rapidly advancing our understanding of the movement ecology of foraging seabirds before introducing my thesis aims. This is followed by: methods, presenting the species, study sites, and technologies and techniques used. Results and discussion summarising the main findings of the thesis, and ending up with the conclusions and my perspectives gained at the end of this work.

## Seabird life-history

At 66 years old, 'Wisdom' is a mother again, as I write this in February 2017 she is rearing a chick (Fig. 3.). As the oldest recorded breeding bird (a record that she keeps breaking year after year), she, a Laysan Albatross (*Phoebastria immutabilis, Rothschild, 1893*), makes news headlines around the world (e.g. Fears 2015; Milman 2015). She is an extreme example, but still representative of the general life-history strategy of seabirds, which have long lives, delayed sexual maturity, and low fecundity (Ricklefs 1990, Gaston 2004). This life-history strategy reflects the constraints imposed on the movement of seabirds during the breeding period, when they need land to breed. They feed on often unpredictable and patchy marine prey, which limits the rate at which they can feed their chicks, and thus also the number of chicks that can be reared at one time. Breeding in dense colonies, often on small offshore islands, parents are constrained in their ability to rear young. As they cannot form foraging territories, they have to travel further to forage on shared resources. This often leads to relatively long foraging trips of several hours or days (see 'Central-place foraging' below). Together these factors are thought to have driven the evolution of monogamy across seabirds, with bi-parental care required to both feed their chicks at a sufficiently high rate and to allow one parent to be present at the colony to incubate or guard the brood (at least for young chicks). This then necessitates that the male parent is confident of paternity (Griffith et al. 2002, Gaston 2004), thus leading to low levels of extra-pair paternity in seabirds, usually <<20% (Quillfeldt et al. 2012).

Many different life-history strategies have been described across biology leading from different trade-offs between reproduction and survival (Jones et al. 2014). These different strategies are generally explained with the slow-fast continuum (Ricklefs and Wikelski 2002), with the opposing extremes of 'live slow, die old' or 'live fast, die young'. Seabirds live their lives at the slow end of this continuum, having low fecundity but long life-spans. Their long-lives lead to significant trade-offs between current and future reproductive attempts (e.g. Chastel, Weimerskirch & Jouventin 1995), and indeed as variance in reproductive success between individuals within a colony is often low, survival may be a greater determinant of life-time reproductive success (Moreno 2003).

**Fig. 3. 'Wisdom', a 66 year old Laysan Albatross with her chick on 7th February 2017**
(Photo: Naomi Blinick/USFWS Volunteer/CC BY-NC 2.0)

Wandering Albatross begin breeding at a mean age of ten years, and rarely visit their breeding colony until 5 years old (Weimerskirch et al. 2014); this an illustrative (if extreme) example of the typically delayed sexual maturity of seabirds (Gaston 2004). Why delay breeding so long? The main theory for this pattern is that seabirds learn about their environment in their first years (juvenile or immature life-stages), improving their foraging success thus increasing their potential for successful breeding. Learning foraging skills may also be important; for instance diving efficiency improves in early life for King Penguin (*Aptenodytes patagonicus*, Miller, JF, 1778) (Orgeret et al. 2016). Juvenile and immature birds (both non breeding) show lower foraging efficiency and less association with productive marine areas than adults in several species; Cory's Shearwater (*Calonectris borealis, Cory, 1881*) (Missagia et al. 2015), Manx Shearwater  (Fayet et al. 2015), and Wandering Albatross (Weimerskirch et al. 2006, Riotte-Lambert and Weimerskirch 2013). These studies support the theory that younger seabirds explore their environment, learning the location of more productive foraging grounds. However, a potentially confounding factor for all these studies are that the young birds are not breeding, thus are not as constrained in their foraging behaviour as the older, usually breeding, adult birds (e.g. in maintaining body reserves during incubation). A study comparing diet, inferred from stable isotope profiles, in Cory's shearwaters (of a different population than in Missagia *et al.* 2015) found no difference in diet between sabbatical (i.e. non-breeding) mature shearwaters and immature (also non-breeding) shearwaters, but did find differences in diet between breeding mature birds and the sabbatical birds (Campioni et al. 2016). Campioni et al. (2016) suggest that differences between immature and mature seabirds are more likely a result of greater foraging constraints on the breeders ('the reproductive constraint hypothesis'), with intra-specific niche segregation then resulting between breeders and non-breeders (often immatures).

Though older birds are generally more successful than younger birds, in late life they may senesce, with increased annual mortality rates for older birds observed across several species: Southern Fulmar (*Fulmarus glacialoides*, Smith, A, 1840) (Jones et al. 2014) and Common Tern (*Sterna hirundo*, L., 1758) (Zhang et al. 2015); and reduced breeding success in very old age: Common Murre (Reed et al. 2008), Southern Fulmar (Jones et al. 2014), and Common Tern (Zhang et al. 2015). These patterns are complex though; Wandering Albatross show declining breeding success with age but also apparently anticipate their final demise, giving higher reproductive investment to their final breeding attempt when their expectation of future reproductive output should be low, thus offsetting their senescence (Froy et al. 2013). Further, ageing is unlikely to be constant, for instance in Thick-billed Murres (*Uria lomvia, L. 1758*) rates of biological aging (inferred from rates of telomere shortening) vary between colonies with rates higher at a colony with poor environmental conditions (Young et al. 2013).

## Coloniality in seabirds

Nearly all seabirds are colonial (Gaston 2004), that is their territories "contain no resource other than nest sites" (Danchin and Wagner 1997), with birds breeding gregariously (Fig. 1.). Coloniality is common across birds having evolved independently over 20 times (Siegel-Causey and Kharitonov 1990), and its evolution has been reviewed for seabirds (Coulson 2001) and for auks specifically (Birkhead 1985). Many explanations have been given for why seabirds are usually colonial, and most of these are not mutually exclusive, the two most commonly cited reasons being a shortage of suitable nesting sites, or protection from predators.

As seabirds' primarily forage at sea, but must nest on land, they are expected to breed on coasts or islands as close to their foraging grounds as possible to limit travel costs. Offshore islands are often the closest sites available, but may be small, thus forcing seabirds to nest close together. Gaston (2004) suggested a close parallel to this situation with cave-nesting swiftlets (*Collocalia spp.*), that also feed on mobile and patchily distributed prey (insects) and have rare nesting habitat (caves). Protection from predators likely interacts with the shortage of suitable nesting sites, forcing seabirds to nest even closer together to reduce predation risk, as above a certain breeding density it is likely more effective to clump together at relatively safer sites (e.g. cliffs) than try to hide (Wittenberger and Hunt 1985).

Other reasons given include the ‘hidden lek’ (Wagner 1999), where males cluster nests to individually get more opportunities for extra pair matings; and the ‘information centre’ (Ward and Zahavi 1973), that by breeding close together birds can benefit by getting information from others nesting nearby (reviewed recently in Evans, Votier & Dall 2015), which may be particularly beneficial in seabirds foraging on ephemeral and patchily distributed prey (Clode 1993).

During breeding, seabirds’ foraging ecology is driven largely by their colonial living, with the need to return to their nesting location between foraging bouts. These conditions thus lead to competition for foraging being higher near the colony where there is a high density of birds, hence seabirds normally have to travel some distance to forage.

## Optimal-foraging theory

Seabirds forage in a challenging environment, their prey are at first glance hidden from view, usually being underwater, and though prey are often aggregated, the distribution of prey aggregations changes day to day. How then does a seabird forage most effectively? To answer this question we should consider the general challenge of optimal foraging for any predator-prey system. Then we can apply these insights to seabirds, then look at the consequences of restrictions on movement placed by breeding, usually colonially (see above), which lead to central-place foraging.

The ideal free distribution (IFD) (Fretwell and Lucas 1969) is the basic model of optimal-foraging theory developed in the 1960s, then subsequently expanded and adapted (MacArthur and Pianka 1966, Charnov 1976, Bernstein et al. 1988, Kacelnik et al. 1992). IFD gives the expected distribution of predators with respect to prey, it essentially predicts that predators should be distributed in proportion to the prey available at a patch (*i.e.* density dependence). IFD makes various simplifying assumptions, including: that resources are distributed in patches; travel time between patches is negligible; that predators know the potential intake rate for all patches; and the rate of intake decreases with increasing number of predators in a patch.

The assumption that prey are distributed in patches is rarely met in the strict sense, where prey are only found in patches, and within patches prey are uniformly distributed (Arditi and Dacorogna 1988). However, both seabirds (Certain et al. 2007) and their prey have been found to be patchily distributed, but this is highly scale dependent, with for example fish organised in shoals at 10s of metres scale, patches at km scale, and patches also aggregated at 100s km scale (Weimerskirch 2007, Fauchald 2009, Wakefield et al. 2009a). To what extent seabirds in general track their prey is unclear. In one study, the distribution at sea of Common Murre and Atlantic Puffin (*Fratercula arctica*, L. 1758) were found to be closely associated with the distribution of their main prey, Capelin (*Mallotus villosus*, O. F. Müller, 1776) (Piatt 1990). This association was scale dependent, being strongest at ca. 2.5 km, suggesting imperfect tracking of prey by the seabirds, and the apparent preferred densities of prey differed between the murres and puffins (Piatt 1990). The stability of patches over time is also dependent on spatial scale, with productive patches stable at larger (10 – 100 km) scales but ephemeral at fine scales (Weimerskirch 2007). Stable oceanographic fronts may provide reliable areas of high primary productivity at large scales, so be areas of predictably high prey abundance which seabird foraging may be associated with during both breeding (Scales et al. 2014a, b) and migration (Mcknight et al. 2013). A striking example of this are Manx Shearwater breeding at four islands separated by 100s km along the western British Isles but all foraging at the Irish Sea Front (Dean et al. 2015). This is a productive marine area (Dickey-Collas et al. 1997) ranging from 120 – 375 km distant from the breeding colonies, yet visited on over 50% of long (>200 km) trips across all four shearwater colonies.

The temporal and spatial structure of foraging patches is a key determinant of to what extent predators can track their prey resources, and thus match their foraging distribution to that of their prey (McNamara and Houston 1985, Bernstein et al. 1991). Learning about the distribution of prey across years (at larger scales), and at small scales across hours or days may help seabirds track their prey distribution (see: 'Competing to feed: individuals').

## Central-place foraging: Where to breed and feed?

Early models of optimal foraging assumed that animals were free to move anywhere across the environment, the 'free' in the IFD model (Fretwell and Lucas 1969). However, during breeding, seabirds are certainly not 'free' to move anywhere, for they must return to their colony to incubate their clutch, to brood, or to feed their chicks. This situation is a classic example of *central-place foraging* (CPF), where an animal is tied to a central-place, here the colony, to which it must return between bouts of foraging activity (Orians and Pearson 1979). CPF theory has been developed in two directions to look at: where the animal should locate its central-place; and where and how it should optimise its foraging from that place (Orians and Pearson 1979). The first question is relevant to where seabird colonies are located, where the options are often very restricted in the marine environment, with seabird colonies usually either on relatively inaccessible stretches of mainland coastline (e.g. steep cliffs, Fig. 1.), or offshore islands (see 'Coloniality in seabirds'). The second question focusses on all the aspects above ('Optimal-foraging theory'), plus how prey are brought back to the brood, how frequently the brood must be fed, and the balance between parental (i.e. self-) and chick-provisioning.

## Where to breed?

Where should a seabird breed? For colonially breeding seabirds, there are two components to this question, firstly where and how are seabird colonies initially established, and secondly how do seabirds disperse between colonies? Seabirds are generally highly philopatric (Gaston 2004), usually returning to breed in the same colony as where they were born, and rarely switching between colonies once they have begun breeding. There are exceptions, with gulls and terns apparently more flexible than many other seabird species; for instance, Caspian Tern are particularly noted for their flexibility in establishing new colonies, with even whole colony abandonment and emigration occurring (Väisänen 1973). Understanding how seabird colonies become established is crucial to conservation programmes introducing species to former or new colony sites, so much of our knowledge comes from this application. A key insight of these studies is that social attraction plays a strong role in colony recruitment, so seabird colony restoration projects often use e.g. decoys and tape-playback of breeding birds (Jones and Kress 2012). Animals may either remain at their natal colony (philopatry), they may disperse before their first breeding attempt (natal dispersal), or they may disperse between breeding seasons (breeding dispersal) (Greenwood 1980).

Earlier studies of seabird dispersal focussed on individually marked birds (i.e. ringed birds) that could be observed across colonies, these studies (12 species across 5 families reviewed along with other bird species in: Clarke et al. 1997) suggest that seabirds follow the generally observed patterns in birds of female biased dispersal (Greenwood 1980, Clarke et al. 1997). The processes by which seabirds move between colonies is still largely unknown, as it is difficult to observe even with tracking devices, unless data can be remotely downloaded. A few detailed studies have been carried out where large numbers of individuals are colour ringed, and re-sighted. European Shags were observed across a large number of neighbouring colonies, showing that 10% of birds dispersed from their natal colony, and that most dispersed shags moved to quite nearby colonies (Barlow et al. 2013).

