Gull over-travels?

Consequences of diverse migration strategies in a generalist seabird

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Publication date
2022

References

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Summary

Samenvatting

Aknowledgements

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Chapter 2. Long-distance migrants vary migratory behaviour as much as short-distance migrants: an individual-level comparison from a seabird species with diverse migration strategies

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JMB, JSB and WB conceived the idea for this study. CJC, LL, WM, CT, and JSB led the tracking projects. JMB analysed the data under consultation with EvL. JMB wrote the manuscript. All authors provided comments on the manuscript.

Chapter 3. Acceleration as a proxy for energy expenditure in a facultative-soaring bird: comparing dynamic body acceleration and time-energy budgets to heart rate

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JMB, JSB and WB conceived and led the study. CJC helped design and facilitated data collection in the field. BAN facilitated data collection in captivity and advised on data analysis. JMB analysed the data and wrote the manuscript. All authors provided comments on the manuscript.

Chapter 4. Migrating further does not affect annual energy expenditure but increases variation in daily energy expenditure in lesser black-backed gulls

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Chapter 5. Equal survival and reproductive parameters between short- and long-distance migrating lesser black-backed gulls

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All authors conceived the idea for this study. CJC leads the ongoing monitoring work on Texel. CJC and RK conducted field work, CJC managed the colour-ring database. JSB assisted with GPS tracking. RK led the analysis, with contributions from JMB. JMB led the manuscript writing, with contributions from RK. All authors provided comments on the manuscript. * JMB and RK contributed equally to this work and share co-first authorship.

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Summary

Geese honking overhead, filling the sky with their characteristic chevron flight formations. A river turned pink with salmon on their terminal trip to their freshwater spawning grounds. The thunder of hooves from a line of wildebeest crossing the savanna, looking for greener pastures. Migration, the directed movements of animals between two or more distant habitats or regions, is a widespread phenomenon within the natural world. The distances animals cover by walking, flying or swimming during migration can be great, and they often move in large numbers, either together or separately. Animal migrations herald the change of seasons, they are beautiful, they are epic.

Why do animals migrate? Many animal migrations are linked with seasonal changes in weather, which in turn causes predictable increases and decreases in food availability. Seasonal migrations allow animals to move into areas with seasonally fluctuating environments during the part of the year when food is plentiful and the weather is nice. Animals often breed in these areas, which provide abundant food, potentially allowing a parent to raise and feed more young. The return migration journey then allows animals to retreat when weather deteriorates and food becomes scarce, conditions which may decrease their chances of surviving if they remained.

While animals can clearly benefit by following these seasonal changes in food and weather, there are also disadvantages to migrating. Animals must use a lot of energy to travel between distant areas. Migrating takes time away from other tasks they need to carry out. These journeys can also be dangerous. Animals may run out of energy. Predators congregate along migration corridors. Storms may interrupt birds trying to cross water or deserts, while roadways or dams may block the pathways of animals that walk or swim. These so-called costs are likely to increase the further an animal migrates.

How far then, and to where, should an animal migrate? Ideally, animals should move between areas that maximize the benefits they receive by migrating while minimizing the costs. Calculating how much an animal may gain or lose by migrating between two areas is, however, not a simple task, and the results may be difficult to predict. This is because these costs and benefits can interact with each other and change throughout the year. For example, while an animal may use a lot of energy migrating, this could be offset by not having to use as much energy to stay warm during the winter. Or, the increased chance of surviving the winter gained by migrating may come at the cost of fewer breeding opportunities if migrants are delayed when returning to their summer breeding areas.

The main aim of this thesis is to understand how the decision of where to migrate (which I call a 'migration strategy'), influences the costs, benefits, and challenges an animal faces while migrating. One way of calculating the costs, benefits and challenges of

using different migration strategies is to measure and compare them between individuals from a single population that migrate to different areas. One species which has a lot of variation among individuals in their migration strategies is the lesser black-backed gull (Latin name: *Larus fuscus*). Within breeding colonies in the Netherlands, you can find lesser black-backed gulls nesting side-by-side that range from short-distance migrants traveling 250 km to winter in the UK, to individuals that migrate over 4500 km to West Africa. For 15 years we have been following the migratory journeys of lesser black-backed gulls by attaching GPS loggers to their backs, as well as monitoring their survival and breeding attempts. This creates an opportunity to measure the consequences of different migration strategies in the natural world.

