

PhD-Dissertation Reviews

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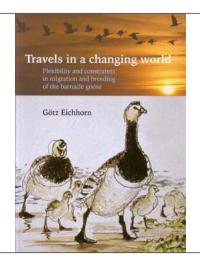
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PhD-dissertation reviews

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Eichhorn G. 2008. Travels in a changing world. Flexibility and constraints in migration and breeding of the barnacle goose. PhD thesis, University of Groningen, The Netherlands. ISBN 978-90-367-3449-3. Paperback, 238 pp. Available at http://irs.ub.rug.nl/ppn/312686560.



Götz Eichhorn was the last (65th) PhD student of Rudi Drent and his thesis is a beautiful example of the inspiring view on migration and breeding Rudi gave his students. The story focuses on the barnacle goose *Branta leucopsis*. A species which has done very well in the last decades, with a phenomenal increase in population size and the establishment of new breeding populations moving in breeding range from the high Arctic to temperate regions. The barnacle goose is now among the

fastest growing breeding bird populations in The Netherlands but also the Arctic populations are still increasing in numbers. A proper timing is crucial in migrating birds with direct repercussions on reproductive success and survival. This thesis gives a wonderful insight on how the geese now display a wide array of adaptive strategies which we never imagined beforehand. The stories are highly relevant in a changing world where many studies focus on the effect of climate change and where predictions of change are merely projections of present behaviour into the future.

Management of time and energy are coupled in this thesis. The species relies on body reserves for successful migration and breeding. Götz has quantified fat reserves and organ composition as energy storage, and migration and nest attentiveness as energy expenditure. The difference in breeding birds of the same species provided a framework for comparison of all these data. The detailed measurements allow us to understand different strategies using calculations with site-related values.

Since the early 1990s an increasing share of the Arctic breeding population delays its departure from the wintering quarters in the Wadden Sea by about four weeks. With GLS tags, small data loggers attached to the leg ring of the birds that register daylight, Götz was able to calculate positions and timing of the entire spring migration. The birds staying behind in the Wadden Sea, skipped the Baltic as a fuelling station. According to old predictions the Baltic would be an indispensable site in a sensitive chain of stopover sites used to replenish and build-up body reserves. However, the fuelling rate in the Wadden Sea has improved over time and made a longer jump northwards possible without large repercussions for the body condition that is left when birds arrive at their breeding place. Detailed calculations translated these behavioural changes into fattening rates in grams per day and into the targeted fat and protein content of body reserves of the geese.

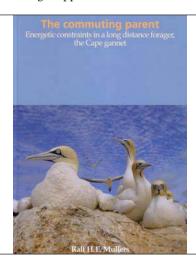
The flight skills of birds enable them to use resources over vast geographical areas and bird migration might be regarded primarily as an adaptation for exploiting seasonal peaks of resource abundance and avoiding seasonal resource depression. Most interestingly, despite an impressive advance of six to seven weeks in laying date compared to arctic breeders temperate-breeding barnacle geese breed too late to match peak food resources with growth of their young. This mismatch will remain as long as both adults preparing for breeding and offspring depend on the same food peak.

Major life-history traits changed in temperate breeding barnacle geese. For example, clutch size appeared to decrease with latitude. Surprisingly and counter-intuitively, the contribution of endogenous stores to incubation was higher in temperate breeding than arctic-breeding geese. However calculations showed that many of the eggs laid by breeding birds in The Netherlands do not produce a fledgling at all.

The thesis comprises three parts: "Tools and techniques", "Travel to breed" and "Why travel to breed: arctic and temperate breeding compared". These parts are divided in boxes and chapters. The boxes made it possible to publish data which were not vet fully developed into research papers but also help to provide background information and fill in some gaps. Even in the general discussion, new original data are presented on both amino acid and isotope composition of the food during spring staging to discuss the strategies of fuelling barnacle geese. All in all, the thesis is easy to read and clearly structured. The list of authors, originating from seven different countries, reveals the whole team involved in this truly international cooperative study. With a summary in Dutch, German and Russian, Götz Eichhorn pays a tribute to all his partners and his own background.