Tracking technologies, and especially GPS, promise to reveal the processes by which individual birds disperse (Ponchon et al. 2013). For example, following breeding failure Black-legged Kittiwake (*Rissa tridactyla*, L. 1758) make long prospecting trips to visit neighbouring colonies, in contrast to the general pattern for seabirds, males visited more distant colonies than females (Ponchon et al. 2017). Locating new colonies, and even returning to the natal colony (often following long distance migrations) relies on having well developed navigational abilities (see e.g. Bonadonna et al. 2003, Wiltschko and Wiltschko 2003, Papi 2006, Holland 2014), both with respect to remembering the location of alternative colonies (a 'cognitive map') and of then relocating those colonies through map-and-compass cues (Kramer 1961) (e.g. magnetic compass, olfactory cues). Studies of navigation in seabirds suggest that we should expect olfactory cues to be important, at least in the tube-nosed or Procellariiforme species (Bonadonna et al. 2003, Papi 2006, Nevitt 2008, Gagliardo et al. 2013, Pollonara et al. 2015) and a recent study suggests that this may be true for Laridae too (Wikelski et al. 2015). However, locating new sites need not be an exclusively individual explorative process, as individuals may also learn from others where colonies are though social learning (Evans et al. 2016). These types of processes are used by naïve Cape Gannet individuals to learn of and locate feeding sites from their conspecifics (Thiebault et al. 2014), and we may imagine the reverse of this process allowing individuals at a common foraging site to learn of colony locations by following others returning to their own colonies. Then when at a novel colony, a seabird may assess the colony quality based on the breeding success of current breeders (Boulinier and Danchin 1997, Ponchon et al. 2013). Though tracking studies can indicate that individuals from different colonies use common foraging areas (e.g. Dean et al. 2015), without either tracking many individuals simultaneously, or using video loggers, we cannot directly observe social learning.

## Where and how to feed?

Where seabirds should feed will vary by breeding stage, as the constraints placed by CPF differ, with longer foraging trips possible pre-laying and during incubation, then shorter trips during the chick-rearing stage (Cleeland et al. 2014, Quillfeldt et al. 2014). The majority of the albatross and petrel (Procellariformes) species perform a pre-laying exodus, that is a long foraging trip performed during egg building (Warham 1990). This behaviour is commonest in females but often present in males too; in females the role is thought to be to gain the additional nutrition required for egg production; in males to have an energy store to use during the first incubation shift that often lasts several days. These long trips are thought to allow petrels to forage at greater distances from their colonies in areas of high productivity (Warham 1990), which tracking studies now support (Phillips et al. 2006, Guilford et al. 2009).

There is much variation in how chicks are fed across seabirds, with a range from feeding of fully intact prey carried back externally in the bill (e.g. murres and puffins), to partially digested prey carried internally (e.g. most gull species), to the pre-digested prey (stomach oils) of albatrosses and petrels (Gaston 2004). How prey are brought to the chick places a specific limitation on foraging behaviour; when feeding the brood with fresh prey, or partially digested prey, the potential foraging range will be constrained by the need to minimise food degradation during the return to the colony (Gaston 2004). Stomach oils are thought to have evolved to relax this limitation, thus allowing parents to forage further from the colony (Warham et al. 1976, Roby et al. 1997). In single prey loaders, which carry a single prey item externally in their bill (Fig. 2.) to their chick, parents are particularly constrained, generally their foraging (for chick provisioning) will be ruled by an optimal diet-choice model (Lessells and Stephens 1983), where they cannot opt to catch many small prey but must bring back a single prey item of good quality. This prediction is supported for Common Murre, a single prey loader, which optimise for prey size and quality (Burke and Montevecchi 2009), though will increase provisioning rate (thus frequency of foraging trips) when the quality of available prey is low (Kadin et al. 2016). This contrasts with the related alcid, the Atlantic Puffin, a multi-prey loader, capable of carrying multiple prey in their bills, which compensate, at least partially, for smaller sized prey by carrying more prey (Barrett 2015).

A central fitness trade-off for all animals with multiple breeding episodes is between their current and future reproductive investment, and thus between investment in offspring versus in self-maintenance (Drent and Daan 1980, Ricklefs 1983, Zera and Harshman 2001). Given the typically low fecundity and long life of many seabirds (see 'seabird life-history'), this trade-off is likely to be particularly extreme (Ricklefs 1990). Trade-offs in foraging decisions may be increased further when the nutritional requirements of adults for self-maintenance differ from those of their chicks for growth. Whether chicks and parents have different dietary requirements is unclear; in Common Murre chick growth is more limited by dietary energy content than nutrient composition (Benowitz-Fredericks et al. 2006), while Western Gull (*Larus occidentalis,* Audubon, 1839) parents switched diet between incubation and chick-hatching (Annett and Pierotti 1989) possibly suggesting differing dietary requirements. Support for trade-offs between current and future reproduction are stronger. Under very poor foraging conditions parents may decide to abandon a breeding attempt altogether. Chastel, Weimerskirch & Jouventin (1995) tested this prediction by comparing three sympatrically breeding seabirds: a long-lived species, the Blue Petrel (Halobaena caerulea, Gmelin, JF, 1789); and two shorter lived species, Common Diving Petrel (*Pelecanoides urinatrix,* Gmelin, JF, 1789) and Slender-billed Prion (*Pachyptila belcheri,* Mathews, 1912). They found that under years of poor foraging conditions, when the adults' condition (body weight) were low at the start of breeding the long-lived Blue Petrel were likely to abandon breeding, whereas the shorter lived species continued to breed. Thick-billed Murre adults breeding in the Hudson bay, Canada trade-off their own condition with that of their chick (Gaston & Hipfner 2006); in years of poor foraging conditions they reduce chick-provisioning rates, but more they reduce their own condition (their body weight), apparently offsetting poorer foraging conditions. However, like the Blue Petrel, they appear to have a lower threshold of body weight below which they will cease breeding that season (Gaston & Hipfner 2006).

The dual-foraging strategy of many seabird species may provide a partial resolution of this trade-off. Here, chick-rearing adults have a bimodal distribution of foraging trip ranges (i.e. distance) and durations, with long-trips used more for self-provisioning, and short-trips for chick-provisioning (Weimerskirch et al. 1994). Blue Petrels use a combination of long trips of ca. 7 days duration and short trips of ca. 2 days duration (Chaurand and Weimerskirch 1994, Weimerskirch et al. 2003). During the long trips the petrels gain weight, then on short trips they appear to use this stored energy, losing weight (Weimerskirch et al. 2003). Further support for the dual-foraging role of the bimodal trip durations are found in a study of Manx Shearwater, when their chicks received supplementary feeding, the parents performed a higher proportion of long trips than usual, presumably because of the relaxed need for chick-provisioning (Hamer et al. 2006). A later GPS tracking study at the same colony suggests that these long trips are used to visit more productive marine areas lying at distance from the colony (Dean et al. 2015), with a similar finding for Cory's Shearwater (Magalhães et al. 2008).

The dual foraging strategy was initially proposed for procellariform species (Weimerskirch et al. 1994) mostly performing multiday trips, with the short trips <4 days, and the long trips of >5 days. However, this general strategy likely also operates for species with much shorter trips, which there is some support for amongst the auk species. Little Auks (*Alle alle, L., 1758*) perform both short (ca. 2 h) and long (ca. 10-17 h) trips, which appear to fit with a dual foraging strategy (Welcker Jorg et al. 2009), with long trips allowing exploitation of productive distant foraging grounds (Jakubas et al. 2016). Thick-billed Murre in the NE Pacific breeding at three different colonies (Harding et al. 2013) may be more able to reduce the conflict between self- and chick-provisioning than in the Hudson Bay area cited above (Gaston and Hipfner 2006). At all the colonies adults perform relatively short daytime trips in the vicinity of their colony, but also make longer overnight trips in which they visit more productive shelf-break waters (Harding et al. 2013).

## Ashmole's halo

There are few formal tests of optimal foraging theory in seabirds, but one key prediction which has been tested is 'Ashmole's halo'. Ashmole (1963) proposed that because breeding seabirds will preferentially forage close to their colony, minimising travel costs, they will deplete prey close to the colony more than that further away, this idea is now termed 'Ashmole's halo'. The idea predated much of the development of CPF ideas, yet the essential predictions and theory are the same. Ashmole (1963) suggested that the limited foraging range during breeding limits colony sizes by introducing a density dependent process for foraging during breeding. Though the theory is now half a century old, it is only recently that really firm progress has been made in empirically testing it. There are two approaches to testing the prediction, either to compare various foraging and breeding parameters across seabird colonies of different sizes, or to relate foraging parameters and prey quality or quantity to the distance from a single seabird colony (Gaston et al. 2007).

Following the first approach, the rate of colony growth in Northern Gannets (*Morus bassanus*, L., 1758) was shown to be inversely proportional to their colony size (Lewis et al. 2001), with GPS tracking across colonies later showing that the likely mechanism for this was density dependent competition during foraging (Wakefield et al. 2013). Similarly, in Adelie Penguins (*Pygoscelis adeliae*, Hombron & Jacquinot, 1841) foraging trip duration and individual metabolic rates positively correlate with colony size (Ballance et al. 2009), and at the largest colonies the energy gained during foraging does not compensate for that expended during foraging (Ballance et al. 2009). Potentially Ashmole's halo should be more pronounced and clearer in isolated oceanic islands away from productive continental shelf-waters, where prey may be depleted more rapidly: Masked Booby (*Sula dactylatra*, Lesson, R, 1831) foraging trips were tracked with GPS during both chick-rearing and incubation at Ascension and St Helena, two South Atlantic islands with very contrasting seabird population sizes (Oppel et al. 2015). Boobies from the larger of the two colonies performed much longer duration trips to greater distances than those from the smaller colony, and they also made more overnight trips at the large colony, potentially suggesting a compensatory dual-foraging strategy (see 'Where and how to feed', above). Further, a recent meta-analysis related species specific maximum foraging ranges to the population size of seabird colonies for 43 species and 28,263 colonies (Jovani et al. 2016). A strong correlation between the maximum species specific colony size and the species specific maximum foraging range was found, suggesting that those species that can exploit a larger foraging area during breeding can attain a larger maximum colony size; though there was a weaker relationship for median species colony size.

Gaston, Ydenberg & Smith (2007) suggest that the theory of Ashmole's halo could be most effectively tested through detailed studies within seabird colonies. So far there have been few studies following this second approach. One of the first studies to do this (predating that paper) compared fish abundance in bays nearby and further away from two Double-crested Cormorant (*Phalacrocorax auritus*, Lesson, R, 1831) colonies (Birt et al. 1987), finding that those bays within the cormorants' foraging ranges had significantly lower abundances of fish than those outside their foraging ranges. Similarly, the energy content of fish brought back to chicks by Thick-billed Murre parents were found to be proportional the square-root of the foraging distance (suggesting a relationship with available foraging area), implying that larger and higher quality prey were increasingly depleted closer to the colony (Elliott et al.

2009). However, this correlational result could likely be more parsimoniously explained by murres being more selective of prey when foraging at greater distances, as optimal foraging models predict (Lessells and Stephens 1983). A recent study correlated maximum individual foraging ranges with the fluctuating population size of a single colony of European Shag (*Phalacrocorax aristotelis*, L. 1761) across several years (Bogdanova et al. 2014). This study found that foraging ranges were greater in years when the breeding population was higher, and further that this relationship only held under years of low breeding success, thus suggesting a density dependent mechanism. Under years of high breeding success the shags are presumably less limited by prey availability thus do not need to travel so far to forage.

There is then support for the Ashmole's halo hypothesis, but really detailed studies looking at trade-offs between foraging close and far from seabird colonies are lacking. Studies of this type are likely to be most able to explain the underlying behavioural ecology behind the patterns observed in the studies cited. Integrating together the ideas of the dual-foraging strategy (Weimerskirch et al. 1994) with those of Ashmole's halo (Ashmole 1963) and placing these in a wider optimal foraging theoretic context could be a productive avenue to furthering our understanding of generalities in the foraging ecology of seabirds.

## Competition for food: populations and species

The maintenance of biological diversity and how apparently similar species may live in sympatry is a recurring question of biology (Gause 1934, Hutchinson 1959, Macarthur 1965), and is a key topic of interest to seabird ecologists in understanding how different species can co-exist on a common prey base, or how large populations of several species of seabird can breed on a common island.

The classic theory for species coexistence at the same trophic level (a species community or guild) in a common environment is that of niche partitioning (Gause 1934, Hutchinson 1957). This, usually applied at the species level as the *fundamental niche*. That is the set of environmental conditions under which the mean fitness of individuals in a population will be unity or more; *i.e.* that the population will be stable or increasing (Holt and Gaines 1992). In the simplest form species are separated ecologically along a single axis of variation (or a single dimension) such as diet. However, in reality, niche space is multi-dimensional, with many different axes of variation contributing to niche separation between species, a concept introduced by Hutchinson (1957) as an n-dimensional *hypervolume,* each dimension some measure of the environment.

Seabirds as colonially living species forming dense breeding aggregations with common foraging grounds were of interest already in the earliest works on niche partitioning between species. Gause (1934, pp. 19-20), in his seminal work, cited (unpubl. study by A. N. Formosov) the example of four sympatrically breeding tern species on a Black Sea island. Already at that time Gause had a good idea of how they partitioned resources amongst themselves according to their foraging behaviour, habitats, and prey:

> "…there is a sharp difference between them [the four tern species], for every species pursues a definite kind of animal in perfectly definite conditions. Thus the sandwich-tern [*Thalasseus sandvicensis*, Latham, 1787] flies out into the open sea to hunt certain species of fish. The blackbeak-tern [Gull-billed Tern, *Gelochelidon nilotica*, Gmelin, JF, 1789] feeds exclusively on land, and it can be met in the steppe at a great distance from the sea-shore, where it destroys locusts and lizards. The common-tern [*Sterna hirundo*, L. 1758] and the little-tern [*Sternula albifrons* (Pallas, 1764)] catch fish not far from the shore, sighting them while flying and then falling upon the water and plunging to a small depth. The light little-tern seizes the fish in shallow swampy places, whereas the common-tern hunts somewhat further from the shore. In this manner these four similar species of tern living side by side upon a single small island differ sharply in all their modes of feeding and procuring food."

Most simply different predatory seabird species may be expected to feed on different prey species, thus partitioning the environment between them by dietary specialization. This is supported by stable isotope studies, giving indirect measures of diet (Young et al. 2010, Navarro et al. 2013, Linnebjerg et al. 2013, Kokubun et al. 2015), and the level of dietary niche partitioning between species may differ between years according to prey availability (Barger and Kitaysky 2012, Moreno et al. 2016). However, many studies have also found broadly overlapping diets amongst sympatric species (Shealer 2001). An early study of eight seabird species on an equatorial Pacific island (Ashmole and Ashmole 1967) concluded (similarly to Gause, above):

> "…coexistence [between species] … depends mainly on differences in feeding methods, feeding zones and feeding times."