To begin, it is useful to know whether an individual always migrates to the same place, or whether they can change their strategy year-to-year. We answer this question in **Chapter 2**, using GPS tracking data from gulls that have been followed for multiple years. As well as looking at whether gulls can change their migration strategies, we examine how much they change their behaviour within a migratory journey across years, such as when they depart and arrive on migrations, the routes they follow, and whether they roost and forage in the same areas within their winter region. These are important decisions to make, because the better an animal can match their migratory movements to patterns of food and weather in a given year, the more they can benefit from their migration journeys.

The information animals use to make these decisions may depend on how far they migrate. Because short-distance migrants have winter ranges near to their breeding range, these areas are likely to be influenced by similar weather systems. This means short-distance migrants can use information in their current area to predict what conditions may be like at their destination, resulting in behaviour that changes among years. Long-distance migrants, on the other hand, being further from their destination, are more likely to experience separate weather systems. Disjunct weather between breeding and wintering areas makes predicting future and distant conditions unreliable, and instead it may be safer for long-distance migrants to move based on averages of past weather conditions. This would results in long-distance migrants having very little variation in their migratory behaviour across years. Concern has therefore been raised regarding whether long-distant migrants will be able to change their migratory behaviour alongside our rapidly changing climate.

In **Chapter 2** we found that over-all gulls were inclined to behave similarly across years, with an individual tending to migrate around the same time, using a similar route, and moving to the same area. However, we also found a few exceptions for each trait we examined. This included a handful of individuals that completely changed their migration strategy. Importantly, behavioural variability was not linked with migration distance, and different individuals were often among the most variable for each of the different traits we examined. This leads us to believe that any individual could behave flexibly if required, though their preference is to use strategies that they have used in the past.

Next we wanted to examine the energy and time costs of using different migration strategies. Alongside taking GPS positions, our trackers also measure body movement patterns in three dimensions (forwards, sideways, and vertically), using accelerometers. These patterns can be used to identify whether a gull is flapping, soaring, walking, floating on water, or resting. Because it takes energy to make these movements, adding up the acceleration over a recording segment, called dynamic body acceleration, might also enable us to estimate how much energy the gull was using at that time. First, we needed to figure out how much energy expenditure increases for every increase in dynamic body acceleration. We also needed to determine whether this conversion is the same across the different types of movement modes gulls use. We study this in **Chapter 3**, by measuring acceleration alongside heart rate, a more familiar method of estimating energy expenditure. We found that both heart rate and acceleration showed similar increases and decreases across most movement types. However, acceleration while floating was higher than while resting, whereas heart rate indicated energy expenditure was similar among these behaviours. However, this is likely because acceleration also detects movement from waves (which does not cost a gull any extra energy). We also compared different ways of estimating daily energy expenditure using accelerometers, by either averaging patterns of acceleration over the day, or by creating a time-energy budget, where the proportion of time an animal spends in a behaviour is multiplied by the average energetic cost of that movement type and summed over the day. Both methods produced similar results, though each underestimated daily energy expenditure on days with higher resting heart rates, and overestimated on days with lower resting heart rates. This shows that acceleration methods may miss some changes in daily energy expenditure that are the result of changes in resting metabolic rate (such as energy needed to maintain body temperature, digest food, fight an infection, or grow new feathers), which cannot be detected by movement alone.

In **Chapter 4,** we applied the acceleration method to tracking data of migrating gulls, to estimate how much energy they spend on movement-related activity throughout the year**.** We combined the acceleration estimates of energy expenditure with a heat-exchange model that estimates the energy needed to stay warm based on the weather the individual was experiencing in its location. We found that the total amount of energy used by gulls during the year was on average equal across different migration strategies. However, individuals within the same strategy could differ a lot from each other in how much energy they used. We also found that, for short-distance migrants, energy expenditure was rather constant through time, whereas long-distance migrants had periods of the year where they had high energy expenditures, while during other periods they had below-average energy expenditure. Next, we divided the year into different stages, including breeding, migrating, stopover (days during the migration period when birds aren't actively moving towards their destination), and winter. Energy use was highest during late breeding and on migration flights, and lowest during winter, as well as on long-autumn stopover where gulls are likely replacing their body feathers (an extra energy costs we didn't account for). Gulls changed their behaviour in similar ways during each of these stages, regardless of their migration strategy. For example, they increased their time in flight while breeding, spent more time walking during autumn, and reduced movement activity during winter.

Energy expenditure and time allocation may contribute towards an individual's survival and reproductive outputs. Combined, these traits determine the contribution of an individual's genes to the next generation, and determine the growth rate of a population. In **Chapter 5** we examine whether a gull's migration distance influences when they lay their eggs, the size of their eggs, and the probability of those eggs hatching, all traits which can influence their reproductive output. We also looked at whether migration distance influences survival probability, using reported observations of colour-coded rings on winter areas as well as in the breeding colony. We found no effect of migration distance on reproductive traits or survival, suggesting migration strategy does not result in any fitness consequences or trade-offs.