The flexibility shown in the successful study species gives hope for the future. The still existing constraints show that not everything is possible but alternative life strategies can provide solutions to new problems. The thesis is relevant for everyone thinking about the future for birds in a changing world.

Maarten J.J.E. Loonen, Arctic Centre, University of Groningen, A-weg 30, 9718 CW Groningen, The Netherlands (m.j.j.e.loonen@rug.n1) Mullers R.H.E. 2009. The commuting parent. Energetic constraints in a long-distance forager, the Cape gannet. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-3813-2, paperback, 167 pp. Available at http://irs.ub.rug.nl/ppn/317897853.



Seabirds, the world over, face deteriorating feeding conditions. Either periodically, as the sea is a highly dynamic and always changing environment, or structurally, as man is impacting this environment by (over) fishing or more subtly, through climate change. Seabirds may react to change in many different ways, as reviewed in the opening chapter of this thesis. In brief, if the food moves out of range of the birds, the birds may move after the food, switch to other foods or change their behaviour. Moving after the food might be difficult – even for widely ranging seabirds – during the breeding season, when they need to commute between their nest and the offshore. Switching to other food species is only possible if such alternatives are available and if the bird is not too specialized. Changing behaviour is always possible; the question is to which extent? Behavioural adaptations to poor food conditions are the central theme of this thesis.

The study species is well-chosen because it keeps the problems within limits. The Cape Gannet *Morus capensis* has a limited distribution, breeding in only two countries (South Africa and Namibia), with a limited population size (150 000 pairs) distributed over only six colonies. The total population size has been monitored since 1956 and shows a gradual decline, particularly in the north-western four colonies. Two of the supervisors, Rob Crawford and Les Underhill had already established that the breeding success and, in the long run, the population size of these gannets is

PhD-dissertation reviews 391

correlated with the abundance of anchovy and sardine (pelagic forage fish with a high energy density) within range. The gannets are under pressure because these fish have been gradually moving out of the birds' range, in response to the changing climate. Only birds from one colony still have access to sufficient food. Bad for the birds but this offers interesting research possibilities. Although the birds are highly specialized foragers, they are flexible to some extent and will also feed on fisheries waste, particularly in the Northwest where the good fish have gone. Last but not least, these gannets are easily caught and caught again, at the nest.

This setting has attracted quite a lot of attention from ornithologists. It even appears that not only the birds are competing (with conspecifics, other piscivores and fishermen) but that also the scientists are competing for limited resources here. Curiously, papers on the same topic, on the same birds in the same colonies, and using exactly the same methodology have been published by different authors, in different journals. The findings in the key chapters in this PhD thesis have been published in three scientific journals (ICES J. Mar. Sci., Ardea, Behav. Ecol.) but mimicking papers can be found elsewhere, authored by others (e.g. in MEPS 350: 127-136; Proc. Roy. Soc. B 275: 1149-1156; Biol. Cons. 142: 2361-2368). When reading both sets of papers, one get the impression that Ralf Mullers' hands were tied to some extent as 'the competing authors' only mention Ralf's work briefly in passing and often offer more in-depth analyses. Be this as it may, the collection of papers comprising the thesis give an interesting overview of the problems that a highly specialized, and until recently, successful seabird, faces today, in a world that is rapidly changing, and not for the better.