Similar findings were made for sympatric auks (Alcidae) (Cody 1973) interpreted to segregate foraging spatially, though subsequently suggested to relate more to other differences in foraging methods (e.g. diving depths, and bill morphology) (Bédard 1976). Further a study comparing the diets of six species during chick-rearing on a sub-Antarctic island in the South Atlantic (Croxall et al. 1997) found all but one species to feed primarily on Antarctic Krill (*Euphausia superba*, Dana, 1850), there the niche partitioning between the seabird species mostly operated on the different sizes and states (sex and reproductive status) of the krill taken and time of foraging.

Perhaps this overlap of prey species between seabird species should not be a surprise, for in many areas one or more highly abundant prey fish, known as forage fish, predominate. These are super-abundant pelagic fish (though the abundant crustacean, krill, are generally included too) on which many different marine predators feed, in many areas representing a high proportion of diet (Pikitch et al. 2014). Thus, declines in forage fish populations resulting from industrial fishing are now a concern for the viability of many seabird populations (Cury et al. 2011).

Across seabirds there are three general foraging guilds according to the where and how they catch their prey. These are: diving (usually offshore), allowing the capture of prey at depth; coastal and inshore foraging, where prey are often abundant and forced to the surface; and pelagic foraging, where large distances are covered allowing foraging on quite dispersed prey (Shealer 2001). A fourth potential strategy is of kleptoparisitism, the taking of prey from other predators. This strategy may be favoured by predators unable to exploit prey distributed at depth (i.e. by diving); kleptoparisitizing seabird species in the Peruvian coastal system usually parasitize seabirds performing deeper dives than themselves (Duffy 1980). These different strategies represent one level of foraging specialism across seabirds.

Two extremes from generalism to specialism are represented by the larger gull species (*Larus spp.*) and murres (*Uria spp.*), respectively. Large gulls often forage on both marine and terrestrial food sources (Götmark 1984, Yoda et al. 2012, Camphuysen et al. 2015), and as opportunists also exploit anthropogenic sources of food, especially from refuse dumps (Duhem et al. 2008) and fisheries discards (Cama et al. 2012, Tyson et al. 2015). Murres conversely have evolved a highly specialized foraging ecology, catching prey deep in the water column (Croll et al. 1992). This specialization for diving is illustrated by sympatric Common Murre performing deeper dives and generally using less flight during foraging trips than the similarly sized Razorbill (*Alca torda*, L., 1758) which has a relatively lower wing-loading (Thaxter et al. 2010, Linnebjerg et al. 2013).

## Competition for food: individuals

A broad species niche may arise either from all individuals within a population being generalists, or from specialist individuals with different narrower niches, such that these individual niches sum to a broad population level niche (Bolnick et al. 2003, Bearhop et al. 2004). For example, Green Turtle (*Chelonia mydas,* L., 1758) show consistent individual specialization over time, though the population level niche is broad because individuals specialize on different habitats with different associated diets (Vander Zanden et al. 2013).

Many seabird species have sex differences in foraging behaviour or diet, including: Common Murre (Thaxter et al. 2009), Audouin's Gull (*Ichthyaetus audouinii,* Payraudeau, 1826) (García-Tarrasón et al. 2015), Northern Gannet (Stauss et al. 2012), and Wandering Albatross (Weimerskirch et al. 2014). These differences may result for a variety of reasons: morphological differences (probably a proximate reason) between sexes in e.g. bill shape (Navarro et al. 2009) or wing area and shape (Wakefield et al. 2009b); sex specific nutritional requirements such as for egg-producing females (Blount et al. 2004, Sorensen et al. 2009); or risk partitioning, whereby within breeding pairs those where the male and female have different foraging strategies have higher breeding success (Elliott et al. 2010).

**Fig. 4. Black-browed albatross (immature)**
(Photo: Tom Evans/CC BY-NC 4.0)

Individual specialization is linked to the related concepts of individual repeatability (Bell et al. 2009), consistency (Bolnick et al. 2003, Patrick and Weimerskirch 2014), and personality (Dall and Griffith 2014), and this may have considerable implications for how individuals forage (Spiegel et al. 2017). Individual specialization is now thought to be widespread across seabird species (Ceia and Ramos 2015), though the level of specialization may vary within a population (Ceia et al. 2012, Patrick and Weimerskirch 2014). How differences in levels of foraging specialization within seabird populations are linked with fitness, thus maintained in a population is currently unclear. In Black-browed Albatross (Fig. 4., *Thalassarche melanophris*, Temminck, 1828), the more specialist individuals (those consistent in habitat and site use) have comparatively higher breeding success than more generalist individuals within a year (Patrick and Weimerskirch 2014). Herring gulls, despite being generalists as a species, show individual specialization in diet and foraging site use (Davis 1975, Pierotti and Annett 1987, Tyson et al. 2015). For these gulls, dietary specialization *per se* was not linked to increased reproductive success, but individuals that specialize on better quality prey do achieve larger clutch sizes (Pierotti and Annett 1987). Most studies of individual specialization have been restricted to a single breeding season, showing short-term consistency only (Ceia and Ramos 2015). Recently though Northern Gannets have been shown to be consistent in their use of specific foraging areas both within and across years, and this appears to be driven by dietary specialization based on consistent individual stable isotope profiles across years (Wakefield et al. 2015), and an earlier study using only stable isotopes suggested a similar pattern in Wandering Albatross (Ceia et al. 2012).

We will gain increased understanding of how individuals within and between species partition their foraging behaviour as more tracking studies are performed and more detailed analyses are made of these data. A recent study following this approach found differences in foraging strategies through GPS tracking of two sympatric albatross species, finding different strategies within (largely sex-based) and between the species (Conners et al. 2015). Individual movement strategies are also likely to shape what information they use in their foraging (Spiegel et al. 2017), when repeatedly using the same foraging sites they likely rely more strongly on their own information (memory), whereas if visiting new foraging sites they may follow conspecifics or other individuals learning of new foraging sites (Thiebault et al. 2014, Evans et al. 2016).

## Diving and flight

The extreme mobility of seabirds below and above water is a large determinant of their foraging ecology. Some species cross vast distances at low cost by dynamic soaring (Weimerskirch et al. 2000), others dive to >500 m (Wienecke et al. 2007), while still others can dive >200 m yet can still fly (Croll et al. 1992)! These abilities allow them to exploit a large part of the World’s oceans. Though diving and flight operate in different fluids (water and air, respectively), birds experience some of the same challenges in both environments, with their movement a function of both their own locomotion, and of the fluid's movement (winds and currents) (Chapman et al. 2011). Though it may seem tough to move through the water fluid, diving has a lower cost of transport than flight (Ellis and Gabrielsen 2001), though clearly flight can be considerably quicker.

The cost of flight varies with airspeed, the speed the bird moves relative to the air around it, rather than to the ground. The specific airspeed optima for a bird is predicted by the flight power-curve (Hedenström and Alerstam 1995, Pennycuick 2008) from which two optimal speeds are obtained, the minimum power speed (*Vmp*) where the instantaneous rate of energy expenditure is minimised, and the maximum range speed (*Vmr*) where the cost of travel per unit distance is minimised. *Vmp* is unaffected by wind, but if a bird flies at its *Vmr* speed, then it should alter its airspeed depending on wind conditions experienced. Under tailwinds *Vmr* is reduced, whereas under headwinds *Vmr* increases (Pennycuick 1978), likewise *Vmr* is affected by cross-winds, with it increased as cross-wind speed increases (Liechti et al. 1994).

Wind may also influence how high birds fly, for at low altitude wind speed decreases rapidly as the sea-surface is approached due to the air being decelerated by friction with the water surface (Geiger et al. 2009). Soaring seabirds exploit this vertical wind speed gradient using dynamic soaring (Rayleigh 1883, Weimerskirch et al. 2000), whereas flapping seabirds may be expected to adjust their altitude depending on the wind direction, if beneficial they may fly higher, yet if a hindrance they may fly closer to the sea-surface.

Costs of both diving and flight are largely determined by drag forces and wing-loading, thus anything that changes the profile of a bird may increase the cost of transport through increased drag, or any increased load will increase wing-loading. These factors are of special relevance to how biologging devices are designed and deployed on birds (Bowlin et al. 2010, Vandenabeele et al. 2012, Pennycuick et al. 2012). The amount of drag is mostly a function of the device frontal cross-sectional area, but is also influenced by shape. External antennas potentially increase drag forces dramatically during both swimming and flight (Wilson et al. 2004, Pennycuick et al. 2012), while using a tear drop shape can reduce drag for a given cross-sectional area (Todd Jones et al. 2013).

# The biologging revolution

That Wisdom is now 66 years old (see Seabird life-history, Fig. 3) we know thanks to researchers uniquely marking her with a ring on her leg in 1956. That same year, in Sweden the Nobel Prize in Physics was awarded for the development of the transistor (Nobel Media AB 2015). Two apparently unlinked events, yet the second would go on to transform seabird research. Much has been learned by the detailed observation of seabirds during breeding, especially when paired with individually marked birds, such as Wisdom. However, how she and other seabirds like herself survive and successfully bring back food to rear their chicks was largely unknown before we could follow their lives at sea. This all changed when the promise of the transistor came of age, as millions of transistors were sent out to Space on satellites beaming signals back to the hundreds of GPS tags sent out to sea on the backs of seabirds.

Many seabird species dive to catch their prey underwater, and it was this vertical dimension that biologging devices first revealed. To study these movements we use time-depth recorders (TDRs), these record water pressure over time, with depth obtained from the pressure reading. Before the development of miniature electronic TDRs, dive data were obtained through a number of techniques. Common Murre dive times and durations were recorded by breaks in the VHF signal from bird-borne radio-tags (Wanless et al. 1988), or without electronics at all, maximum dive depths were recorded using capillary tubes dusted inside with a soluble indicator such as icing sugar (Burger and Wilson 1988). One of the earliest seabird TDR studies (Huin and Prince 1997) looked at dives made during foraging trips by Grey-headed Albatross (*Thalassarche chrysostoma*, Forster, JR, 1785) using TDRs originally developed for marine mammal research. The TDRs revealed that the albatrosses were most active midday and at dusk.

Individual movements of seabirds at sea were first recorded using platform transmitter terminals (PTTs), these devices transmit a radio-signal which is then picked up by satellites, using the Doppler effect allows the inference of location. Early studies showed that seabirds foraged at greater distances from their colonies than previously expected. King Penguin (*Aptenodytes patagonicus*, Miller, JF, 1778) travelled ca. 500 km, allowing them to forage on productive waters at the polar front (Jouventin et al. 1994), whilst Wandering Albatross travelled up to 15,000 km in a single foraging trip, and were more nocturnally active on nights around the full-moon (Jouventin and Weimerskirch 1990).

For most seabirds the long-term attachment of back-mounted tags, such as PTTs or GPS (below) is not feasible. Long term attachment by taping to feathers is not possible because of moult, and most seabirds appear to be disturbed by harnesses (Phillips et al. 2003), with the exception of gulls (Thaxter et al. 2014). Light-level geolocators (GLS) have revolutionised studies of migration in seabirds, for these simple devices are small enough to be attached to a leg-ring. These were first developed and used to study Northern Elephant Seals (*Mirounga angustirostris*, Gill, 1866) during their migrations (Delong et al. 1992). GLS record light-level at a regular interval using an accurate internal clock, from which the time of sunrise and sunset can be inferred. As day-length changes with latitude, and the time of sunrise and sunset change with longitude, it is possible to estimate a geographic position (Hill

1994). One of the earliest seabird studies revealed that Grey-headed Albatross circumnavigate the Antarctic continent during their migration (Croxall et al. 2005). By now the miniaturisation of GLS tags allows the tracking of even the smallest of seabird species. A <1g GLS was used to track the ca. 45 g Leach's Storm Petrel (*Oceanodroma leucorhoa*, Vieillot, 1818) from its breeding grounds in Nova Scotia, Canada, to its wintering area off the coast of Brazil (Pollet et al. 2014).

In the late 1990s the first GPS tracks were obtained from wildlife, first Moose (*Alces alces*, L., 1758) (Edenius 1997) and African Elephant (*Loxodonta africana*, Blumenbach, 1797) (Douglas-Hamilton 1998), then a few years later the largest seabirds, Wandering Albatross were tracked with 105 g devices (Weimerskirch et al. 2002). GPS works by a network of satellites transmitting down radio signals, which the GPS unit receives, using signals from multiple satellites allows highly accurate positions, accurate to within a few metres. Today we can study the majority of seabird species with GPS, thanks to the continued miniaturisation of the technology.

Future developments in biologging are largely focussed on either gaining information about behaviour or the environment through which the animal moves, data which can complement the positional data. Bird-borne cameras are revealing novel behaviours, such as Thick-billed Murre foraging on fish associated with jellyfish (Sato et al. 2015), or how juvenile seabirds may follow experienced adults to foraging sites (Yoda et al. 2011). Accelerometers give detailed information on body movement, which may be used to infer energy usage (Amélineau et al. 2014) or classify whether birds are using soaring or flapping flight (Berlincourt et al. 2015, Shamoun-Baranes et al. 2016).

## Movement ecology, using biologging to inform ecology

Nearly all processes in ecology have a spatial element, and this is certainly the case for seabirds, which must decide where to breed, and daily must decide where to feed (see ’Central-place foraging’, above). These decisions are in turn made based on the external environment: Where is there a suitable island or sheltered cliff? Where are the easiest fish to catch? Can it fly against such a strong headwind? But also, on the bird’s internal state: Is it ready to breed? How are its energy stores? This broad way of considering how the movement decisions of a seabird are made up of a number of intricately linked, yet distinct components: its internal state, its motivation, and of the external environmental conditions: is unified under the term *movement ecology* (Nathan et al. 2008). The explosion of animal tracking data (Hussey et al. 2015) offers the potential to open up new avenues in ecology, but to do so requires careful consideration of the research questions to be asked (Jeltsch et al. 2013, Börger 2016) and perhaps especially in this data rich field, analytical approaches able to make sense of such complex data (Demšar et al. 2015).