It is remarkable that a 20-fold increase in migration distance, as well as spending the winter in regions that range from cold Britain, where birds forage at garbage dumps and on pig feed, to the rice field and cities of Spain, versus the sunny beaches of Africa where surface-feeding fish can be caught throughout the winter, seemed to have little influence on any of the properties we studied. Most of our understanding and assumptions relating to the costs, benefits and challenges of migrating stems from work on smaller avian migrants, which have specific food preferences and are more susceptible to harsh weather. Gulls, however, are a very different type of animal. They have learned to forage on a variety of different food types, including fish (often from fisheries), insects (often in agricultural fields), and human waste. This provides them with many foraging alternatives in the face of unexpected changes to their landscape. They are large, well-insulated birds, making them more robust in the face of winter weather. Gulls can also rest on both water or land, which may lessen the survival risks of migrating. What we can take away from this is that migration does not always present a cost. Through their behavioural flexibility, gulls could adjust to the different challenges presented by their respective migration strategies, allowing them to manage their time and energy budgets throughout the year, and providing them with equal chances of surviving and reproducing when they return to their colonies. By carrying out research on less 'traditional' migratory species, we obtain broader insights into the limits posed by migrating as well as how animals can overcome them.

Samenvatting

Translated by Dr. Marwa Kavelaars

Ganzen vliegen gakkend over, de lucht vullend met hun typerende V-formatie. Een rivier kleurt roze door de zalmen die op weg zijn naar het paaigebied, hun laatste bestemming. Hoeven klinken donderend door de Savanne, van gnoes op zoek naar groener land. De trek van dieren tussen twee of meer verre habitats, oftewel migratie, is een wijdverspreid fenomeen in de dierenwereld. De afstanden die dieren vliegend, zwemmend of lopend afleggen kunnen enorm zijn, en ze bewegen zich vaak in grote aantallen voort, samen of alleen. Migratie kondigt op een mooie en epische manier de verandering van de seizoenen aan.

De vraag is waarom dieren migreren. Migratie is vaak gelinkt aan seizoensgebonden veranderingen in het weer, die op een voorspelbare manier invloed hebben op de voedselbeschikbaarheid. Door migratie kunnen dieren verkassen naar gebieden waar de weersomstandigheden op dat moment beter zijn en er genoeg voedsel is. Vaak planten ze zich in die gebieden voort omdat de grote beschikbaarheid aan voedsel de ouders in staat stelt om meer jongen groot te brengen. Wanneer de (weers-)omstandigheden vervolgens verslechteren en er minder voedsel te vinden is, kunnen ze weer verder trekken of terug migreren, daarmee hun overlevingskansen vergrotend.

Dieren hebben duidelijk profijt van het meebewegen met de seizoensgebonden veranderingen in het weer en de voedselbeschikbaarheid, maar er zijn ook nadelen aan migratie. Van het ene naar het andere gebied trekken kost veel energie, met eventueel uitputting tot gevolg. Bovendien kunnen tijdens deze lange reis andere belangrijke taken niet uitgevoerd worden en ligt er veel gevaar op de loer. Zo komen roofdieren samen op belangrijke knooppunten van trekroutes en bemoeilijken stormen de oversteek van vogels over de zee of woestijn, terwijl wegen of dammen de paden van lopende of zwemmende dieren blokkeren. De kosten die met al deze hindernissen gepaard gaan zullen waarschijnlijk toenemen naarmate de afstand groter wordt.

Hoe ver en waarheen moeten dieren dan migreren? Idealiter zouden ze tussen gebieden trekken die zo voordeling mogelijk voor hun zijn, terwijl ze de kosten zo laag mogelijk proberen te houden. Berekenen hoeveel voordeel er uit trek gehaald kan worden, is echter geen gemakkelijke taak en het is vooraf moeilijk te voorzien wat het resultaat zal zijn. Er is namelijk een wisselwerking tussen de kosten en de baten, die ook nog eens verandert door het jaar heen. Migreren vereist bijvoorbeeld veel energie, maar waarschijnlijk minder dan de hoeveelheid die nodig is om in de winter warm te blijven in een koud gebied. De kans om de winter te overleven is groter in een gebied met een milder klimaat, maar de afstand naar het broedgebied is dan soms zo groot dat er in geval van vertraging onderweg bij aankomst minder broedplekken over zijn.