Question 1 of the thesis is if fishery waste can replace the now depleted fish that the gannets have long been specializing on. The answer is no. A high percentage of fishery waste in the diet coincides with low breeding success and starvation and predation of nestlings. The study reveals some remarkable predators of gannet chicks, such as the Great White Pelican Pelecanus onocrotalus and Cape Fur Seals Arctocephalus pusillus. Although this first paper appears to present a clear answer to a clear question (fishery waste, fashionably named junk food, cannot replace the real thing), it is not the strongest paper in this thesis and questions remain. As only percentages of different foods are given, we cannot work out if good fish went down, or waste went up over time, or both. The authors maintain that the low energy density of waste is the measure of its poor quality, but no attempt has been made to measure the total amount of kilojoules needed or provisioned. This is only touched upon in the final chapter of the thesis but a clear table of amounts of kilograms and kilojoules ferried in is lacking. Also nothing is said on the level of individual birds: are some birds able to keep on finding good fish while others bring home only waste and how does this play out? It is clear, however, that a high proportion of fishery waste in the diet comes with poor growth, and much predation and starvation of chicks. Gannets are geared to eat high-quality foods, spending a lot of energy getting it. Such birds are in evolutionary dire straits if the good food runs out: they cannot spend the energy to find and ferry back faraway for low quality stuff (Österblom et al. 2008, Oikos 117: 1075-1085). This does not mean to say that all that fishery waste is all bad news. Adult survival over the whole year may be better with fishery waste abundantly available and the decline in population size may be slowed down because of this resource. This does not help the starving chicks of course, but one should be careful in dismissing the value of junk food.

Given its title, one would expect results for individual parents or pairs, in relation to their specific diet, from individually marked parents or nests in the next chapter, which is on variation in parental provisioning. As it turns out, the birds were indeed individually marked (quite cleverly, for that matter, with a marking device on a long stick) but in the end results were mostly grouped for male and female parents (one year and a half worth of data) and for years (one bad year and one not so bad year). Only birds at the edge of the colony were used, under the assumption that these would not differ in performance from birds in the core. A tricky assumption and based only on a very limited check, done many years ago when feeding conditions were still good. One could have argued that now that things have gone bad, particularly birds at the edge of the colony would be at risk, making them excellent material for studying environmental deterioration. But this is not further pursued. It turned out that parents looked better after themselves than after their chicks, which is in fact the normal strategy for long-lived seabirds. Parental body condition did go down slightly as the breeding season progressed, but between-year variation was slight at best (note that data for only two years are available so power is low). In the bad year the parents worked even harder than in the not so bad year, as indicated by longer foraging trips and lower frequency of visits to the nest. Despite the hard work in the bad year, chick growth was slower and mortality higher. Predation was the main cause of death, but presumably predation only came before the inevitable starvation in many cases. In the bad year, chicks were left

unattended more often, for longer periods and at a younger age and this, of course, is asking for trouble. But what can a parent seabird do, when left with an empty sea? The most interesting find of this part of the thesis is that male and female parents behaved quite differently under stress. The females have a slightly higher body mass than their partners, and make longer trips. They also increased trip length more than the males (making them staying more at home) under poor feeding conditions and thus seem better equipped for long-distance flight. This is surprising, given their presumably higher flight costs (wing lengths are equal between the sexes so wing-loading is higher in females). Here, individual maternal skills come into play. Only efficient foragers, i.e. mothers that managed to find food quickly, kept their offspring alive. Variations in male skill did not seem to matter much: mothers rule! Why and how this male-female difference has evolved is still unclear. Here, the authors state that "we need at-sea data to look into this more specifically".

This insight did not take the author to the sea. Instead, he let the birds do the work and equipped a large number of them (646 from two colonies during three and four seasons, respectively) with GPS loggers. Here their good catchability was important as birds had to be caught at the onset of a foraging trip and again at their return, to retrieve the logger and the data. The analysis of all these data is remarkably lean. A map of only one (example) GPS track is presented in Chapter 5 and the data are reduced to means and standard deviations of trip duration, total flight distance, time spent flying, hunting and drifting. From these, it turns out that, in contrast to what was found earlier, birds with long foraging flights did best. Presumably this is because they went after good but far-away fish, rather than for easy pickings behind nearby trawlers. Without maps showing where the birds went, where the fish was and where the trawlers were, this is hard to judge. The necessary information does in fact exist, and quite a lot more on this can be found in the competing papers mentioned earlier.