In seabirds individuals' foraging decisions are made at different levels, from the decision of when to initiate a foraging trip, on where to go, then on when to stay within a foraging patch and when to move on in search of a better patch. Therefore, the analysis of seabird tracking data must be connected with environmental data which is of an appropriate spatiotemporal scale to address the scale at which a movement decision is made (Wakefield et al. 2009a). An aspect of temporal scale is predictability and persistence of foraging patches and conditions (Mueller and Fagan 2008). Under more predictable environments we may expect seabirds to rely mostly on previously acquired knowledge of their local area, whereas at intermediate levels seabirds may benefit from following conspecifics which have recent knowledge of foraging conditions, then when resources become highly unpredictable more random search strategies are likely favoured (Spiegel et al. 2017).

# Thesis aims

The movement ecology of diving and flying guillemots and gulls during breeding

The aim of this thesis was to investigate the movement ecology of seabirds, focussing on their general patterns of foraging activity, on how this activity is shaped spatiotemporally across scales, and how they vary their foraging behaviour in response to their environment: spatially (e.g. habitat), and temporally (e.g. influence of weather). This context is further used to gain more general insights into how birds use their environments, looking at how they vary their flight behaviour and how they explore their environments. Fives species are followed, four of the more closely related con-generic gulls (*Larus* spp.) and one auk species, the Common Murre. These breeding at two field sites in the Baltic Sea.

Before summarising the findings from these studies I must introduce our cast, the study species, our scenes, the two study sites, and our props, the electronic devices which will tell use so much about the movement ecology of these seabirds.

# Methods

## Study sites

The studies took place at two of the most important seabird breeding sites in Sweden, both located in the Baltic Sea (Fig. 6.). The Baltic Sea is a 'mediterranean sea' (in the oceanographic sense), being nearly completely enclosed with limited exchange of water between it and the nearby North Sea. This leads to an unusual brackish marine environment with water of progressively lower salinity going north, and also very steep gradients both horizontally and vertically in nutrients, oxygen levels, salinity, temperature, and pH (Leppäranta and Myrberg 2008). The physical oceanography is now quite well understood (Omstedt et al. 2014), and increasingly how this connects with the ecosystem too. During the 1980s, the Baltic Sea underwent an ecological regime shift from a top-down regulated system, with high populations of Atlantic Cod (*Gadus morhua*, L., 1758) and lower densities of clupeid species; European Sprat and Baltic Herring (*Clupea harengus membras*, Wulf, 1765); to a bottom-up regulated system of abundant sprat and herring, but low cod numbers (Möllmann et al. 2009). This followed from an earlier regime shift from a seal dominated system at the beginning of the 20th century (Österblom et al. 2007). The regime shift from cod to clupeids was driven by a combination of overfishing of cod and environmental changes (Casini et al. 2008, Möllmann et al. 2009) with complex interactions with human drivers (socio-economic) in the system (Lade et al. 2015). As clupeid abundance increased, following predatory release, there was greater competition for zooplankton, thus clupeid condition declined (Casini et al. 2011).

### The island of Stora Karlsö

Every year during April to July, thousands of seabirds congregate on the Karlsö islands. Stora Karlsö and Lilla Karlsö together represent one of the principle seabird breeding sites of the Baltic Sea, thus are listed as Important Bird and Biodiversity Area and Natura 2000 sites (Birdlife International 2015a, Natura-2000 2015). My research took place on the larger island of Stora Karlsö, Gotland, Sweden (57.28° N, 17.97° E) a small island (2.5 km$^2$) lying 7 km to the west of the larger island of Gotland in the central Baltic Sea (Fig. 6.). At Stora Karlsö there are large breeding populations of Common Murre, Razorbill (*Alca torda*, L., 1758), Great Cormorant (*Phalacrocorax carbo*, L., 1758), European Herring Gull, Arctic Tern (*Sterna paradisaea*, Pontoppidan, 1763), and Lesser Black-backed Gull, with smaller numbers of other species (Hentati-Sundberg et al. 2012, Hermansson and Wizèn 2014).

Stora Karlsö hosts the Auk Lab, a unique research platform; this is an artificial nesting cliff primarily developed for Common Murres, but also used by Razorbills (Hentati-Sundberg et al. 2012). It is constructed of a steel frame enclosed by oak wood with limestone slabs or shelves on the outside where the auks breed. Effectively the structure acts as an artificial cliff, with researchers able to walk through the structure 'behind' the cliff face. The Auk Lab construction (Fig. 5.) was completed in 2008, however, as it takes time for murres to recruit into a colony (Parker et al. 2007), the artificial ledges has been gradually occupied over time. This study makes use of a raised floor at the base of the structure, below which is a natural rock ledge with ca. 100 established pairs of Common Murre. Through trap-doors in the raised floor these birds could be accessed (Fig. 5.).

For the generalist foraging gulls breeding on Stora Karlsö, the large (>3,000 km$^2$) nearby island of Gotland provides potential terrestrial foraging habitat. There is an agricultural area on the nearer part of Gotland to Stora Karlsö, with arable fields where gulls may feed on earthworms and other invertebrates. In contrast to many other studies of gulls, there are no nearby open refuse sites.

## The Björn Archipelago at Fågelsundet

The Björn Archipelago at Fågelsundet, is located on the east coast of Sweden (17.72° E, 60.63° N, Fig. 6), in the northern part of the Baltic Sea and south-eastern area of the Gulf of Bothnia. Here several seabird species breed across numerous small skerries and a few islands, the whole area is ca. 5x5 km, though we only worked in the north-western part, over a few skerries spread <1.5 km apart. In the archipelago breed the following gull species (preceded by mean numbers of pairs for 2010-2014): 222 Herring — (*Larus argentatus*, Pontoppidan, 1763), 184 Lesser Black-backed — (*Larus fuscus*, L. 1758), 25 Great Black-backed — (*Larus marinus*, L. 1758), 737 Black-headed — (*Chroicocephalus ridibundus*, L. 1766), and 381 Mew Gull (*Larus canus*, L, 1758). There are also significant of terns; 86 Caspian Tern (*Hydroprogne caspia*, Pallas, 1770), 403 Common Tern (*Sterna hirundo*, L. 1758), and 582 Arctic Tern (*Sterna paradisaea*, Pontoppidan, 1763), along with waterfowl species (U. Lötberg, unpublished data, BirdLife International, 2017). The Lesser Black-backed Gull are of the nominate sub-species (*L. fuscus fuscus*, L. 1758), which breed predominantly in the Baltic Sea. Numbers of each breeding species have fluctuated over the last two decades, and breeding success is variously impacted by predation by

**Fig. 5. The Auk Lab at Stora Karlsö with inset photos of the author using a noose-pole to recapture a Common Murre with a GPS through a trap-door in the floor** (main photo: Tom Evans, inset photos ©Aron Hejdström)

introduced American Mink (*Mustela vison,* Schreber, 1777*)*, the larger gull species (Herring and Great Black-backed gulls), and more recently by White-Tailed Eagle (*Haliaeetus albicilla*, L. 1758; U. Lötberg, unpublished data). The mink have been controlled in the archipelago for more than 15 years resulting in increasing numbers of breeding seabirds with especially positive trends for lesser black-backed gulls (Roos and Amcoff 2010).

The birds studied were on archipelago islands/skerries ca. 2.5 km from the closest part of the mainland (Fig. 6B). Across the area a range of potential foraging habitat for generalist gull species. The mainland area is composed of mixed land use, with coniferous forest predominating, some areas of arable fields, and small towns and villages. Further afield are a couple of larger urban areas (cities Gävle and Uppsala, respectively 40 and 85 km distant). Across the area are several landfill/waste management centres. The marine area is composed of shallow coastal waters (mostly 1-20 m deep) around the archipelago and along the mainland coastline, with deeper offshore waters (20-50 m), around 10 km out from the coast with some shallow reefs.

## Study species

Five species of seabird are studied in this thesis, with two contributing to the majority of the studies (Common Murre and Lesser Black-backed Gull), and three further species included in one study (Mew Gull, Herring Gull, and Great Black-backed Gull). Here I will give a more detailed account for the first two species, and a shorter accounts for the three other gull species.

### Common Murre

Common Murre (Fig. 2, *Uria aalge*, Pontoppidan, 1763) are a medium sized alcid seabird (typically 800 – 1000 g). They have a circumpolar distribution, being present in the boreal to low-Arctic regions of the North Atlantic and Pacific oceans. The species has a large global population of ca. 18 million individuals, with an IUCN Red List classification of least concern (Birdlife International 2015b). However, in Europe there have been steep population declines over the last 20 years, leading to a European Red List classification of near threatened (BirdLife International 2015). Common Murres, along with the congeneric Thick-billed Murre (*Uria lomvia*, L., 1758), have become *de facto* model species in seabird biology, with over 1000 publications on the two species to date (search in Zoological record on 2017-02-23: ‘TS = "uria aalge" OR TS = "uria lomvia", Timespan: All years’. Returned 1,360 results). This provides a rich context of previous work within which to research the species and test more general theories.

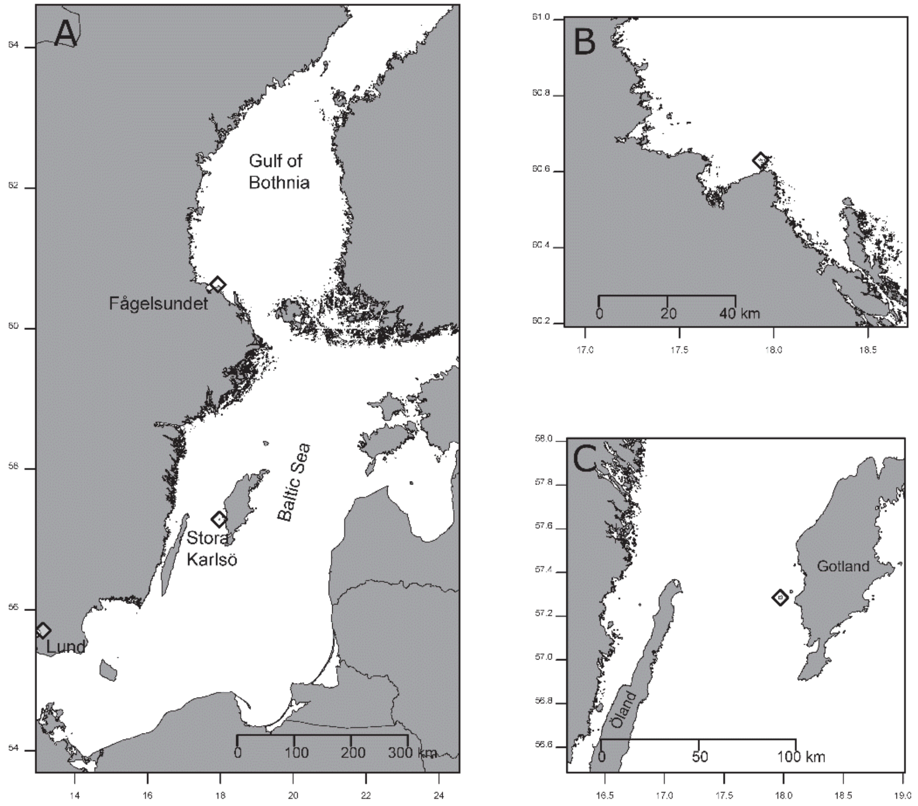

**Fig. 6. Location of study sites**
A. Large scale map showing location of both study colonies (diamonds). B & C, small scale maps of immediate area of Björn Archipelago at Fågelsundet (B) and Stora Karlsö (C)

Common Murre feed primarily on fish, which they catch by pursuit diving (Bradsheet and Brown 1985). The main prey species of the murres throughout their range are forage fish, especially clupeid species (Clupeidae, G. Cuvier, 1817) and sand lance (or sandeel, Ammodytidae, Bonaparte, 1832), plus also the youngest age classes of larger species, such as gadids (Gadidae, Rafinesque, 1810) (Buren et al. 2012, Kadin et al. 2012, Erikstad et al. 2013, Anderson et al. 2014, Gladics et al. 2015). At the study colony of Stora Karlsö clupeids are common and especially European Sprat (*Sprattus sprattus*, L., 1758) (Kadin et al. 2012). Common Murres have very high wing loading and relatively low aspect ratio wings, higher than the congeneric Thick-billed Murre (Kokubun et al. 2015), limiting them to almost exclusively flapping flight (not flap-gliding) (Pennycuick 1987). This flight style leading from their adaptation for wing-propelled diving (Watanuki et al. 2006, Elliott et al. 2013) allowing foraging at depths >100 m (Fort et al. 2013) and apparently swimming at relatively high speeds for their body mass (Watanuki et al. 2006), potentially to avoid dramatically increased drag at lower swim speeds (Watanabe et al. 2011).

Common Murres are socially monogamous and form multi-year pair bonds, with the pair occupying the same spot usually on a rocky ledge or plateau, where they lay their egg and rear the chick, this forms the smallest territory of any bird, being not much larger than a single adult murre (Harris and Birkhead 1985)! The female produces a single egg, with both parents active in incubation and chick-rearing, throughout this period the egg then chick are constantly attended (Harris and Birkhead 1985), except under extremely poor environmental conditions (Ashbrook et al. 2008). Murres are single-prey loaders, provisioning the chick by returning from foraging trips with a single fish held length-ways in their bill (Fig. 2.) (Bradsheet and Brown 1985). This provisioning style likely limits their ability to increase the rate of chick-feeding as the chick grows. Thus leading to murres' semi-precocial breeding strategy, where the chick leaves the colony while still flightless at around one third of adult weight at ca. 20 days of age, when it is attended by the male parent for a couple of months at sea (Birkhead 1977). During the winter period murres will usually move offshore to more productive marine areas, the male migrates with its chick (Birkhead 1977, Olsson et al. 1999), thus is limited to a swimming migration, whereas the female can fly. They then undergo their primary moult, during which they are flightless for a period. Common Murres typically migrate shorter distances than Thick-billed Murre, up to ca. 1000 km (Fort et al. 2013, McFarlane Tranquilla et al. 2014), with timing and destination areas consistent across years within individuals (McFarlane Tranquilla et al. 2014).