Het doel van dit proefschrift is om te begrijpen hoe de keuze van een dier om naar een bepaald gebied te migreren (vanaf nu ‘migratiestrategie’) invloed heeft op de kosten en baten van migratie en de uitdagingen die daarmee gepaard gaan. Een manier om de kosten, baten en uitdagingen van verschillende migratiestrategieën te bepalen is om deze te berekenen en te vergelijken tussen individuen die naar verschillende gebieden migreren. De Kleine Mantelmeeuw (*Larus fuscus*) is daar uitermate geschikt voor door de grote variatie aan migratiestrategieën tussen individuen. In de broedkolonies van Nederland kun je individuen vinden die korte afstanden afleggen, bijvoorbeeld 250 km naar het Verenigd Koninkrijk, maar ook vogels die 4500 km naar West-Afrika vliegen. Gedurende 15 jaar hebben we deze Kleine Mantelmeeuwen gevolgd met behulp van GPS trackers, terwijl we ook hun overleving en broedpogingen volgden. Dit stelde ons in staat om de consequenties van de verschillende migratiestrategieën te bepalen.

Om te beginnen is het nuttig om te weten of individuen altijd naar dezelfde plek migreren of dat ze hun strategie van jaar tot jaar kunnen aanpassen. Dit wordt uitgezocht in **hoofdstuk 2** met behulp van GPS data van meeuwen die meerdere jaren gevolgd zijn. Naast dat we bestuderen of meeuwen hun migratiestrategie kunnen aanpassen, onderzoeken we ook hoeveel hun migratiegedrag verandert tussen verschillende jaren, bijvoorbeeld de timing (wanneer ze vertrekken en aankomen), de routes die ze volgen en of ze op dezelfde plek slapen en foerageren in het overwinteringsgebied. Dit zijn belangrijke keuzes, want hoe beter dieren hun verplaatsingen kunnen aanpassen aan de weersomstandigheden en de voedselbeschikbaarheid, hoe meer voordeel ze uit hun migratie halen.

De informatie die dieren gebruiken om deze keuzes te maken hebben mogelijk te maken met de afstand die ze moeten afleggen. Korte-afstandsmigranten blijven in de winter in de buurt van hun broedgebied, waar de omstandigheden waarschijnlijk door hetzelfde weersysteem beïnvloed worden, terwijl dit bij lange-afstandsmigranten niet het geval is. Als de weersomstandigheden in het broed- en overwinteringsgebied niet aan dezelfde veranderingen onderhevig zijn, is het moeilijk om op afstand een inschatting te maken van de situatie op de bestemming. Voor dieren die ver migreren zou het daarom veiliger kunnen zijn om uit te gaan van de gemiddelde weersomstandigheden in het verleden, met als resultaat geringe variatie in migratiegedrag tussen verschillende jaren. Dit zou echter kunnen betekenen dat lange-afstandsmigranten zich onvoldoende kunnen aanpassen aan snelle veranderingen in het klimaat.

In **hoofdstuk 2** vonden we dat meeuwen over het algemeen elk jaar hetzelfde gedrag vertonen. Individuen migreerden rond dezelfde tijd, gebruikten dezelfde route en hadden dezelfde bestemming. Er waren echter ook een paar uitzonderingen. Enkele individuen veranderden hun migratiestrategie zelfs compleet. Variabiliteit in gedrag was niet gerelateerd aan de migratieafstand, en voor ieder gedrag dat we onderzochten, waren het weer andere individuen die het meest variabel waren. We kwamen daarom tot de slotsom dat individuen zich flexibel kunnen gedragen wanneer dat nodig is, maar dat ze de voorkeur geven aan een strategie die ze in het verleden hebben gebruikt.