No information is provided on individual birds. As it is unlikely that all 646 recorded trips were from 646 different individuals, an unknown amount of autocorrelation must be present in the data analysed. In any case, the sexes appear to go to more or less the same places but trips of females were only longer because they spend more time sitting on the water's surface. Males and females provisioned similar amounts of food: the females just needed more time to get this food (or needed more time and food for themselves). Differences in breeding success between the two

colonies only correlated with time spent flying during trips, and diet. Chicks in the colony with a high fisheries waste percentage in their provisions did poorly. In broad terms, their parents ferried in more food in terms of kilograms, but less in terms of kilojoules.

Chapter 4 describes a handicapping experiment. One parent per pair (n = 75) was (slightly) handicapped by taping the two outer primaries together in both wings, thus reducing wing area and increasing flight costs. Even though gannets often have missing or growing primaries and secondaries, these birds doubled their foraging trip duration and reduced nest attendance. Their partners compensated for this to some extent, by increasing their nest attendance when chicks were small, and by increasing feeding trip frequency when chicks were older. Not surprisingly (these birds were already under great stress from poor feeding conditions), the partners could not fully compensate for the poor performance of their mates. Interestingly however, the loss of foraging capacity affected the chicks rather than the parents. The adults kept their body mass and thus opted for better times in future breeding seasons: exactly what a long-lived seabird is supposed to do under the circumstances.

Chapter 6 addresses the energetic costs of parental foraging as a function of wind conditions. This is a rarely explored feat in seabird ecology. Dive success probably varies with wind speed (fish may be less visible in choppy seas); soaring is more costly without wind and flapping flight more costly in a storm. Ambient conditions have rarely been considered for pelagic seabirds. In this case of the breeding gannets, the birds cannot afford to sit out periods of unfavourable wind, as they must deliver food daily. Two colonies are compared that have different wind conditions. Of course everything else is also likely to differ between these colonies, so it is not quite clear why the study did not focus on within-colony differences: there is more than enough heterogeneity as it is! Doubly labelled water experiments showed that birds at either colony worked equally hard, at 5.5×BMR. Birds in the windy colony dived less, but their chicks did slightly better, indicating that feeding conditions were better than in the other colony. Here, parents made nearly twice as many dives per trip, which is costly, and presumably the take-offs after all these dives were also relatively costly, without sufficient wind. With a similar DEE to the 'windy' birds, these birds had to compensate by spending more time resting (recovering) at the sea sur-

Chapter 7 sums it all up and also presents some new data and figures. Fishery waste features most

PhD-dissertation reviews 393

prominently at the start of the breeding season (in the colony most affected) and is later on replaced by natural fish (saury). It is a natural food that the gannets take instead of the apparently preferred anchovies and sardines, but what exactly is wrong with these sauries, that make up a large proportion of the provisions, is not revealed. The energy density of these fish cannot be the problem as this is only marginally less than that of the presumed preferred anchovies (6.20 vs. 6.74 kJ/g according to the *Proceedings* paper). Chapter 7 also provides two much-missed maps of distribution at sea, from the GPS loggers. These figures, however, lump the data for more years so that trends over time cannot be seen and are printed in black-and-white while clearly designed in colour. As a result, much information that

must be available remains in the dark. The text is more revealing, mentioning that foraging ranges have increased over the years and are now so large, that birds stray into the feeding ranges of neighbouring colonies, thus increasing between-colony competition.

All in all, the Cape Gannet faces a bleak future. Devoid of good forage fish at the traditional sites near its (few) colonies, unable to use other resources successfully, and surrounded by hungry predators in the colony, this highly specialized seabird, can only go downhill further, it seems. Specialization is a risky evolutionary strategy.

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