### Lesser Black-backed Gull

The Lesser Black-backed Gull (*Larus fuscus*, L., 1758) is a relatively large gull species and are sexually dimorphic in body size, with males (750 – 1000 g) typically slightly larger than females (500 – 850 g) (Olsen and Larsson 2004). The species (*L. fuscus spp.*) has a breeding distribution across northern Europe, from Iceland in the west to the White Sea in the east. Its IUCN Red List status is of *least concern*, both globally (Birdlife International 2012) and regionally on the European list (BirdLife International 2015). However, the nominate sub-species (*L. f. fuscus*, L., 1758) studied here (Fig. 7) has been under steep decline, thus is classified in Sweden as *endangered* (ArtDatabanken 2015). The species is part of the wider Herring Gull

(*Larus argentatus*, Pontoppidan, 1763) species complex. Previously this was given as a classic example of a ring species, as it has a circumpolar distribution, though genetic data now suggests that this is not the case (Liebers et al. 2004, Liebers-Helbig et al. 2010). The primarily Baltic Sea breeding sub-species, *L. f. fuscus*, has genetic support to be considered a sub-species (Liebers and Helbig 2002), with the two more western sister sub-species (*L. f. graellsii*, Brehm, AE, 1857; *L. f. intermedius*, Schiøler, 1922) less clearly separated. This is reflected in the migration of Lesser Black-backed Gulls, which winter in Iberia, north-west Africa, and along the Nile River, south to Lake Victoria in sub-equatorial Africa (Olsen and Larsson 2004). With *L. f. fuscus* mostly in east Africa and further south than *L.f. intermedius* and *L. f. graellsii* which both winter in north-west Africa and the Iberian peninsula (Kylin et al. 2011), and are increasingly resident year-round in north-west Europe (Burton et al. 2013).

**Fig. 7. Lesser Black-backed Gull of the 'Baltic' sub-species *Larus f. fuscus***
(Photo: ©Aron Hejdström)

Lesser Black-backed Gulls are colonial breeders, typically breeding in open and flat areas between vegetation, which provides shelter (Kim and Monaghan 2005, Ross-Smith et al. 2015). They breed at a much lower density than Common Murres (above), but nests are clustered within a colony (Davis and Dunn 1976, Götmark 1982). They form socially monogamous pairs, and have biparental care, with both sexes incubating and then feeding the chicks. Females lay a clutch of usually 3 eggs, though it is rare for all eggs to hatch and for all chicks to reach fledging (Harris 1964, Brown 1967, Ross-Smith et al. 2015).

Typical of other large gull species (genus Larus), Lesser Black-backed Gull are generalist predators, thus use a wide variety of habitats across their annual cycle. *L. f. fuscus*, studied here, uses mostly marine food sources during breeding (Strann and Vader 1992, Kubetzki and Garthe 2003) of which they are thought to be more reliant than other subspecies (*L. f. graeslii, L. f. intermedius*) (Götmark 1984). Gulls are also increasingly using anthropogenic food sources including fisheries discards, refuse dumps, and agricultural land (Duhem et al. 2008, Navarro et al. 2010, Tyson et al. 2015); with potential for conflict with human activities (Ross-Smith et al. 2014). Some species are apparently benefitting from these food sources, though others are not. A decline in the population of Glaucous-winged Gull (*L. glaucescens*, Naumann, JF, 1840) has been attributed to a switch in diet from marine to terrestrial food sources (Blight et al. 2015) while conversely Yellow-legged Gull (*L. michahellis*, Naumann, JF, 1840) have benefited from a greater availability of anthropogenic food sources (Duhem et al. 2008).

In common with their generalist diet, Larus gulls have a flexible flight style, having medium aspect ratio wings, allowing them to use both gliding and flapping flight (Shamoun-Baranes and Loon 2006). At sea larger gull species use primarily flapping flight (Spear and Ainley 1997) as strong rising air conditions (thermals or orographic lift) are rarely available over water.

Gulls at sea mostly forage by either taking prey directly from the surface or through shallow plunge dives (Schwemmer and Garthe 2005), though increasingly they also make use of anthropogenic sources of food, especially from fisheries discards (details above). Gulls may also forage through: commensal foraging where predatory fish drive schools of small fish to the surface, making these available to gulls (Colblentz 1985); or kleptoparasitism of seabird species that are able to access prey beyond the gulls reach (Duffy 1980), such as auks catching fish at great depths then bringing these to the surface.

In Sweden, the total population of lesser black-backed gulls of both *L. f. intermedius* and *L. f. fuscus*, was recently estimated to approximately 18,000 pairs (Ottosson et al. 2012), with the *Larus f. fuscus* sub-species predominantly breeding in the Baltic Sea with an estimated population size of 8,300 (Ottosson et al. 2012).

## Mew, Herring, and Great Black-backed gulls

The Mew Gull (or Common Gull, *Larus canus*, L. 1758) is the smallest of the gulls studied herein. They breed throughout northern Europe, Asia, to north-west North

America, though the nominate subspecies (*L. c. canus*, L. 1758) here studied is restricted to the west of this range mostly in Europe (BirdLife International 2016a, Olsen and Larsson 2004). They are not of conservation concern (*least concern*), having a large global population size and distribution (BirdLife International 2016a). They are nationally listed as *least concern* too, but have experienced a decline of 23-40% over the last 30 years (ArtDatabanken 2015). In common with the other *Larus* species, Mew Gull are sexually dimorphic in body size though less so than the other species studied here, the males (328-390 g) larger than the female (322-376 g) (Olsen and Larsson 2004). They are short to medium distance migrants, the Scandanavian breeding population wintering from southern Scandanavia to central France. They mostly forage in estuaries, in the intertidal area, on agricultural fields, and in coastal waters. Terrestrial prey include earthworms, beetles, and some vegetation (grasses and berries), intertidal/estuarine prey include crustaceans, molluscs, and polychaetes, and marine prey, fish (Götmark 1984, Kubetzki and Garthe 2003).

The Herring Gull (*Larus argentatus*, Pontoppidan, 1763) is intermediate in size between the Lesser Black-backed gull and the Great Black-backed Gull. They breed throughout northern Europe and across to Iceland (BirdLife International 2016b, Olsen and Larsson 2004). Globally they are not currently of conservation concern (*least concern*), having a large global population size, however they are declining but this is thought to be following a larger population size in the mid-20th century with the availability of refuse that is now more restricted in availability (BirdLife International 2016b). However, in Sweden they are listed as *threatened*, having had a population decline of 20-30% in the last 10 years which is expected to continue; the population in Sweden is of 61,000 pairs, with the majority (>60%) on the east coast (i.e. the Baltic Sea coast) (ArtDatabanken 2015). In common with the other *Larus* species, Herring Gull are sexually dimorphic in body size, the males (800-1500 g) larger than the female (750-1400 g) (Olsen and Larsson 2004). They are sedentary or short distance migrants, the Baltic Sea breeding population mostly winters along the southern Baltic Sea coasts and into the Kattegat and some in to the North Sea (Olsen and Larsson 2004). Like the Common Gull, they forage in estuaries, in the intertidal area, on agricultural fields, and in coastal waters, but they also forage more on anthropogenic food sources, especially refuse/landfill sites and fisheries discards both at ports and offshore (Götmark 1984, Garthe and Scherp 2003, Kubetzki and Garthe 2003).

The Great Black-backed Gull (*Larus marinus*, L. 1758) is largest of the *Larus* gulls. They breed along coastlines throughout the North Altantic, across north-west Europe, Iceland, southern Greenland, and eastern North America (BirdLife International 2016c, Olsen and Larsson 2004). Globally they have a large population size and are not significantly declining, so are not of conservation concern (*least concern*) (BirdLife International 2016c). In Sweden they are also listed as *least concern*, though the population is thought to have declined dramatically in the last 10 years by up to 50%, though there is much uncertainty in these numbers, thus they may be revised to *near threatened* in the near future (ArtDatabanken 2015). Great Black-backed Gull are the most sexually dimorphic in body size of the species studied herein, the males (1.1-2.2 kg) larger than the female (1.0-2.0 kg) (Olsen and Larsson 2004). They are sedentary or short distance migrants, the Baltic Sea breeding population mostly winters along the southern Baltic Sea coasts and especially the Kattegat and some into the North Sea (Olsen and Larsson 2004) and some migrate as far as southern Britain (author, *unpublished data*). Like the other gulls, they forage on a range of habitats including estuaries, the intertidal area, and in coastal waters, like Herring Gull they also forage on anthropogenic food sources, including refuse/landfill sites and fisheries discards both at ports and offshore, during the breeding period they can eat large numbers of eggs and chicks of other breeding birds (Götmark 1984, Garthe and Scherp 2003).

In the Björn Archipelago area the Herring and Great Black-backed gulls breed earliest, laying from early to mid-May, then the Lesser Black-backed and Mew gulls some two-weeks later from mid- to late-May.

# Instrumentation

## GPS tracking

Global Positioning System (GPS) tracking provide highly accurate location information, usually with horizontal positional errors <20 m and often <5 m. In addition to recording latitude and longitude, measurements are obtained of instantaneous velocity, heading, and altitude. In my research I have used two types of GPS devices, one a logging device where it is necessary to recapture the birds to recover the data from its tag, the other with short-range wireless radio download.

To study the foraging trips of chick-rearing murres, during June of three years (2009, 2014, & 2015) I tagged the murres with GPS logging devices (i-gotu GT-120 by Mobile Action Technology, Taipei, Taiwan). This GPS (Fig. 8.) is widely used in seabird studies as it is inexpensive and provides between 4-8 days of data depending on the GPS logging interval. The disadvantage is that devices must be retrieved.

For two years (2014 & 2015), plus a small-pilot deployment (2013), I also used UvABiTs GPS tags on some of the Common Murres. These tags provide additional data to the GPS fix, by also giving accelerometry, which can be used to infer wing-beat frequency for example.

From 2011 – 2015 I followed the year round behaviour of Lesser Black-backed Gulls at Stora Karlsö by using GPS tags developed at Amsterdam University, the UvABiTS system (Bouten et al. 2013). These devices are ca. 18 g, are solar-powered and have a short-range communication system. Using a base-station sited near where the gulls nest we were able to download data when they attended the colony, and further we could also change the configuration of the tags remotely. Thus, we could change the GPS schedule depending on the study questions. During 2012-2016, the UvABiTS system was also deployed in the Björn Archipelago, where we following four sympatrically breeding gull species.

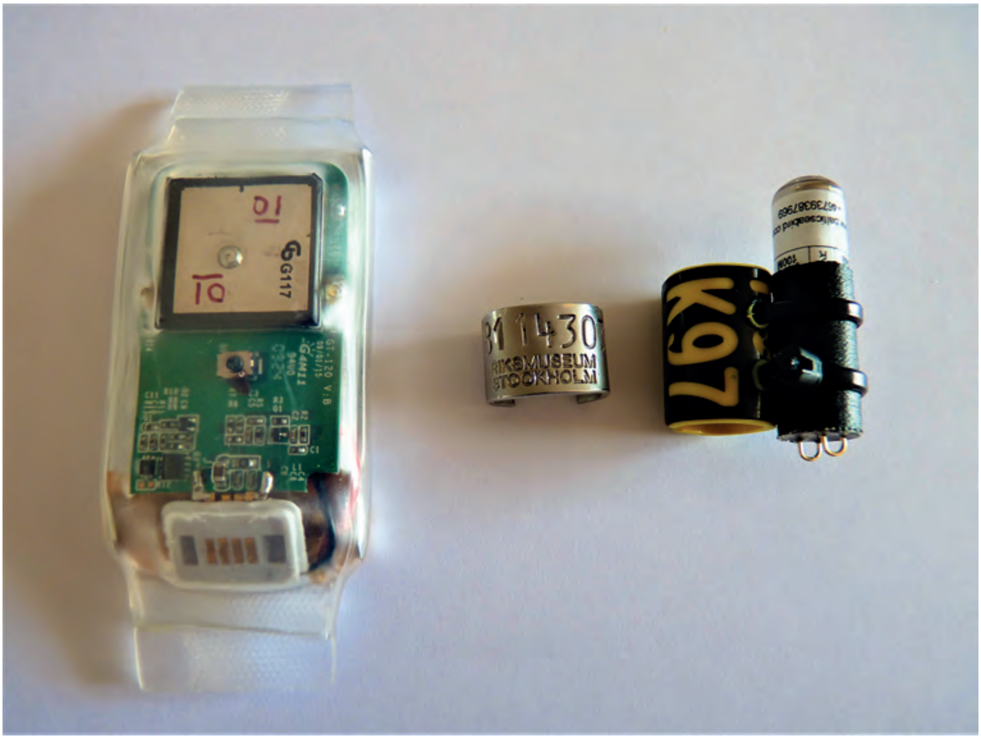

**Fig. 8. Devices used to follow the movements of Common Murre above and below the water**
GPS (left), metal ID ring (centre), and TDR together with plastic ring (right) (Photo: Tom Evans/CC BY-NC 4.0)

## Time-depth recorders (TDR)

To study the diving activity of chick-rearing Common Murre, I used TDRs (Fig. 8, model LAT 1500, Lotek Wireless, Newmarket, Canada). In addition to recording pressure over time, for detailed dive depth-time profiles, these also record temperature and wet-dry state, which together allow detailed time-activity budgets to be obtained (Linnebjerg et al. 2014). Combining deployments of TDRs and GPS on the same birds allowed the connection of dive activity with location.