Vervolgens wilden we onderzoeken hoeveel energie en tijd de verschillende migratiestrategieën kosten. Naast GPS posities, leggen de trackers die de meeuwen bij zich dragen met behulp van een versnellingsopnemer ook hun bewegingen in drie richtingen vast (voorwaarts, zijwaarts en verticaal). Deze bewegingspatronen kunnen gebruikt worden om een indruk te krijgen wat de meeuw doet: met de vleugels slaan, zweven, lopen, dobberen of rusten. Al deze bewegingen kosten energie, en door de versnellingen in de drie richtingen tijdens zo'n opnamemoment bij elkaar op te tellen (vanaf nu 'dynamische lichaamsversnelling') kunnen we een inschatting maken hoeveel energie een meeuw op dat moment verbruikt. Daarvoor is het belangrijk om er eerst erachter te komen hoe het energieverbruik verhoogd wordt met iedere verhoging in dynamische lichaamsversnelling en of dit hetzelfde is voor alle verschillende bewegingen die een meeuw maakt. We bestuderen dit in **hoofdstuk 3** door naast versnelling ook de hartslag van meeuwen te meten, een veel gebruikte methode om een inschatting te maken van het energieverbruik. Tijdens de meeste bewegingen hadden de hartslag en versnelling dezelfde toename. Echter, tijdens het dobberen op zee was de versnelling hoger dan tijdens het rusten, terwijl de hartslag op hetzelfde energieverbruik wees. Dit kan verklaard worden doordat de versnellingsopnemer ook bewegingen vastlegt die door de golven van het water worden gemaakt, terwijl dat deel geen extra energie kost. We vergeleken ook verschillende manieren om met de versnellingsopnemer een inschatting te maken van het dagelijkse energieverbruik. Ten eerste kan dit bepaald worden door het gemiddelde te nemen van alle versnellingen over een dag. De tweede manier is door een tijd-energie budget te berekenen, waarbij het aandeel van de tijd waarin een bepaald gedrag vertoond wordt, te vermenigvuldigen met de gemiddelde energetische kosten van dat gedrag, en dat vervolgens voor de gehele dag bij elkaar op te tellen. Beide manieren kwamen uit op hetzelfde energieverbruik, maar ze geven allebei een onderschatting van het dagelijkse energieverbruik op dagen met een hogere rusthartslag, en een overschatting op dagen met een lage rusthartslag. Dit toont aan dat de berekeningen op basis van versnelling misschien kleine veranderingen missen in het dagelijkse energieverbruik die te maken hebben met het rustmetabolisme (bijvoorbeeld het warm houden van het lichaam, ruien, afweersysteem of voedselvertering) en dus niet met bewegingen gedetecteerd kunnen worden.

In **hoofdstuk 4** hebben we de versnellingsmethode toegepast op de tracking data van de migrerende meeuwen om te bepalen hoeveel energie ze spendeerden tijdens activiteiten gedurende het hele jaar. We combineerden de schattingen van het energieverbruik, die bepaald werden door middel van versnelling, met een *heat-exchange* model dat een schatting geeft van de energie die nodig is om warm te blijven bij de weersomstandigheden waarin de meeuw zich bevindt. Het totale energiegebruik was over het algemeen vergelijkbaar tussen meeuwen met verschillende migratiestrategieën. Onderling kon er echter een groot verschil zijn tussen individuen met dezelfde strategie. Daarnaast vonden we dat korte-afstandsmigranten een redelijk constant energieverbruik hadden, terwijl lange-afstandsmigranten tijdens sommige periodes een hoger energieverbruik hadden en op andere momenten juist een lager dan gemiddeld energieverbruik. Vervolgens verdeelden we het jaar in verschillende fases: broedperiode, migratie, stopover (dagen tijdens de migratieperiode waarop individuen zich niet actief verplaatsen naar hun bestemming) en overwintering. Meeuwen gebruikten de meeste energie aan het einde van het broedseizoen en tijdens de migratievluchten, en het minste tijdens de winter en de lange stopovers in de herfst wanneer ze hun veren ruien (de energie die ze hiervoor gebruiken hebben we niet meegerekend). Ongeacht welke migratiestrategie meeuwen hadden, veranderden ze hun gedrag op dezelfde manier in al deze fases. Zo spendeerden ze allemaal meer tijd vliegend tijdens de broedperiode, liepen ze meer in de herfst en hadden ze minder bewegingsactiviteit in de winter.

Hoeveel energie verbruikt wordt en hoeveel tijd een individu besteedt aan bepaalde gedragingen kan invloed hebben op de overlevings- en voortplantingskansen. Samen bepalen ze hoeveel van hun genen individuen aan hun nakomelingen kunnen doorgeven en hoe snel een populatie groeit. In **hoofdstuk 5** hebben we bestudeerd of migratieafstand invloed heeft op factoren die te maken hebben met de voortplanting van de meeuwen: wanneer ze hun eieren leggen, de grootte van de eieren en de waarschijnlijkheid dat deze eieren uitkomen. Ook keken we of de afstand een invloed heeft op de overlevingskans met behulp van ringaflezingen in het overwinteringsgebied en de broedkolonie. Er was geen effect van migratieafstand op elk van deze eigenschappen, wat suggereert dat migratiestrategieën geen consequenties hebben voor het voortplantingssucces.