## Handling and capture

I studied Common Murre during their breeding period, late April – early July, on Stora Karlsö island. At this time murres regularly attend their breeding ledge for incubation then chick guarding and brooding. For tracking studies I caught murres during chick-rearing, catching them using a noose pole (Fig. 5, constructed of a long 5-10 m fishing rod, with a noose loop of mono-filament nylon fishing-line at the end). Murres were weighed, and various biometric measurements were taken. TDR and GLS devices were attached to plastic leg-rings by cable-ties. GPS devices were attached to the back feathers using several strips of black marine fabric tape.

The gulls were studied using solar-powered remotely downloadable GPS devices (see above). Gulls were caught during incubation at both Stora Karlsö and on the Björn Archipelago islands by use of walk-in cage traps placed over their nests. As these GPS devices are solar-powered they can be deployed over the longer-term, thus harnesses were used for attachment, these were constructed of tubular Teflon™ ribbon (Bally Ribbon Mills 8476-.25") with a 1 mm braided nylon wader shelf string (British Trust for Ornithology) inserted, used  either with a wing- (2011) or body- harness (2012, 2013, 2014) (Thaxter et al. 2014). During handling various biometric measurements were taken, with gulls sexed morphologically (most were also sexed molecularly, below) by the head plus bill measurement (Coulson et al. 1983), using a colony-specific discriminant threshold of 113.5 mm (< female, > males).

The majority of murres and gulls were sexed molecularly (Griffiths et al. 1998) from either blood or feather samples taken at the time of device deployment.

## Land based observations

To study how Lesser Black-backed Gulls from Stora Karlsö used land based foraging, observations were made on an area of farmland on Gotland where the GPS data indicated the gulls visited. Ten transects of 300m were set along roadways, with fields bordering each transect surveyed. Transects were selected to include at least one field where gulls were known to have been foraging, either from direct observation (Fig. 9), or where a GPS tracked gull had been present during the preceding period, plus at least one control field where gulls had not been recorded. Fields were surveyed during

June and early July 2013, representing late incubation or early chick-rearing through to late chick-rearing. At each field on several observation occasions we counted the numbers of other bird species present while also quantifying earthworm availability. We walked along a 4x25 m gate transect at a speed of one footstep per second and counted how many earthworms were seen within a 1 m perimeter, similar to the method described in Dänhardt (2009). The vegetation characteristics of each field were surveyed during three observation periods across the season.

**Fig. 9. At dawn, two Lesser Black-backed Gull (middle distance) forage on an arable field on Gotland**
(Photo: Tom Evans/CC BY-NC 4.0)

# Results and discussion

Included in this PhD thesis are six different studies, below I summarise each discussing key findings with an illustrative figure for each [NB this section is unreferenced, the fully referenced ideas included may be found in the full papers that follow in the printed version of the thesis.]

## Paper I: Foraging behaviour of common murres in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices

The foraging trip of a Common Murre takes it from its nesting cliff on land out over the sea born by its rapidly beating small wings to a foraging site at sea, where it then uses these same wings to carry it deep below the sea surface in search of small fish. To study these foraging trips in detail we must follow the murres' movements both above and below water. As a result of the miniaturisation of biologging devices it is increasingly possible to follow multiple aspects of activity simultaneously. In this study we followed chick-rearing murres both above water with GPS, and below water with time-depth recorders (TDRs), being the first published study to acquire such detailed data simultaneously.

Foraging trips by the murres usually started with a short flight (mean distance 0.3 km), then a period sitting on the sea surface, 'splash-down', before either starting to dive or fly onto a subsequent foraging site. Several bouts of diving occurred per trip sometimes with short flights between these. The final dive bout generally occurred close to the maximum distance reached during the trip. After this final dive bout, the murres usually flew directly back to the breeding-ledge.

The murres had strong daily activity patterns (Fig. 10), with foraging trips leaving earlier in the day being of short duration (<6 h) and distance, usually 5-10 km from the colony. Trips departing in the late afternoon/evening were long duration (usually >6 h), and murres travelled out to more distant foraging sites 25-40 km from the colony. Dives showed a crepuscular pattern, with more dives made around sunset and sunrise, and dive depths were greatest around midday and least around midnight.

During the outbound flights murres usually had quite high groundspeeds, likely aided by tail-winds, but on inbound flights groundspeeds were low, likely owing to headwinds. The murres also seemed to avoid cross-winds, flying with or against the wind. Paper III looked in more detail at this.

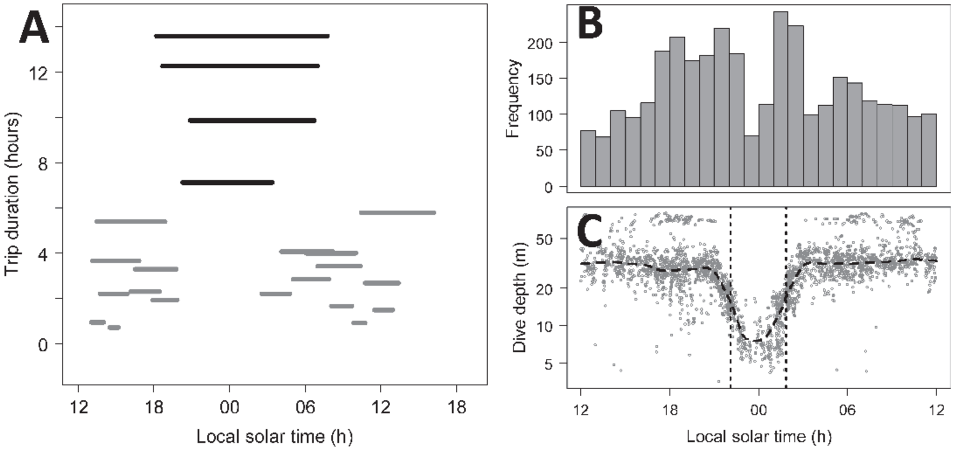

**Fig. 10. Foraging activity in common murres by time of day.**
Trip durations by trip start time (A) (n = 22), with overnight trips (black) and daytime trips (grey) indicated. Frequency of dives in one hour bins (B) and depth (log axis) of dives (C, all individual dives shown by small grey open circles) with a smooth line fitted. Local solar time (UTC+1:10) displayed, with sunset and sunrise indicated by vertical dashed lines (C). [Fig 5. of **Paper I**]

Overall, the murres appeared not to be affected by carrying the two devices (reported in supplement 2 of the paper), with breeding success unaffected, yet we did observe mass losses over the course of the device deployments. Unfortunately, as we did not have a control group for body mass, we could not be sure whether these mass losses corresponded to previously observed mass losses between incubation and chick-rearing or resulted from carrying the devices. This was the starting point for the next study (Paper II).

## Paper II: Back-mounted tags have limited effects on a flying and diving seabird

Biologging data provides researchers with rich information on the movement and behaviour of wild animals, as illustrated in Paper I. We implicitly assume that the data recorded are representative of animals without devices; yet, this assumption is rarely tested in detail. As researchers we also have an ethical obligation to minimise our impacts on the animals we study. Seabirds that both fly and dive, such as Common Murre, may be affected both during flight through air and during diving underwater.

Using the experimental approach from Paper I, we followed individual murres both carrying the small leg-mounted TDR with the larger back-mounted GPS, and with just the TDR. Using a split cross-over approach, where half the murres had the GPS and TDR in the first period then the TDR only in the second, the other half having the reverse order. This allowed their detailed, TDR recorded, activity to be compared when with and without the GPS. Concurrently, a number of control murres were studied, with their breeding success and body condition (mass) measured.

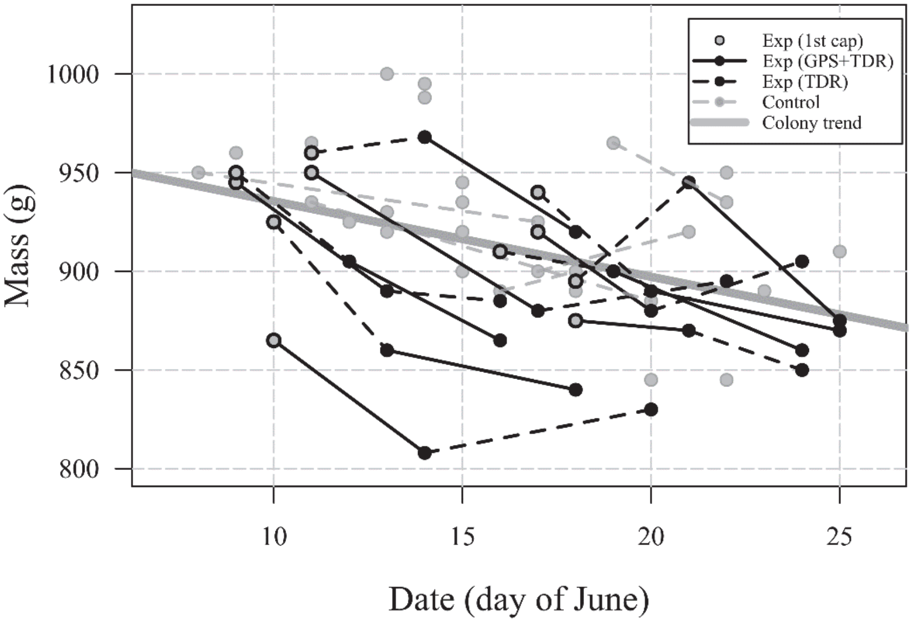

**Fig. 11. Mass changes for Common Murre across the chick-rearing period compared between murres with and without tracking devices.**
Individual masses and mass trajectories for experimental murres ('Exp', with GPS and TDR devices), and control murres (no device). The first captures of all murres were used to derive the seasonal trend in mass, with a significant reduction in mass through the chick-rearing period (linear regression line shown, grey thick-line). [Fig 2A in **Paper II**]

Breeding success was unaffected, but we did find effects on body condition. For, though all murres lost mass during chick-rearing, more mass was lost during the GPS deployments, than when with only TDR or no device (Fig. 11). This suggested that the murres were impacted in some way by carrying the GPS. However activity was largely unaffected: diving performance, time-activity budgets, and daily patterns of activity showed no changes. We did find some changes in the depth distribution of dives performed by the murres, but these results were ambiguous, differing between the two experimental groups depending on the order in which devices were deployed.

Why GPS tracked murres lost more mass is unclear, in the paper we provide some suggestions, such as through increased energy consumption during flight, or from reduced foraging performance, thus reduced energy intake rates.

## Paper III: Adaptive adjustment of flight height and airspeed in relation to winds in two morphologically distinct seabird species

For seabirds, covering long distances during foraging flights, wind can have a significant impact on the cost of travel and on their travel speeds. Empirical studies have found wind to influence foraging activity, the energetic costs of flight, and influence flight behaviour. While theoretical studies on flight optimality suggest how birds may most beneficially respond to wind conditions by altering their behaviour. Birds are predicted to alter their flight altitudes to experience more beneficial winds, and to vary their airspeeds to improve flight economy.

Common Murre and Lesser Black-backed Gull contrast in their flight mechanics. The murres have small wings, with high wing-loading, and use only flapping flight at high airspeeds. Whereas, the gulls, although of a similar mass, have much larger wings, thus low wing-loading, and they are flight generalists using both flapping and soaring flight styles with lower airspeeds. Using GPS tracking, we followed both species on their inbound flights, returning to their common colony at the end of their central-place foraging trips.

Both species adapted their flight behaviour depending on winds, but they did so differently (Fig 12). Only the gulls adjusted their flight altitude, increasing their flight height to obtain higher wind speeds under beneficial winds, but flying low, close to the sea surface where wind speeds are reduced under conditions of unfavourable winds (head-winds and strong cross-winds). The gulls and murres adjusted their airspeeds according to wind speed and direction. Interestingly, they responded both to the head-tail (assistance) and cross-wind components. Though this is theoretically predicted for flying animals, adjusting airspeed to cross-winds has only been demonstrated in a few cases.

The study raises some interesting questions about how the two species detect winds, to be able to adaptively respond to them. It may also have practical relevance in providing a more mechanistic understanding for how and why birds vary their flight heights, providing a basis for better predictive collision risk models for bird strike with aircraft or with off- and on-shore wind turbine developments.

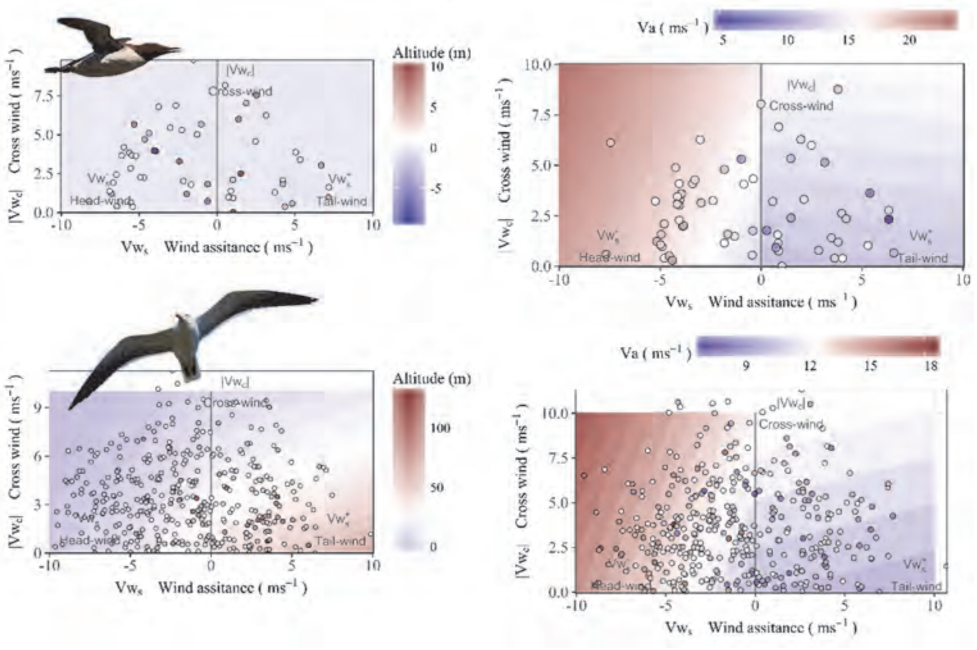

**Fig. 12. Affect of wind on flight altitude (left) and airspeed (Va, right) in GPS tracked Common Murre (top) and Lesser Black-backed Gull (bottom)**
Each plot shows model predictions for altitude and airspeed as a coloured background, with intervals of 5 m altitude (left) and 0.5 $ms^{-1}$ velocity (right). Original data are shown as coloured points, with median values for each flight plot according to the colour scales [adapted from figs. 5, 6 in **Paper III**]. Photos of two species ©Aron Hejdström.

## Paper IV: Land or sea? Foraging area choice during breeding by an omnivorous gull

The large gulls (Laridae) are well known for their dietary and habitat generalism. Many species forage both on land and at sea. In this study we investigated how Lesser Black-backed Gull breeding on an offshore island choose between land and sea foraging at three time scales: over the course of a day, across the breeding season, and over three years.

We followed individual gulls with GPS across their full breeding period and some across several years too. Achieving this with solar-powered harness mounted GPS devices. Complementing these data, for one year, we visited the main land foraging area used by the gulls. This was an area made of up of mixed-arable farmland on the large nearby island of Gotland. Within this area we made a series of road transects, making observations on fields along each transect. On three occasions around 10 days apart we visited each transect morning and evening. On each visit we noted both the composition of the fields (crop plant species, groundcover, and crop plant height) and the presence or absence of gulls.

We found that gulls made significant use of both land and sea foraging, but that this changed markedly across the season (Fig 13). Early in the season, around the time of pre-laying and incubation, >50 % of foraging trips were to land. Late in the season, in late chick-rearing/post-breeding <10 % of foraging trips were to land, most being to sea. This may suggest dietary switching by the gulls at the onset of chick-rearing, or alternatively may reflect seasonally changing foraging conditions. Our field observations give some support for the latter. Over the season, crops obviously grow! Less obviously this may impact the gulls' foraging. For they are known to forage on earthworms and other invertebrates associated with cropland. On exposed ground these can be found more easily, and additionally as gulls forage on land by walking they can be impeded by high dense vegetation. Throughout the crop-land visits gulls were more commonly observed on fields with less groundcover and shorter vegetation, and the availability of these types of field was reduced across the season.

Within days, gulls were more likely to forage on land in the early morning and under days with wetter conditions (more rainfall). This pattern is consistent with feeding on earthworms which come closer to the soil surface at night, and especially so under damper conditions.

Individual gulls varied in their tendency to forage on land or at sea, though this did not appear to vary between females and males. It does suggest some level of individual dietary specialization in this population.

The results of the study inform on how generalist species make foraging decisions, and in this declining population may also suggest that effective conservation may include management of farming practises in the area.

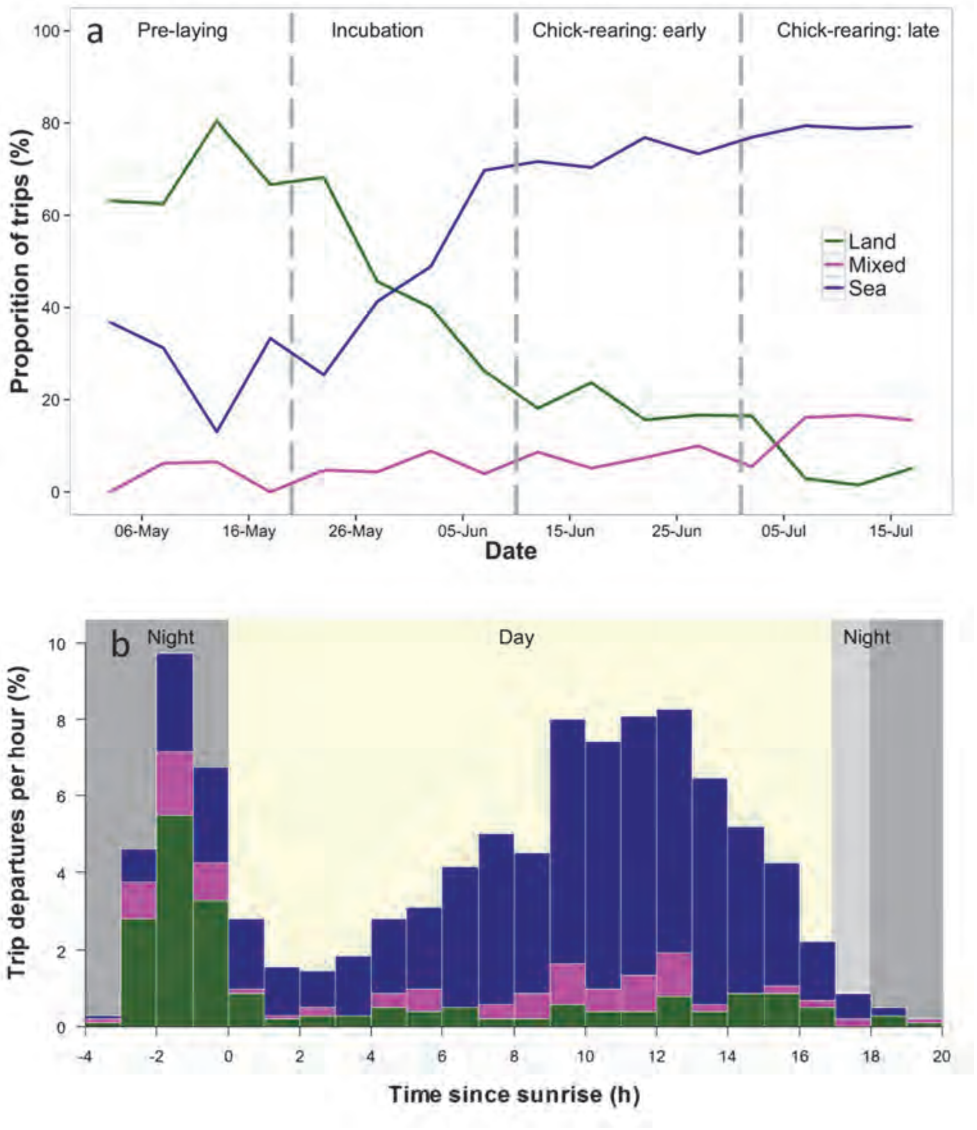

**Fig. 13. The proportion of foraging trips by GPS tracked Lesser Black-backed Gull classified as land, sea, or mixed: throughout the breeding period (a), and by time of day (b).**
(a) For each 5 day period (all 3 years pooled) with breeding stages indicated (vertical broken grey lines).
(b) Proportion of all foraging trip departures occurring each hour relative to time of sunrise for data pooled. Period of day is indicated, with night (dark grey), and day (light yellow); as the length of night was not constant throughout the study the maximum- (light grey) and minimum- (dark grey) night duration are indicated. [Fig. 4 in **paper IV**]

# Paper V: Niche sharing and partitioning during foraging among a quartet of coastal gulls

A central theme of ecology is in understanding how communities of species are structured. How do so many species live in one area? For species with apparently overlapping diets feeding at the same trophic level (i.e. members of an ecological guild) this a challenging question to answer. Add that these species are generalists foraging across a wide array of habitats on many different prey and it is harder still; this was the context for this study. On the Björn Archipelago in eastern Sweden, four gull species (Laridae *Larus spp.*) breed near together across a handful of small coastal islands. Previous studies at other sites have looked at how these species differ in their diets, habitat use, and to a lesser extent their foraging behaviour.

GPS tracking provides a very detailed view of foraging, at least with respect to activity in space and time, and more when combined with other data sources (e.g. habitat maps). From such data many different metrics can be extracted, and then compared between species. However, this also raises a challenge, for ideally we should combine these metrics to summarise the information in an ecologically meaningful way. This was the main aim for this study.

Here, we GPS tracked individuals of the four gull species simultaneously during the peak breeding period, from late incubation through to mid chick-rearing. These GPS tracks were then broken down into their constituent foraging trips. Three-types of metric were then extracted for each foraging trip for: movement and behaviour (distance travelled and time in flight), habitat (proportion of trip spent at sea/ on land), and time of day (departure times relative to sunrise and solar-noon). The variation between foraging trips in 16 metrics were then collapsed down to five common dimensions of variation (PCA), or principle components (PCs). E.g. positive values on PC3 were suggestive of foraging at sea with tortuous flight. Finally, foraging trips were grouped together (clustered) if they shared similar values across the five PCs (hierarchical clustering). The analysis suggested seven meaningful groupings of foraging trips (Fig. 14), with each potentially interpretable as a sub-niche available for foraging gulls to use in this area.

Variation within and between species in the types (i.e. clusters) of foraging trip they used were then looked at using diversity indices and overlap measures. At Fågelsundet, our analysis high-lighted interesting differences between the species in individual foraging strategies. Both Herring- and Great Black-backed gulls were species level generalists, using foraging trips from several clusters. However, this arose from different individual strategies, with the Herring Gull generalists also at the individual level. Whereas, individuals within the Great Black-backed gulls mostly performed foraging trips from just a couple of clusters (specialists), but as individuals

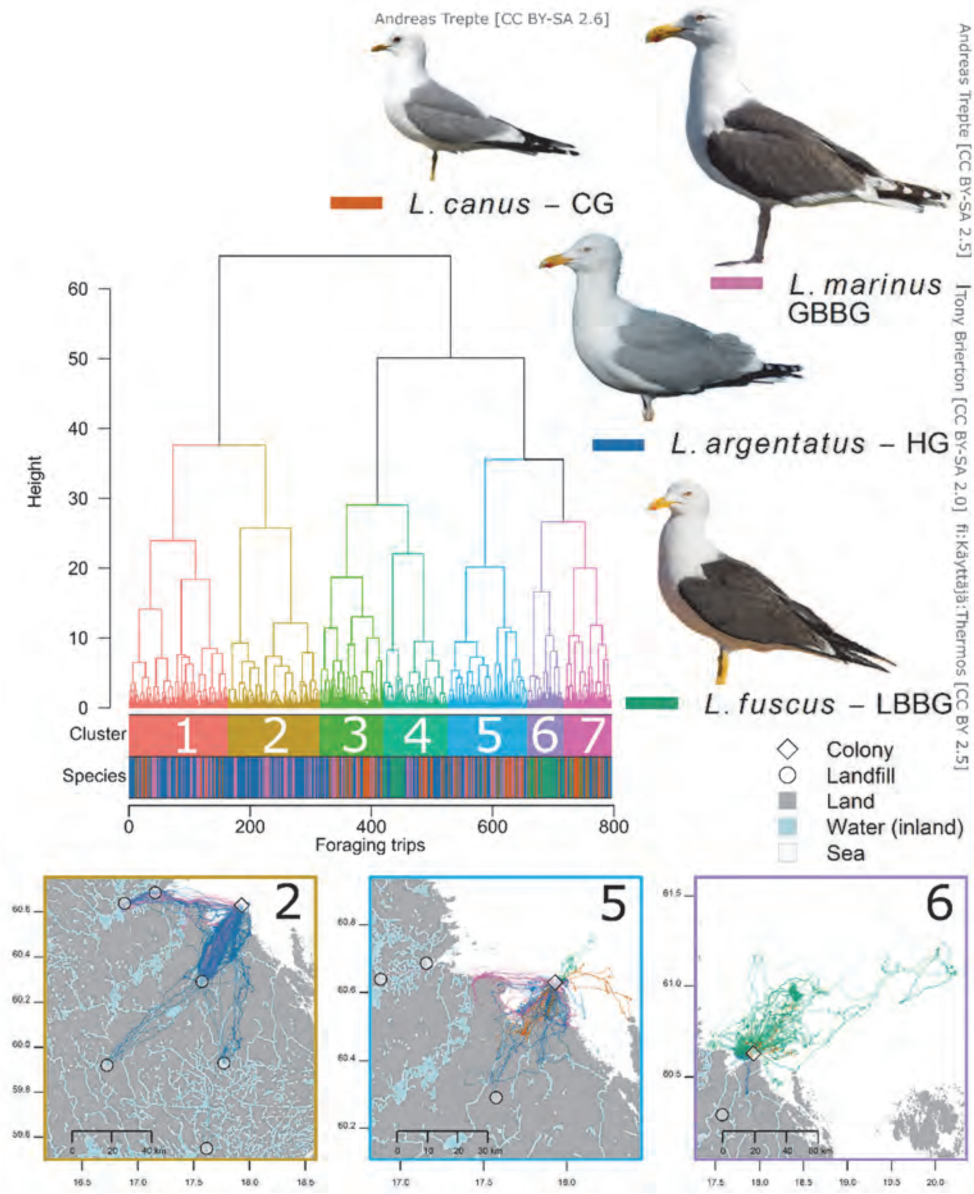

**Fig. 14. Hierarchical cluster analysis of foraging trips, showing dendrogram (top left) and three exemplar clusters mapped for four species (photos).**
The 7 clusters are indicated by colours. The distribution of foraging trips across clusters by species (see colour below each gull photo) is indicated by the lower coloured bar. Species are shown aproximately to scale, given with scientific name and abbreviated English common name). Maps (see legend) show all foraging trips (lines coloured by species) by cluster (2, 5, 6), indicating movement patterns and area use, with relative density of locations in area indicated by opacity. [adapted from fig. 2 in **Paper V**]. Photos adapted and re-used under creative commons licences (shown in margin) from commons.wikimedia.org

showed limited overlaps in the types of foraging trip performed, this resulted in a wider diversity of trip types across the species as a whole (species level generalism).

The approach developed and applied promises to be useful in quantifying shared and unique variation in foraging at different levels of organisation (individuals, populations, and species) and in revealing hidden patterns in biologging data that are ecologically meaningful.