Naast de enorme verschillen in migratieafstand, zijn er ook uiteenlopende omstandigheden tijdens de winterperiode, zoals in het koude Verenigd Koninkrijk waar de meeuwen op vuilnisbelten foerageren of varkensvoer eten, in Spanje waar ze vooral in de stad of op rijstvelden te vinden zijn, of de zonnige stranden van West-Afrika waar ze gemakkelijk aan vis kunnen komen. Het is dus opmerkelijk dat deze verschillen maar weinig invloed hebben op de factoren die we hebben bestudeerd. Onze voorkennis en veronderstellingen over de kosten, baten en uitdagingen van migratie zijn voornamelijk gebaseerd op onderzoek aan kleinere trekvogels, die specifiekere voedseleisen hebben en kwetsbaarder zijn voor slechte weersomstandigheden. Meeuwen zijn echter heel anders.

Ze kunnen allerlei verschillende voedselbronnen gebruiken, van vis (meestal bijvangst van vissers) tot insecten (vaak op akkers) en afval. Dit zorgt ervoor dat ze veel alternatieven hebben wanneer ze geconfronteerd worden met onverwachte veranderingen in het landschap. Het zijn grote vogels die beschikken over een dik verenkleed, waardoor ze bestand zijn tegen koud winterweer. Daarnaast kunnen ze rusten op land en water, wat ervoor zorgt dat migratie minder risicovol is. Wat we hier dus uit mee kunnen nemen is dat migratie niet altijd kosten met zich meebrengt. Door hun flexibiliteit in gedrag kunnen meeuwen zich aanpassen aan de verschillende uitdagingen die horen bij hun migratiestrategie. Daardoor zijn ze in staat om het hele jaar rond hun energie- en tijdsbudget goed af te stemmen en hebben ze dezelfde kansen op overleving en voortplanting wanneer ze terugkeren naar hun broedkolonies. Door onderzoek te doen naar een minder 'traditionele' trekkende soort, hebben we bredere inzichten gekregen in de beperkingen die zich voordoen tijdens migratie en hoe dieren deze te boven kunnen komen.

Acknowledgements

Almost five years ago, I was excitedly getting off a plane in Amsterdam for the first time. I was nervous about my upcoming interview at the UvA for my dream PhD project: an immense, high resolution dataset where I could examine how a bird' behaviour throughout the year might be impacted by the migration strategies they use. My one reservation about the project, that I would be working with gulls (large, noisy, impossible to identify) was quickly set a side after meeting my potential new supervisors, **Judy** and **Willem**. It was clear from the beginning, that you both had an open and compassionate way of communicating. Looking back over my time here, I can confirm that I was not mistaken. You were there week in and week out, whether I was excitedly sharing a new result, looking for a heated debate, or crying my way through my latest setback.

Judy, your passion and excitement for ecology and birds especially is infectious. Thank you for many enthusiastic discussions about migration and animal behaviour. I'm sorry for knocking on your door so many days at 5pm to ask a quick $_{\text{(30+ minute)}}$ question. In addition to sharing many scientific interests, it was an unexpected bonus to connect about life outside of work. I've enjoyed our walks in the park, AME falafel parties, Paradiso concerts, and discussions about swimming and martial arts. I'm fortunate to have you as a mentor.

Willem, you come to every meeting with a smile. Your unflappable positivity in face of every issue I brought to the table was at times baffling, but ultimately left me with the confidence to keep barrelling on. I am slowly learning the lesson that 'no dataset is perfect'. It was always a treat to have a work retreat at your house - even if we couldn't always find the solution to whatever analysis I was struggling with at the time, having a peaceful lunch with you and Inge in your garden was the perfect way to put work problems into perspective.

I would likely not have undertaken a PhD where it not for superb mentorship and support from my past supervisors. **Chris,** I remember, several years after my BSc, you pondering how I ended up in your lab in the first place. I still can't honestly remember, but I'm so glad I did. Looking back it seems like an absurd idea commuting back and forth between Long Point all autumn while also following courses. However, you trusted me to do it, and look how it's influenced the last decade of my life. It's been great reconnecting over the years, either doing fieldwork at Long Point, at the Lund course, or while corresponding over your and Yolanda's papers. **Phil**, I had so much fun doing my MSc project with you. You left us with so much freedom to figure out our projects while still supporting us the entire way. I

fondly remember Dom and I tracking your movements based on your ebird lists when you were missing from the office. Thank you for always being so encouraging, I hope to find an excuse to travel back to Nova Scotia to visit sometime.

To the members of my reading committee, **Kyle Elliott, Samantha Patrick, Theunis Piersma, Isabel Smallegange, André de Roos, Emiel van Loon and Bart Nolet,** thank you for taking the time to read my thesis. **Emiel**, my memories of our earlier interactions are of you dropping by the PhD office to distract Elspeth and I with unusual facts and insights about the Netherlands. Through time I've come to appreciate how much you genuinely care about the progress and wellbeing of those you work with. Thank you for responding so thoughtfully and enthusiastically to the many long, extensively detailed emails about the statistical oddities I was struggling my way through. Who knows, maybe one day we will manage to turn one of those blunders into a paper! **Bart**, thank you for stepping in at the last moment to help facilitate the heart rate pilot studies, it seems like ages ago now. You always found the time to join a co-author meeting or to watch a practice presentation (even when it was 30 degrees and sunny out). It's been great having you involved in several of my papers, I've appreciated your insightful contributions.

This thesis would not exist without a lot of effort put into collecting data in the field. For this I have to thank **Kees** for his continuing dedication to the kelderhuispolder, **Roos** who's joined him for most of my PhD, **Suus** who was finishing her own PhD as I began, as well as numerous volunteers and students over the years . **Kees**, thank you for your continuing dedication to the gulls. While our working relationship was a bit of a roller-coaster in the early days, I've grown to appreciate your vast knowledge about gulls and natural history in general. It's been great having you involved in all my papers, I feel like these works have benefited from several hearty conversations. Thanks for bringing me along on colony rounds, and helping facilitate the heart rate project. **Roos**, it was always a pleasure spending a day in the colony with you, or just catching up over a gull tea in the office. I so glad that that our interests collided and we had the opportunity to work together for the final data chapter of my thesis. It was nice bouncing back and forth over the drafts as the paper came together. I wish I could have spent more time out in the colony with you both.

David, thanks for lending your scalpel to the project. You were full of energy and enthusiasm. Thanks for inviting me into your vets practice and I'm glad you could join us in the field a few times. Your flexibility and willingness to accommodate our unpredictable schedule made the uncertainty of catching gulls much easier to manage. **Edwin** and **Gerrit**, your ingenuity helped wrangle a lab-based heart rate transmitter into a functional

field system. We only had the one field season to do it, and it work excellently. **Tanya, Pascale** and **Mary,** thank you for your quick responses and willingness to help, especially with my many last minute car rental requests.
Wendt, **Luc**¸and **Chris T.,** thank you for giving me the opportunity to bring our gull data together for the repeatability paper. Sometime it seemed like it was never going to come to an end, so thanks for your input and support throughout the many revisions.

Something I've learned during the pandemic is that research is a lot more fun with an enthusiastic group of likeminded people to share it with. To that end I'm grateful to have had so many wonderful people to work alongside in the Animal Movement Ecology research group. Thank you **Elspeth, Maja, Jens, Bart K., Hans, Bart H., Roos, Stacy, Berendt, Johannas, Eldar, Fiona, Nelleka, Kees, Ji, Leo, Wouter, Thomas, Lisbeth,** and other AME members past and present for many fun discussions and feedback. **Jens,** I hope someday you discover the joys of lunchtime food beyond sandwiches. Beyond AME, I was fortunate to have been welcomed warmly into the greater TCE (and groupies) P(h)D community. **Louis, Silke, Lotte, Jacques, Kat, Jun, Zsófia, Jasper, Sietze, Tom, Floor, Catalina, Romain, Hannah**, thanks for many strange lunchtime conversations and Friday night beers + fries at Oerknal. Cake club, thank you for making Fridays that much better.

Beyond UvA, I was fortunate to spend several months over the past few years on Texel, working at the NIOZ. Thank you to **Thomas** and **Emma** for letting me stay in your apartments while you were away, and to **Suus** for allowing me to crash on your couch. **Eva**, it was fun going swimming and running at the GRC. And thank you to many others at COS for dragging away from my desk for coffee break or helping me find my way around.

It was fun having a consortium of PhDs from other universities likewise tackling the mystery of the gull. **Anouk, Marwa, Suus, Liam,** and **Cara,** I always enjoyed reconnecting at our gull symposiums. **Anouk** and **Marwa**, what fun that you're now both back in Amsterdam, I hope we get to spend some more time bouldering together before I leave. **Marwa**, I cannot express how grateful I am that you offered to help translate my summary into Dutch! Best of luck to all of you.

Christine and **Isabeau**, you were there for me when I was at my some of my lowest points during this project. It made the world of a difference to have two bad-ass sisters in science to turn to back home.