## Paper VI: On the move for food or a new home? Long-distance return movements by Lesser Black-backed Gull during breeding

Dispersal is an important process shaping the connectivity between populations, and allowing animals to improve their breeding potential through moving to better breeding locations. For informed dispersal animals must explore potential alternative breeding sites, termed *prospecting* movements. For colonially breeding birds prospecting movements typically occur during the breeding period when the most pertinent information for breeding site selection are available: breeding success of conspecifics, availability of resting sites, and assessment of seasonal foraging conditions.

These movements have been studied through observations of individually colour/metal ringed birds. Showing, for example, that female birds and failed breeders more often make these movements. Ideally though, we should like to follow individual birds as they make these journeys, how many sites do they visit? What triggers their movements? How often do they perform prospecting movements?

By GPS tracking Lesser Black-backed Gull throughout the year with remotely downloaded, solar-powered devices (see **papers III-V**) at two separate colonies in the Baltic Sea we gained a detailed insight into the nature of these movements and under what conditions the gulls chose to make prospecting movements.

Levels of breeding success were low for both colonies (estimated <30%) suggesting poor breeding conditions, potentially owing to high rates of nest and chick predation. Gulls from both colonies made a number of exceptionally long return movements reaching maximum distances from their colonies of >150 km. A minority of these were identified as extended foraging trips visiting more distant marine areas. The majority though included visits to multiple (mean: 3, range 1-15) land locations (Fig. 15), with many of these sites visited by multiple individuals. The trips ranged over a large area encompassing a large part of the Baltic Sea. Though previous studies suggested these types of movements to be more common in females, we found no significant differences between sexes. The trips did differ between the two colonies, however, with those travelling from the northern colony on average making much longer (duration and distance) prospecting movements.

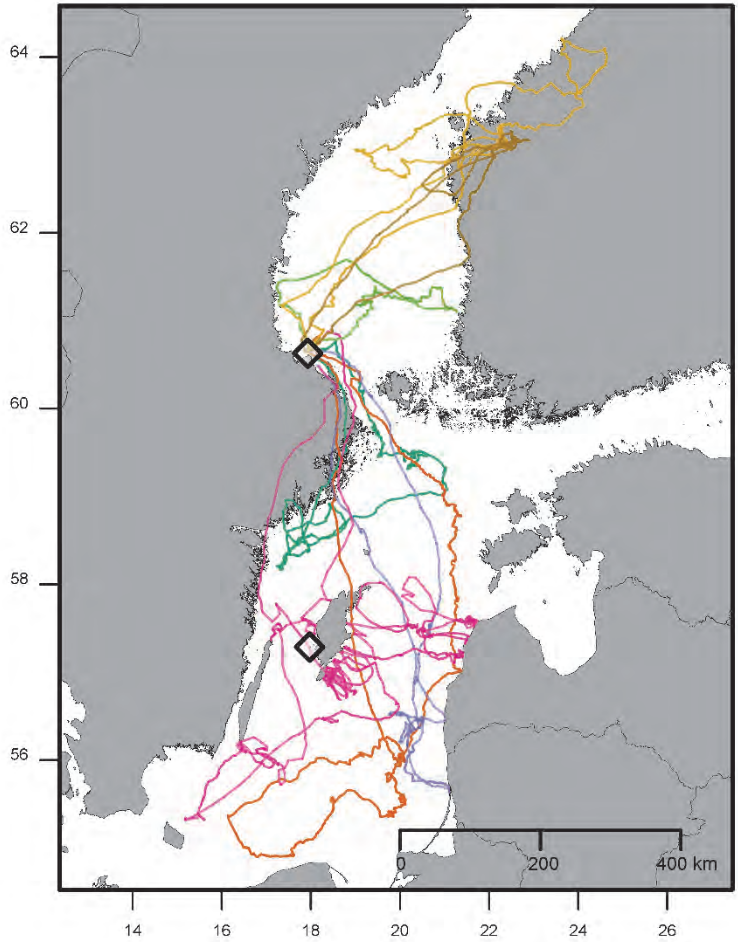

**Fig. 15. Prospecting trips by a Lesser Black-backed Gull from the northern study colony**
A female breeding at Fågelsundet (top open diamond) performing seven trips during the two years she was tracked (2014-2015), visiting a large part of the Baltic Sea including briefly Stora Karlsö (lower open diamond). Individual trips are shown in different colours. [Fig 5A from **paper VI**]

This study suggests potentially high connectivity within the threatened Baltic Sea meta-population of Lesser Black-backed Gull. It also illustrates the great potential of biologging data to allow the observation of previously opaque, yet ecologically important behavioural phenomena.

# Combined discussion and perspectives

The six studies reported herein ranged widely across the movement ecology of five seabird species. Thinking synoptically across the studies a number of general themes emerge relating to foraging ecology during breeding for central-place foraging seabirds, and more broadly for how we may use biologging data in ecology. Each study also raises its own interesting questions suggesting ideas for future studies, here I highlight one question for each paper:

Paper I. Common Murre used long overnight and short daytime trips, visiting more distant foraging areas on the long trips. Are these direct analogues of the dual-foraging strategy (Weimerskirch et al. 1994, Weimerskirch 1998) so far described mostly in the albatross and petrel species? Recent studies in auks suggest longer overnight trips may be used to visit more productive distant foraging grounds (Welcker Jorg et al. 2009, Harding et al. 2013, Jakubas et al. 2016) but how widespread this strategy is across seabirds is unclear. Do long-trips allow murres to improve their condition (self-provisioning) while losing condition on short-trips (chick-provisioning)? These predictions of a true dual-foraging strategy *sensu* Weimerskirch et al. (1994). This could be tested through using weighing platforms at the nesting site (potentially possible to implement at the Karlsö Murre Lab, Hentati-Sundberg et al. 2012), are parents heavier when returning from long trips than from the short trips?

Paper II. We found that Common Murre carrying GPS devices lost more mass than when without the device, though we found no measurable effects on activity. Why do they lose this mass? Whether they have elevated energy expenditures when carrying the tags during specific activities (e.g. diving vs. flight) could be investigated through using miniature heartrate monitors or accelerometers following the same dual-tagging approach used in this paper. Likewise, whether foraging success is affected could be investigated using stomach-temperature loggers or cameras.

Paper III. Both Common Murre and Lesser Black-backed Gull varied their flight behaviour according to winds during their inbound flights returning to their colony, thus, goal-directed flight. Do they do the same during other types of flight? E.g. outbound flights and searching/exploratory movements; during these times the cost of being blown off course is presumably lower (compared to missing their colony).

Paper IV. Lesser Black-backed Gull foraged more on land during the early breeding season, then at sea later in the season. Does this reflect changes in prey availability (external conditions) or in nutritional needs of the parent gulls/offspring (internal state)? This could be investigated by a combination of cross-fostering experiments, dietary analysis of both parents and young, and ideally by directly measuring prey availability (especially of marine prey here).

Paper V. Four gull species overlapped in their foraging behaviour, with common types of foraging trip across species. How closely do clusters of foraging behaviour correspond to more classical dietary niches? This could be investigated by combining the tracking approach used with concurrent studies of diet, from pellets or stable isotope analyses.

Paper VI. Lesser Black-backed Gull made long distance movements visiting many coastal areas, apparently prospecting for alternative breeding sites, presumably for future years. Do they maintain a 'map' of alternative breeding sites? This could be tested through tracking gulls from their first year of life over several years, testing if they repeatedly visit the same sites, and if their movements between/to these sites becomes more directed over time, indicating goal-oriented flight.

Looking across these studies, can we make some more general conclusions about seabird movement ecology?

Three of the studies (papers I, III, and IV) showed that individual foraging activity is dynamically shaped by weather conditions: wind affected how quickly murres and gulls could travel (papers I and III); while gulls chose to forage on land more under damp and cool conditions (paper IV); and both murres and gulls adapted their flight behaviour to improve their cost of transport (distance travelled per unit energy) as wind conditions varied (paper III). These add to a growing body of results: showing how wind conditions can increase (Gabrielsen et al. 1987, Elliott et al. 2014) and decrease (Furness and Bryant 1996, Amélineau et al. 2014) energy expenditure during the flight of seabirds, and thus that wind may affect foraging decisions (Weimerskirch et al. 2012, Lewis et al. 2015, Pistorius et al. 2015).

Using biologging devices, and especially GPS we follow how animals move spatially and how their movements vary over time, i.e. spatiotemporal activity. Three of the studies in the thesis (papers I, IV, V) showed that foraging activity can be best understood when looking at spatiotemporal patterns in movement, rather than e.g. looking in isolation at the timing of foraging trips, or only where birds forage. Common Murre varied both where they foraged by time of day and how they foraged (paper I), travelling further on longer overnight trips than in shorter daytime trips (see question for paper I above) and diving shallower and more frequently around sunset and sunrise than in the middle of the day. Lesser Black-backed Gull varied how much they foraged on land rather than at sea across three temporal scales (paper IV), doing so more in some years than others, more frequently at the beginning of the breeding season, and more often on foraging trips performed early in the day than those with later departures. Similar results for daily activity patterns were shown for four gull species (paper V), these suggesting that certain types of habitat were used by multiple species at the same times of day, this indicative of foraging on a common prey or food source showing daily variation in relative availability (to alternative prey/food). Biologging is thus allowing researchers to revisit some earlier results on how the spatiotemporal patterns of birds and their prey are linked (Sibly and McCleery 1983, Piersma et al. 1988) but this time we can follow the activity of individual animals over time. Future studies will increasingly be able to track both predator and prey, which a few marine studies have already achieved in showing how predators vary their foraging decisions in response to prey density and distribution in the water column (Hazen et al. 2015, Cimino et al. 2016).

As discussed biologging is giving researchers many new insights into the movement ecology of seabirds. However, it is still important to consider the impacts on study animals, from both a welfare perspective, and from a scientific perspective – i.e. are we measuring ‘natural behaviour’? The activity of Common Murre did not appear much affected by carrying back-mounted GPS devices (paper II), though a review of previous studies (also in paper II) suggested there may be device effects. We did not investigate device effects in the gulls, though this has been studied elsewhere (Thaxter et al. 2014, 2015), suggesting minimal effects on survival and reproduction. That biologging gives really novel insights was shown nicely in the final study (paper VI), where we observed a key aspect of population ecology, how animals choose to disperse and how they collect information to inform these movements, when we tracked the remarkable prospecting movements of Lesser Black-backed Gull.

What next for biologging? A continuing challenge for biologging science is how we best exploit the rich possibilities of these new data to address ecological questions (Jeltsch et al. 2013, Demšar et al. 2015, Börger 2016). How should the analysis of the data keep up with the pace of technological development? One aspect of this is to combine biologging data with complementary data on aspects affecting the movement of animals, e.g. to investigate relatively fine-scale behavioural responses to wind conditions during flight (paper III), or of weather conditions on foraging area choice (paper IV). A further challenge is of the complexity and quantity of data now collected, often with many potential variables, e.g. for a foraging trip: the habitat used, the time spent in flight, and the time of day (paper V). We can analyse different components separately, but by combining multiple components into a single analysis we can get a fuller picture of how these operate together. One promising approach is to use clustering or similarity analyses, i.e. the grouping of data by those sharing common properties. There are several ways to do this, usually either clustering by similarity in summary metrics (Louzao et al. 2014, Orben et al. 2015), or to find repeated or similar sequences of behaviour (De Groeve et al. 2016). Using the clustering and data summary approach we looked at how four species of gull varied in the types of foraging trip they performed, and to what extent different types of foraging trip were common across species (paper V).

A great strength of biologging studies is that they can follow individual animals in great detail, but this is also perhaps the biggest challenge for biologging, how to scale back up from individuals to populations. On Stora Karlsö >3,000 Common Murre chicks are ringed each year; in a productive year we will tag just two-orders of magnitude fewer adults with tracking devices! However, following individuals can give insights into how they respond to changes in their environment at the small scale, which can indicate possible mechanisms for population and species level responses to larger scale climate or environmental change (Weimerskirch et al. 2012, Frederiksen et al. 2016), which has been termed environmental demography (Frederiksen 2014). Through tracking over longer time periods, e.g. using solar-powered harness-mounted GPS tags (papers III-VI), we can investigate how foraging changes over the season and across years (IV). Tracking over longer time periods can also reveal rarer movements beyond foraging and migration, such as the prospecting movements (paper VI) which may anticipate breeding dispersal, thus are important in understanding meta-population dynamics.

Most biologging studies follow animals from just one population, or species, including half of the papers (papers I, II, IV) in this thesis! However, clearly many important ecological processes occur above these levels, with interactions between species (paper V, Wilson 2010, Conners et al. 2015), or between populations within a species (paper VI, Hunt, and Hunt 1973, Kubetzki and Garthe 2003, Wakefield et al. 2013). I followed Lesser Black-backed Gull at two sites (papers III-VI), looking into their foraging ecology (papers IV and V), interestingly there were differences between the two sites, gulls from the northern site (Björn Archipelago) exploited nearly exclusively marine resources, while those from the southern site (Stora Karlsö) used both terrestrial and marine habitats. This may suggest greater inter-specific competition at the northern site, where more gulls occur in sympatry, leading to niche segregation, but it may also reflect better availability of marine prey at the northern site. Alternatively, there may be more competition among fish-eating seabirds at the southern site, for here many thousands of the fish-specialist Common Murre and Razorbill breed, thus the more generalist Lesser Black-backed Gull may be displaced to forage on alternative prey. Further investigations will be needed to determine which of these potential mechanisms are responsible.

It is an exciting time to work in ecology, and especially seabird ecology, as these new biologging tools continue to improve, making it possible to revisit old and new questions, and of course to ask new questions too!

**The author with a Lesser Black-backed Gull with a GPS** (Photo: ©Linda Takahashi)

# Tack! Thanks! Diolch! የቐንየለይ Merci!

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# Across landscapes and seascapes

I Evans, T.J., Kadin, M., Olsson, O., and Åkesson, S. (2013). Foraging behaviour of common murres in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices. *Marine Ecology Progress Series* 475, 277–289.

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