Throughout my time in Amsterdam, I've turned to sports for balance (though many would argue that my sports life here was far from balanced...). Regardless, it introduced me to several communities of wonderful people outside of work, which has shaped my time in Amsterdam.

Dear ATAC, I've unfortunately fallen out of touch with most of you during the past year, though still fondly remember exploring the Netherlands with you all on many bike tours. Being a part of this club made me reassess what I'd previously though possible with regards to endurance sports. It was with you that I completed my first century ride, and then went on to do a 250 k solo ride in the longest day of the year challenge during the middle of the covid pandemic. **Abe, Francesco, Daniel, Oscar^2, Martin, Anna, Céline, Erik** and many others, thanks for many epic rides. Especially **Ivo** and **Michal**, thanks for inviting me to be your third wheel throughout the pandemic.

To the Guang Mingers, **Nelson, Quinten, Karel, Marthe, Gaia, Timo, Amber, Lau**, **Jose, Kelly, Joachim, Cyril, Muberra, Daphne, Sabien, Lukas, Jildou, Roos,** and others. I had no idea what wushu was when I first walked in to the Amstel campus gym, but I am so glad I found such a delightful squad to train with these past four years. I am sorry for not speaking Dutch, but thanks for welcoming me into you group regardless. I experience my first sinterkerst with you, had an epic training weekend at ChateauTimo, and even managed to squeeze in my first competition. I still can't believe what a passionate, kind, supportive, and quirky crew you are. **Nelson,** your energy is a continuous source of amazement, thanks for being so inspiring and motivating. **Quinten** and **Karel**, it was wonderful that you both found the time to visit me on Texel, thanks for always being so welcoming. Quinten – thanks for helping me figure out how to convert ECG into heart rate!

Often I looked forward to long weekend boulder sessions with **Louise, Jun, Baptiste, Eileen, Elspeth, Vatsal,** and the many other climbing scientists over the years. **Louise**, you are always a fun and motivational (allez!) climbing companion. **Baptiste,** thanks for inspiring me to take a mountaineering course. One of my regrets is not making it to Fontainebleau while I was in Europe, one day it would be great for reunite with my two favourite French climbers there. **Jun** someday I still plan to take you up on your offer to explore Singapore. **Frenzi**, how wonderful to have an old acquaintance from Nova Scotia reappear in my life in Amsterdam and become a friend. I love your shear enthusiasm every time you show up at Monk. I've enjoyed all of our cooking adventures, and can't thank you enough for introducing Avery and I to Ottolenghi.

Elspeth and **Maja**, I don't even know where to begin. It's been great going through this crazy process together with the two of you. We've been there for each other through all of our ups and downs. Shared so many hikes, dinners, games nights, and drinks. **Elspeth**, I hope we have more NS walks in our future, it was always nice having a companion for a pretentious coffee break. **Maja**, I'll never forgive you for inviting us over for a "quiet movie night", I don't think I'll ever recover. I couldn't be happier that you've both agreed to stand by my side during my defence as my paranymphs. While I'm glad us and the Males (shout out to **Dado** and **Vatsal**), got to escape for a lovely camping trip, I still hope that someday we'll get together again for our wonderful weekend!

Keryll and **Greg**, I have missed so much in your lives while being away. **Greg**, thanks for coming to visit me in Amsterdam. **Keryll**, it's been far too many years since we've lived in the same country. I look forward to many more sibling days with you in the future! **Mom** and **Dad**, you've done so much for me over the years. You've supported me in everything I've done, from driving me dance class and piano, to helping me with my homework (including the impossible task of studying for the weekly dictées, and helping me build a paper mâché sarcophagus that I could fit into). I know it seems like I keep moving away to the furthest corners of the earth, but it means a lot that I can always come home to you.

Avery, every day you amaze me with your selflessness and support. You proofread every chapter of my thesis, made dinner and did the dishes for weeks at a time, acted as my personal masseuse, and organised weekends away, camping trips, and social evenings when I didn't have the energy. You've given me the freedom to pursue my dreams, regardless of where it's taken us. Life in Amsterdam wasn't always the easiest for you, it took you away from your friends, family, work, and nature. Yet we've also discovered many new things we love doing together, like biking through the city, eating ramen, art classes, and cooking 'easy' meals. You're my favourite travel companion, and I'm glad we fit in trips to Norway, Sweden, Portugal, Paris, Barcelona and Venice. I am looking forward to many adventures in the future. I love you.

And finally, to the gulls. My initial reservations have changed to a hesitant affection. I still can't claim to understand your many quirks, but then I've been known to enjoy a good mystery.